22nd Lowell Wakefield Fisheries Symposium

Sea Lions
of the World

Editors: A.W. Trites, S.K. Atkinson, D.P. DeMaster,
L.W. Fritz, T.S. Gelatt, L.D. Rea, and K.M. Wynne

Proceedings of the symposium Sea Lions of the World:
Conservation and Research in the 21st Century
September 30-October 3, 2004, Anchorage, Alaska, USA

Alaska Sea Grant College Program
University of Alaska Fairbanks
AK-SG-06-01

Price: $50.00

Elmer E. Rasmuson Library Cataloging-In-Publication Data:

Sea lions of the world / editors : A.W. Trites, [et al.] – Fairbanks : Alaska Sea Grant College Program, 2006.

664 p. : ill. ; 23 cm. – (Alaska Sea Grant College Program, University of Alaska Fairbanks; AK-SG-06-01)

Proceedings of the symposium sea lions of the world : conservation and research in the 21st century, September 30-October 3, 2004, Anchorage, Alaska, USA.

Includes bibliographical references and index.

1. Sea lions—Conservation—Congresses. 2. Sea lions—Research—Congresses. Title. II. Trites, Andrew W., 1957-. IV. Series: Lowell Wakefield Fisheries Symposium series (22nd : 2004 : Anchorage, Alaska). IV. Series: Alaska Sea Grant College Program report ; AK-SG-06-01.

QL737.P63 P76 2006

ISBN 1-56612-105-1

Citation for this volume is: 2006. A.W. Trites, S.K. Atkinson, D.P. DeMaster, L.W. Fritz, T.S. Gelatt, L.D. Rea, and K.M. Wynne (eds.). Sea lions of the world. Alaska Sea Grant College Program, University of Alaska Fairbanks. 664 pp.

Credits

This book is published by the Alaska Sea Grant College Program, supported by the U.S. Department of Commerce, NOAA National Sea Grant Office, grant NA16RG2321, project A/161-01 and grant NA16RG2830, project A/152-19; and by the University of Alaska Fairbanks with state funds. The University of Alaska is an affirmative action/equal opportunity employer and educational institution.

Sea Grant is a unique partnership with public and private sectors combining research, education, and technology transfer for public service. This national network of universities meets changing environmental and economic needs of people in our coastal, ocean, and Great Lakes regions.

Alaska Sea Grant College Program
University of Alaska Fairbanks
P.O. Box 755040
Fairbanks, Alaska 99775-5040
Toll free (888) 789-0090
(907) 474-6707 fax (907) 474-6285
www.alaskaseagrant.org

Contents

Physiological Ecology

Foraging Ecology

Population Ecology and Dynamics

Conservation and Management

Roundtables

About the Symposium

The goal of the symposium was to bring together scientists and resource managers to address knowledge of world sea lion populations in order to compare them with Steller sea lions, and to identify research needs.

Changes in the worldwide abundance of sea lions is of growing concern to fisheries and conservation groups, because fisheries are feared to threaten sea lions, and/or because sea lions are feared to threaten fisheries. Over the past few decades, major changes have been noted in the abundance of all five species of sea lions around the world. In the North Pacific, the Steller sea lion has been declared endangered in parts of its range and is considered threatened with extinction in others. This is in contrast to the rapid increase in populations of California sea lions in Mexico and California. Elsewhere, the Japanese subspecies of the California sea lion is probably extinct and the Galapagos subspecies is in low numbers. Numbers of New Zealand sea lions and Australian sea lions are also extremely low, with major declines recently reported in Australia. Relatively little is known about the South American sea lion.

This symposium brought the world community of sea lion researchers and policy makers together to share their experiences and knowledge with each other. Interspecies comparisons can shed light on why some populations might decline while others increase. Insights might also be gained on whether trends in the abundance of sea lions are related to fishing activities through food dependencies or more directly through control or conservation measures. A better understanding of the biology of sea lions is urgently needed. The symposium significantly contributed to the understanding of fluctuating sea lion populations, especially as they compare to the Steller sea lion, by synthesizing current knowledge and forging new directions.

The symposium was coordinated by Sherri Pristash, Alaska Sea Grant College Program, University of Alaska Fairbanks. Organizing committee members are Shannon Atkinson, Alaska SeaLife Center; Michael Castellini, University of Alaska Fairbanks, Institute of Marine Science; Doug DeMaster, NOAA Fisheries, Alaska Fisheries Science Center; Lowell Fritz, NOAA Fisheries, Alaska Fisheries Science Center; Tom Gelatt, NOAA Fisheries, Alaska Fisheries Science Center; Andrew Trites, University of British Columbia; Bill Wilson, North Pacific Fishery Management Council; and Kate Wynne, University of Alaska Fairbanks, Alaska Sea Grant Marine Advisory Program.

Symposium sponsors are Alaska Sea Grant College Program, Alaska Department of Fish and Game, NOAA Fisheries, North Pacific Fishery Management Council, Wakefield Endowment, and University of Alaska Foundation.

The Lowell Wakefield Symposium Series and Endowment

Alaska Sea Grant has been sponsoring and coordinating the Lowell Wakefield Fisheries Symposium series since 1982. These meetings are a forum for information exchange in biology, management, economics, and processing of fish species and complexes, and an opportunity for scientists from high-latitude countries to meet informally and discuss their work.

Lowell Wakefield was the founder of the Alaska king crab industry. He recognized two major ingredients necessary for the king crab fishery to survive—ensuring that a quality product be made available to the consumer, and that a viable fishery can be maintained only through sound management practices based on the best scientific data available. Lowell Wakefield and Wakefield Seafoods played an important role in the development and implementation of quality control legislation, in the preparation of fishing regulations for Alaska waters, and in drafting international agreements for the high seas. In his later years, as an adjunct professor of fisheries at the University of Alaska, Wakefield influenced the early directions of Alaska Sea Grant. The Wakefield symposium series is named in honor of Lowell Wakefield and his many contributions to Alaska's fisheries. In 2000, Lowell's wife Frankie Wakefield made a gift to the University of Alaska Foundation to establish an endowment to continue this series.

Proceedings Acknowledgments

This publication presents thirty-seven symposium papers. Each paper was reviewed by two peers, and was revised according to recommendations by associate editors who generously donated their time and expertise: Andrew Trites, Shannon Atkinson, Doug DeMaster, Lowell Fritz, Tom Gelatt, Lorrie Rea, and Kate Wynne. The publisher thanks the editors and the authors of the papers.

Many thanks to the following people who reviewed one or more manuscripts for this book: Milo Adkison, Juan Jose Alava, Lee Alverson, John Arnould, Carrie Beck, Jeff Breiwick, Alexander Burdin, Vladimir Burkanov, Jennifer Burns, Katherine Call, Michael Cameron, Richard Campbell, Humberto Cappozzo, Shane Capron, Dennis Christen, Cheryl Clark, Dan Costa, Randy Davis, Sylvain DeGuise, John Durban, Pat Gearin, Scott Gende, Leah Gerber, Dan Goodman, Frances Gulland, Ailsa Hall, Rob Harcourt, Luis Hückstädt, Susan Inglis, Steve Insley, Peggy Krahn, Jeff Laake, Michelle Lander, Mary-Anne Lea, Qing Li, Libby Logerwell, Tom Loughlin, Sandra Lowe, John Maniscalco, Angela Matz, Lisa Mazzaro, Sharon Melin, Jo-Ann Mellish, Gabriele Müller, Matt Myers, Travis O'Brien, Kathryn Ono, Mark Oosthuizen, Grey Pendleton, Tim Ragen, Kim Raum-Suryan, Lorrie Rea, Diego Rodríguez, Lawrence Schaufler, Michael

Sigler, Beth Sinclair, Carol Sparling, Diana Szteren, Ward Testa, Jeannette Thomas, Dom Tollit, Rod Towell, Andrew Trites, Steve Trumble, Jason Waite, Arliss Winship, John Wise, Graham Worthy, Kate Wynne, Ann York, and Tonya Zeppelin.

Copy editing is by Sue Keller, Alaska Sea Grant College Program (ASG). Layout and format are by Jen Gunderson, ASG. Cover design is by Genesis Design & Media, Fairbanks, Alaska. Index is by Julie Kawabata, of Tigard, Oregon.

Organochlorines in Steller Sea Lions (*Eumetopias jubatus*) from the Western North Pacific

Hiroshi Hoshino
Hokkaido University, Division of Marine Environment and Resources, Graduate School of Fisheries Sciences, Hakodate, Japan

Shouichi Fujita
Hokkaido University, Laboratory of Toxicology, Graduate School of Veterinary Medicine, Sapporo, Japan

Yoko Goto
Hokkaido Kushiro Fisheries Experimental Station, Kushiro, Japan

Takeomi Isono
Econixe Co. Ltd., Sapporo, Japan

Tsuyoshi Ishinazaka
Nihon University, Laboratory of Theriogenology, College of Bioresource Sciences, Fujisawa, Japan

Vladimir N. Burkanov
Natural Resources Consultants Inc., and NOAA National Marine Fisheries Service, National Marine Mammal Laboratory, Seattle, Washington

Yasunori Sakurai
Hokkaido University, Division of Marine Environment and Resources, Graduate School of Fisheries Sciences, Hakodate, Japan

Abstract

The population of Steller sea lions, *Eumetopias jubatus*, has declined in the western North Pacific since the late 1960s. Recently, the Sea of Okhotsk was reported to be polluted by organochlorine contaminants (OCs) including polychlorinated biphenyls (PCBs) and agrochemicals. OCs are known to have toxic effects on phocid species; thus, studies of OCs in sea lions are important for sea lion conservation.

In this study, sea lion blubber samples were collected from the Kuril Islands and Olyutorsky Bay in Russia and Hokkaido in Japan from 1997 to 2004, and OC concentrations in blubber were measured.

1,1′-(2,2,2-trichloroethylidene)bis(4-chlorobenzene) and its metabolites (DDTs) and PCBs were found to be the dominant compounds accumulated in sea lions of the western North Pacific. The DDT and PCB levels were higher in Steller sea lions from Hokkaido than in sea lions from Olyutorsky Bay. The ratio of DDTs to PCBs in sea lions from Hokkaido was also higher than in sea lions from Olyutorsky Bay. A higher number of adult sea lions from Hokkaido exceeded the 2,2′,3,4,4′,5,5′-heptachlorobiphenyl level reported to decrease circulating thyroid hormone in ribbon seals than sea lions from Olyutorsky Bay. DDTs and PCBs were the predominant OCs accumulated in Steller sea lions of the western North Pacific measured in this study. In particular, Steller sea lions from Hokkaido may have higher DDT accumulation than sea lions in the western Bering Sea and may have higher risks of toxicity.

Introduction

The Steller sea lion, *Eumetopias jubatus*, is the largest member of the family Otariidae living in the North Pacific rim from California, U.S.A., to Hokkaido, Japan (Loughlin et al. 1987). Their world population has declined since the late 1960s, and the cause of the decline has been a matter of dispute among marine scientists (Loughlin et al. 1992, Loughlin and York 2002). In the western part of the North Pacific, sea lion rookeries are located on the coast of the Sea of Okhotsk including the Kuril Islands and Kamchatka Peninsula, and the Commander Islands in the western Bering Sea (Fig. 1). The number of sea lions in these areas has declined from the 1960s to date (V.N. Burkanov and T.R. Loughlin unpubl.).

Recently, the Sea of Okhotsk was reported to be polluted by runoff containing organochlorine compounds (OCs): hexachlorocyclohexanes (HCHs), chlordanes (CHLs), polychlorinated biphenyls (PCBs), and 1,1′-(2,2,2-trichloroethylidene)bis(4-chlorobenzene)(*p,p′*-DDT) and its metabolites (DDTs) (Chernyak et al. 1995, Zhulidov et al. 2000). Further, global transportation of pollutants from southeastern Asian countries to the high latitude regions may possibly have impacts on the Sea of Okhtosk (Iwata et al. 1993). These organochlorine compounds are used for the electronics industry and agriculture, and are known as the toxic and endocrine disrupting chemicals. They are highly lipophilic and tend to accumulate in higher trophic animals through the food web (Kawano et al. 1988). In phocid species, some toxic effects of OCs were reported, such as immune system suppression (de Swart et al. 1996) and a decrease in circulating thyroid hormone (Chiba et al. 2001); thus studies of OCs

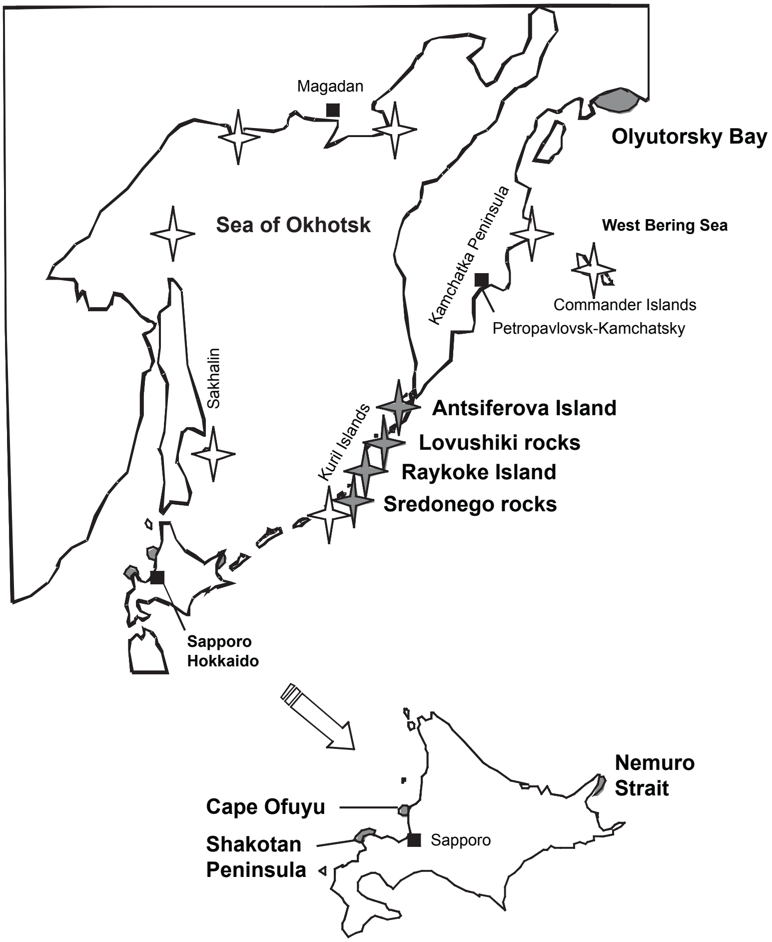


Figure 1. Location of sampling sites and rookeries. Star = sea lion rookery; gray area and gray star = area and rookery where we collected sea lion samples; black squares = major cities.

in sea lions are warranted to determine if similar effects may impair sea lion conservation.

In this study, we measured the concentrations of organochlorine contaminants in Steller sea lions of the western North Pacific and we discuss the risk of organochlorine contamination on Steller sea lions in this area.

Materials and methods

We collected sea lion blubber samples from Hokkaido Island in Japan, the Kuril Islands, and Olyutorsky Bay in Russia from 1997 to 2004 (Fig. 1). In the Kuril Islands, we collected sea lion pups found dead in rookeries from late June to July. We collected fresh or slightly decomposed carcasses following the guideline of Geraci and Lounsbury (1993). Only three females and two males were fresh and the others were decomposed slightly. In Olyutorsky Bay, we collected sea lions taken accidentally by a Russian herring fishery from October to December. In Hokkaido, we collected sea lions from licensed sea lion hunters from January to March. Blubber (200-500 g) was cut from the mid dorsal or breast region, frozen on a ship in Russia, transported by airplane from Russia, and stored at –25ºC until analysis. Blubber collected in Hokkaido was frozen at the field station or laboratory as soon as possible after collection and stored at –25ºC too. The body length, body weight, blubber thickness on the xiphoid process, milk excretion, and pregnancy status of sea lions were checked when possible. Ages and reproductive status were determined in sea lions collected from Hokkaido following procedures described by Isono (1999) and Ishinazaka and Endo (1999). Male sea lions older than 3 years or morphologically mature were classified as adults, and the other males were classified as juveniles. Female sea lions that were not pregnant and younger than 4 years were classified as juveniles. Age of sexual maturity was determined by procedures described by Yamanaka (1986) and Ishinazaka and Endo (1999).

OC analysis was carried out by the method described by Hoshino (2004). Several pieces of blubber (5 g) were cut vertically from the block of blubber to avoid differences in concentration between blubber layers (Severinsen et al. 2000). Pieces of blubber were ground with anhydrous Na_2SO_4, and organo-solvent compounds were extracted into a mixture of dichloromethane and n-hexane (13.5:1 vol:vol) by an automatic soxhlet extractor (Soxtherm S306A, Gerhardt, Bonn, Germany) for 3 hours. Extracted OC solvent was concentrated by nitrogen gas and applied to Bio Beads SX-3 gel permeation chromatography (Norstrom et al. 1986), eluted OC solvent was washed with sulfuric acid and then applied to silica gel high performance liquid chromatography. The lipid concentration was determined gravimetrically using an aliquot of the extracted OCs (Lee et al. 1996). An equivalent mixture of dichloromethane and hexane was used for the mobile phase of gel permeation chromatography, and a mixture of dichloromethane and hexane (2:8 vol: vol) was used for the mobile phase of high performance liquid chromatography. Concentrations of OCs were measured by a Chromatopack 3800 gas chromatography linked to a Saturn 2000 ion trap mass spectrometer (Varian, Walnut Creek, California). The Chromatopack 3800 was equipped with a fused silica capillary column (30 m length × 0.25 mm inner diameter) coated with ZB-1

(Phenomenex, Torrance, California, 0.25 μm bonded phase thickness). We determined the concentrations of 55 polychlorinated biphenyl congeners and 11 organochlorine pesticides. The concentrations of OCs were quantified by comparison with corresponding external standards. An equivalent mixture of Kanechlors 300, 400, 500, and 600 (GL Sciences, Shinjuku, Tokyo, Japan) was used as the external standard for quantification of PCBs (Tanabe et al. 1987). The concentrations of total PCBs were the sum of 55 congeners. The unit of organochlorine concentrations (ng per g lipid) quantifies the number of the nanograms of organochlorine contained in 1g of lipid extracted from the blubber. Recoveries of all PCBs and the other OCs through the analytical procedure were examined by spiking 4 μg of PCBs and 100-200 ng of the other organochlorine standards into about 0.7 g of sea lion lipid. Average recovery efficiencies were 97±13% for the PCB congeners, and 103±16% for the other OCs. And limits of detection were determined followed by the official method (Kankyochou Suishitsu Hozenkyoku Suishitsu Kanrika 1998) and 0.1-10 ng per g lipid for PCBs and 2.3-14 ng per g lipid for others. The nonparametric multiple comparisons test (Steel-Dwass test) was used to compare OC concentrations in sea lions. The Wilcoxon rank sum test was used to compare OC concentrations in sea lions from Hokkaido with those in sea lions from Olyutorsky. Welch's test was used to compare *p,p′*-DDE and PCBs in juvenile sea lions investigated in this study with the data reported by Barron et al. (2004). The 2-sample test for equality of proportions without continuity correction was used to compare the proportion of sea lions exceeding toxic levels in Hokkaido with those from Olyutorsky. The Steel-Dwass test and Wilcoxon rank sum test were conducted with Kyplot (KyensLab Inc., www.kyenslab.com/en/index.html), Welch's test was conducted with web statistic tools (www.clg.niigata-u.ac.jp/~takagi/takagi.html), and the 2-sample test for equality of proportions without continuity correction was conducted with R2.2.0 (CRAN, www.r-project.org).

Results and discussion

In Steller sea lions from the western North Pacific, DDTs (2609±2358 ng per g lipid) and PCBs (1648±1332 ng per g lipid) are significantly higher than chlordanes (CHLs) (896±642 ng per g lipid) and hexachlorocyclohexanes (HCHs) (266±184 ng per g lipid) (Steel-Dwass test, $P \leq 0.05$) (Table 1). This suggests that DDTs and PCBs are the predominant OCs accumulated in sea lions of the western North Pacific measured in this study.

Among adult male sea lions, DDTs and PCBs in sea lions of Hokkaido were significantly higher than those in sea lions of Olyutorsky Bay (Wilcoxon rank sum test, DDTs; $P \leq 0.001$, PCBs; $P \leq 0.01$) (Fig. 2). In addition, the ratios of DDTs to PCBs (DDTs:PCBs) in sea lions of Hokkaido were also significantly higher than those in sea lions of Olyutorsky (Table 1, Wilcoxon rank sum test, $P \leq 0.01$). Sea lions collected off the coast

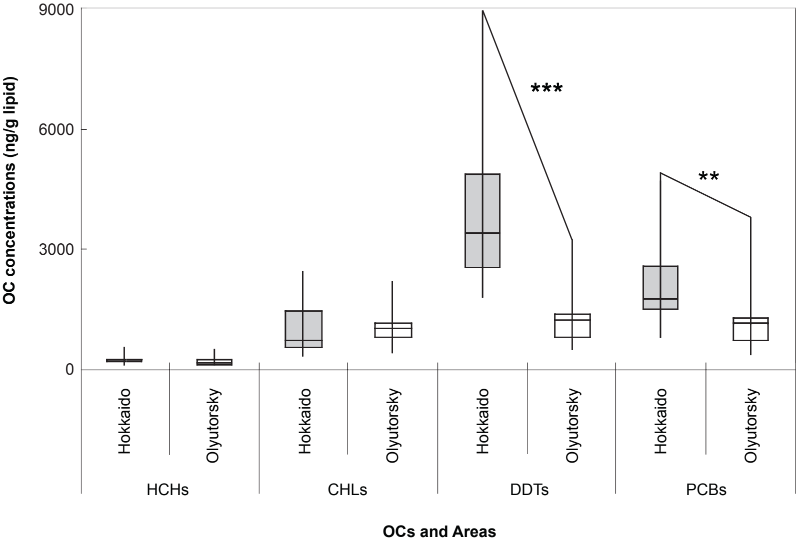


Figure 2. Concentrations of organochlorine compounds accumulated in adult male sea lions of Hokkaido and Olyutorsky Bay. HCHs = sum of α-HCH, β-HCH and γ-HCH. CHLs = sum of oxychlordane, *trans*-chlordane, *cis*-chlordane, *trans*-nonachlor, and *cis*-nonachlor. DDTs = sum of *p,p′*-DDT, *p,p′*-DDE, and *p,p′*-DDD. PCBs = sum of congeners listed in Table 1. Gray box = sea lions of Hokkaido; white box = sea lions of Olyutorsky Bay; whisker = minimum and maximum; lower boundary of box = 25th percentile; center boundary of box = median; upper boundary of box = 75th percentile. Wilcoxon rank sum test; **$P \leq 0.01$, ***$P \leq 0.001$. Asterisks indicate significant differences evaluated by Wilcoxon rank sum test.

of Hokkaido came from the Sea of Okhotsk (Isono and Wada 1999) and most sea lions collected in Olyutorsky Bay are thought to come from the Commander Islands and Kamchatka Peninsula (V.N. Burkanov unpubl.); thus, sea lions of the Sea of Okhotsk may be more contaminated by DDTs and PCBs than sea lions of the western Bering Sea. In particular, DDTs: PCBs showed that contamination of sea lions of the Sea of Okhotsk by DDTs are more advanced than that of sea lions of the western Bering Sea. DDTs are not transported longer distances by the atmosphere than PCBs (Iwata et al. 1993, Andreas et al. 2000), and emission of DDTs is related to agricultural and economical activities (Monirith et al. 2003). Relatively higher human activity in countries surrounding the Sea of Okhotsk than the western Bering Sea may cause a geographical difference in contamination of Steller sea lions.

Table 1. **Concentrations of organochlorine compounds accumulated in Steller sea lions from Hokkaido, Kuril Islands, and Olyutorsky Bay.**

Area	Age class, sex	No. of samples	Mean lipid %	HCHs	CHLs	DDTs	PCBs	DDTs/PCBs
Hokkaido	Adult, male	10	72	266±136	1052±719	4259±2563	2204±1223	2.0±0.6
				191±92	754±504	3091±1899	1595±899	
Hokkaido	Juvenile, male	5	72	391±213	1264±664	4155±2212	2463±1182	1.6±0.2
				283±163	911±501	2988±1641	1773±887	
Hokkaido	Juvenile, female	3	76	183±48	879±624	2745±1713	1665±1111	1.7±0.1
				140±39	670±471	2092±1290	1268±836	
Kuril Islands	Pup, male	7	51	379±334	948±876	3342±3352	2189±2244	1.7±0.8
				167±151	424±420	1394±1413	1002±1109	
Kuril Islands	Pup, female	9	56	221±129	328±193	1031±918	746±419	1.5±0.8
				116±50	179±112	528±384	425±294	
Olyutorsky Bay	Adult, male	12	69	206±105	1013±473	1314±738	1201±879	1.2±0.2
				137±53	689±276	890±430	800±479	
Summary		46	65	266±184	896±642	2609±2358	1648±1332	1.6±0.6
				165±104	586±431	1681±1569	1067±849	

Upper = mean±S.D., ng/g lipid. Lower = mean±S.D., ng/g wet weight).
HCHs = sum of α-HCH, β-HCH, and γ-HCH. CHLs = sum of oxychlordane, *trans*-chlordane, *cis*-chlordane, *trans*-nonachlor, and *cis*-nonachlor. DDTs = sum of *p,p′*-DDT, *p,p′*-DDE, and *p,p′*-DDD. PCBs = sum of 8, 18, 15, 28/31, 52, 49/69, 47/Peak 48, 44, 42, 41/64, 58/74, 66, 91/95, 102, 60, 84/92/90, 101, 99, 97/113, 87/177, 85, 136, Peak 510, 151, 135, 144/149, 118/Peak 515, 132, 128, 105, 153, 176, 138, 178, Peak 74, Peak 617, 187, Peak 77, 180, 170, 198, 201/196.
Number of peaks and PCBs follow Tanabe et al. 1987.

In addition, we compared the level of *p,p′*-DDE in juvenile Steller sea lions of the western North Pacific with that in Steller sea lions of Southeast Alaska and Prince William Sound reported by Barron et al. (2003). The major content of DDTs accumulated in sea lions is *p,p′*-DDE (Lee et al. 1996). This is a preliminary comparison because different analytical methods were used; however, *p,p′*-DDE levels in juvenile sea lions from Hokkaido are slightly higher than those in juvenile sea lions from Prince William Sound (PWS = 1.3±0.6 µg per g wet weight, 19 individuals) (Welch's test, $P = 0.095$). The level of PCBs in sea lions is similar among all areas of the north Pacific. It is possible that more DDTs accumulated in Steller sea lions living in the Sea of Okhotsk than in Steller sea lions in other North Pacific areas. Inter-laboratory studies are needed to clarify contamination in sea lions from all habitats.

In phocid species, immune suppression and a decrease of circulating thyroid hormone due to OCs have been reported. Immunosuppression was observed in harbor seals, *Phoca vitulina,* that had accumulated 2.4 µg per g lipid of *p,p′*-DDT and 16.5 µg per g lipid of PCBs in their blubber (de Swart et al. 1996). No sea lions in this study, however, exceeded the levels of PCBs and *p,p′*-DDT in the harbor seal. In addition, two species of congeners, 2,2′,3,3′,4,4′,5-heptachlorobiphenyl (PCB170) and 2,2′,3,4,4′,5,5′-heptachlorobiphenyl (PCB180), were suggested to decrease the circulating thyroid hormone in ribbon seals, *Phoca fasciata*, that had accumulated 14 ng per g lipid of PCB170 and 43 ng per g lipid of PCB180 in their blubber (Chiba et al. 2001; calculated from mean fat = 92%). We compared the numbers of adult sea lions exceeding the PCB170 and PCB180 levels of ribbon seals in Hokkaido with those in Olyutorsky (Fig. 3). For PCB170, 4 of 10 sea lions in Hokkaido and 2 of 12 sea lions in Olyutorsky exceeded the level of ribbon seals. For PCB 180, all sea lions of Hokkaido and 5 of 12 sea lions of Olyutorsky exceeded the level of ribbon seals. The proportion of sea lions of Hokkaido exceeding the toxic level is significantly higher than that of sea lions of Olyutorsky (2-sample test for equality of proportions without continuity correction, $P \leq 0.01$). These data suggest that sea lions of the Sea of Okhotsk have higher toxic risks than sea lions of the western Bering Sea, although sea lions may not have the same sensitivity to toxicity as ribbon seals.

We concluded that DDTs and PCBs are the predominant organochlorines accumulated in Steller sea lions of the western North Pacific in this study. Steller sea lions from the Sea of Okhotsk may have higher DDT accumulations than sea lions of the western Bering Sea and the eastern North Pacific and may have higher toxic risks, such as decrease of circulating thyroid hormone.

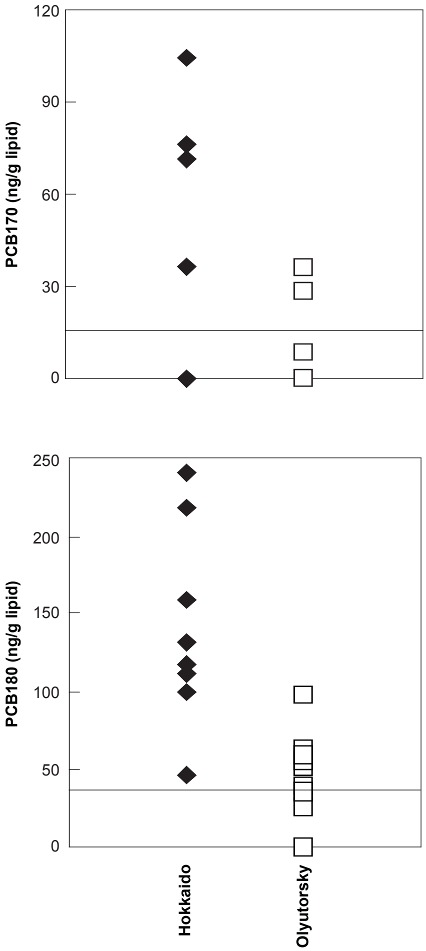


Figure 3. Number of sea lions exceeding toxic levels of ribbon seals. Horizontal lines in figures show levels of ribbon seal (Chiba et al. 2001).

Acknowledgment

We are grateful to Fisheries Agency, Japan; Alaska SeaLife Center; National Marine Mammal Laboratory, U.S.A.; Inui Tasuke Scientific Foundation; and the Amway Nature Center of Japan. We would like to thank Kazuo Wada, Akihiko Wada, Akio Kazusaka, Mayumi Ishizuka, Kenji Konishi, Tatsuya Kariya, and Tomohiro Deguchi. We also give special thanks to colleagues in Russia and at Hokkaido University, Nihon University, and Rakunou Gakuen University for help in collecting samples.

References

Andreas, B., D. Mackay, M. Matthies, F. Wania, and E. Webster. 2000. Assessing long-range transport potential of persistent organic pollutants. Environ. Sci. Technol. 34:699-703.

Barron, M.G., R. Heintz, and M.M. Krahn. 2003. Contaminant exposure and effects in pinnipeds: Implications for Steller sea lion declines in Alaska. Sci. Total Environ. 311:111-133.

Chernyak, S.M., L.L. McConnell, and C.P. Rice. 1995. Fate of some chlorinated hydrocarbons in arctic and far eastern ecosystems in the Russian Federation. Sci. Total Environ. 160/161:75-85.

Chiba, I., A. Sakakibara, Y. Goto, T. Isono, Y. Yamamoto, H. Iwata, S. Tanabe, K. Shimazaki, F. Akahori, A. Kazusaka, and S. Fujita. 2001. Negative correlation between plasma thyroid hormone levels and chlorinated hydrocarbon levels accumulated in seals from the coast of Hokkaido, Japan. Environ. Toxicol. Chem. 20:1092-1097.

de Swart, R.L., P.S. Ross, J.G. Voss, and A.D.M.E. Osterhaus. 1996. Impaired immunity in harbour seals (*Phoca vitulina*) exposed to bioaccumulated environmental contaminants: Review of a long-term feeding study. Environ. Health Persp. 104(Suppl. 4):823-828.

Geraci, J.R., and V.J. Lounsbury. 1993. Marine mammals ashore: A field guide for strandings. Texas A&M Sea Grant College Program. (Translated by T. Yamada and M. Amano, Kaiyusha, Tokyo, Japan. 345 pp.)

Hoshino, H., 2004. Accumulation of organochlorines in Steller sea lions *Eumetopias jubatus* living in the western North Pacific. Ph.D. thesis, Hokkaido University, Hakodate. 112 pp.

Ishinazaka, T., and T. Endo. 1999. The reproductive status of Steller sea lions in the Nemuro Strait, Hokkaido, Japan. Biosphere Conservation 2:11-19.

Isono, T. 1999. Characteristic of morphology and growth. In: N. Ohtaishi and K. Wada (eds.), Migratory ecology and conservation of Steller sea lions. Tokai University Press, Tokyo, pp. 230-247.

Isono, T., and K. Wada. 1999. Migration of Steller sea lions *Eumetopias jubatus* around Hokkaido Island, Japan. In: N. Ohtaishi and K. Wada (eds.), Migratory ecology and conservation of Steller sea lions. Tokai University Press, Tokyo, pp. 230-247.

Iwata, H., S. Tanabe, N. Sakai, and R. Tatsukawa. 1993. Distribution of persistent organochlorines in the oceanic air and surface seawater and the role of ocean on their global transport and fate. Environ. Sci. Technol. 27:1080-1098.

Kankyochou Suishitsu Hozenkyoku Suishitsu Kanrika. 1998. Gaiinseikakuranbushitsu Chousa Zantei Manual (Suishitsu, Teishitsu, Suiseiseibutsu), October, National Institute for Environmental Studies, Chemicals Database, w-chemdb.nies.go.jp/index.html.

Kawano, M., T. Inoue, T. Wada, H. Hidaka, and R. Tatsukawa. 1988. Bioconcentration and residue patterns of chlordane compounds in marine animals: Invertebrates, fish, mammals, and seabirds. Environ. Sci. Technol. 22:792-797.

Lee, J.S., S. Tanabe, H. Umino, R. Tatsukawa, T.R. Loughlin, and D.C. Calkins. 1996. Persistent organochlorines in Steller sea lion (*Eumetopias jubatus*) from the Gulf of Alaska and the Bering Sea, 1976-1981. Mar. Pollut. Bull. 32:535-544.

Loughlin, T.R., and A.E. York. 2002. An accounting of the sources of Steller sea lion mortality. In: D. DeMaster and S. Atkinson (eds.), Steller sea lion decline: Is it food II. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 9-13.

Loughlin, T.R., M.A. Perez, and R.L. Merrick. 1987. *Eumetopias jubatus*. Mamm. Species 283:1-7.

Loughlin, T.R., A.S. Perlov, and V.A. Vladimirov. 1992. Range-wide survey and estimation of total number of Steller sea lions in 1989. Mar. Mamm. Sci. 8:220-239.

Monirith, I., D. Ueno, S. Takahasi, H. Nakata, A. Sudaryanto, A. Subramanian, S. Karuppiah, A. Ismail, M. Muchtar, J. Zheng, B. Richardson, M. Prudente, D.H. Ngyen, S.T. Touch, A.V. Tkalin, and S. Tanabe. 2003. Asia-Pacific mussel watch: Monitoring contamination of persistent organochlorine compounds in coastal waters of Asian countries. Mar. Pollut. Bull. 46:281-300.

Norstrom, R.J., M. Simon, and M.J. Mulvihill. 1986. A gel-permeation/column chromatography cleanup method for the determination of CDDs in animal tissue. Intern. J. Environ. Anal. Chem. 23:267-287.

Severinsen, T., J.U. Skaare, and C. Lydersen. 2000. Spatial distribution of persistent organochlorines in ringed seal *(Phoca hispida*) blubber. Mar. Environ. Res. 49:291-302.

Tanabe, S., R. Tatsukawa, D.J.H. Phillips. 1987. Mussels as bioindicators of PCB pollution: A case study on uptake and release of PCB isomers and congeners in green-lipped mussels (*Perna viridis*) in Hong Kong waters. Environ. Pollut. 47:41-62.

Yamanaka, M. 1986. Developmental stages and characteristics of distribution for Steller sea lions (*Eumetopias jubatus* Schreber) migrate along the coast of Hokkaido. M.S. thesis, Hokkaido University, Hakodate. 78 pp.

Zhulidov, A.V., J.V. Headley, D.F. Pavlov, R.D. Robarts, L.G. Korotova, Y.Y. Vinnikov, and O.V. Zhulidov. 2000. Riverine fluxes of the persistent organochlorine pesticides hexachlorocyclohexane and DDT in the Russian Federation. Chemosphere 41:829-841.

Female Attendance and Neonatal Pup Growth in Steller Sea Lions (*Eumetopias jubatus*)

Randall W. Davis and Elisif A.A. Brandon
Texas A&M University at Galveston, Department of Marine Biology,
Galveston, Texas

Donald G. Calkins
Alaska SeaLife Center, Seward, Alaska

Thomas R. Loughlin
National Marine Fisheries Service, National Marine Mammal Laboratory,
Alaska Fisheries Science Center, Seattle, Washington

Abstract

We studied attendance behavior of lactating Steller sea lions (SSL) and the growth rates of pups in Southeast Alaska, the Gulf of Alaska, and the Aleutian Islands from 1990 to 1997. These rookeries included one (Lowrie Island in Southeast Alaska) in an area of stable population and three (Chirikof and Marmot islands in the Gulf of Alaska and Seguam and Yunaska islands in the Aleutian Islands) in areas where the population of SSL has declined significantly over the past 30 years. Radio transmitters were glued to the fur of lactating SSL and their presence on the rookeries monitored for the first four to six weeks postpartum. Newborn pups were weighed and measured every two weeks over the same period. The time spent onshore (22.5 h ± 8.26 SD) by females did not differ significantly among rookeries. Average foraging trip duration was significantly different among rookeries and ranged from 25.6 h ± 11.64 SD in the area of stable population to 9.4 h ± 3.32 SD in the area of declining population. The average percentage of time spent at sea was significantly different among rookeries and ranged from 51% ± 8.9 SD in the area of stable population to 31% ± 9.99 SD in the area of declining population. Male pups (22.6 kg ± 2.21 SD) were significantly heavier than female pups (19.6 kg ± 1.80 SD) at 1-5 days of age, but there were no significant differences among rookeries at that age. Male and female pups on the same rookery grew at the same rate during the first four to six weeks. Body mass and standard length increased at a faster rate for pups in the Aleutian Islands and the western Gulf of Alaska (0.45-0.48 kg day^{-1} and 0.47-0.53 cm day^{-1}, respectively) than in Southeast Alaska (0.23 kg day^{-1} and 0.20 cm day^{-1}). Overall, average foraging trip duration among rookeries decreased and pup growth rate increased in an east-to-west direction from the area of stable to declining population. There was no evidence that female sea lions and pups were nutritionally stressed during the first six weeks postpartum in the area of population decline.

Introduction

Attendance pattern and foraging trip duration are important indicators of foraging effort in lactating sea lions and fur seals (order Carnivora, family Otariidae). Female sea lions with suckling pups alternate times onshore with foraging trips to sea. Basic information about foraging trip length is an important starting point for understanding maternal investment. The average length of a foraging trip to sea is influenced by prey density and distribution (e.g., in the water column and in relation to the rookery), fasting capacity of pups, and other environmental factors and physiological constraints (Trillmich and Limberger 1985, Ono et al. 1987, Costa et al. 1989, Antonelis et al. 1990, Boyd et al. 1991, Feldkamp et al. 1991, Boyd et al. 1994, Hood and Ono 1997, Francis et al. 1998, Georges and Guinet 2000). Steller sea lion (SSL) pups have little body fat, so their ability to fast is very limited. As a result, the foraging trips of lactating SSL are generally short and limited to the area around the rookery during the first two months postpartum. The earliest studies of attendance pattern and foraging trip duration in lactating SSL were conducted in the 1960s (Sandegrin 1970, Gentry 1970). More recently, there have been a number of observational studies of female attendance behavior at rookeries in California (Higgins et al. 1988, Hood and Ono 1997) and Alaska (Ono 1997, Porter 1997, Milette 1999). Time-depth recorders (TDRs) attached to adult females in Alaska recorded attendance and diving patterns (Swain 1996, Merrick and Loughlin 1997, Andrews 1999). In the present study, we attached radio transmitters to lactating females to examine attendance patterns during the first four to six weeks postpartum. Our study differs from previous research by providing a larger sample size and longer measurement period than has been possible with time depth recorders or observational studies.

Sea lion pups depend entirely on milk for neonatal growth (Bonner 1984). Studies of sea lions and fur seals have shown that if a pup does not obtain enough milk from its mother, it will exhibit poor body condition (i.e., reduced lean mass and total lipid mass for a given age or standard length) and a reduced growth rate (Trillmich and Limberger 1985, Ono et al. 1987). This may have lifelong consequences as neonatal growth is an important factor in determining adult size and survival (Bryden 1968, Innes et al. 1981, Calambokidis and Gentry 1985, Albon et al. 1992, Baker and Fowler 1992, Gaillard et al. 1997, Boltnev et al. 1998, Tveraa et al. 1998, Burns 1999). Due to their large size, aggressive behavior, ease of disturbance, and remote location of rookeries, less is known about the early growth of SSL than most other pinniped species. Higgins et al. (1988) measured body mass of SSL pups on Año Nuevo Island in California, but only reweighed five to measure growth rates. Merrick et al. (1995) weighed SSL pups at a number of locations throughout the Gulf of Alaska and the Aleutian Islands, but did not reweigh them to assess individual growth rates.

Over the past 30 years, the SSL population has declined by more than 80% (Braham et al. 1980, Loughlin et al. 1992, NMFS 1995, Loughlin 1998), resulting in the species being classified as endangered (U.S. Fed. Reg. 62:24345) in the western part of its range and threatened in the eastern region. A number of possible causes for the SSL population decline have been proposed, including pollution, predation, subsistence and commercial harvesting, disease, natural fluctuations, environmental changes, and commercial fishing. A change in the overall distribution, abundance, or nutritional quality of key prey species was hypothesized to be the most significant factor when this research was conducted (1990-1997). If prey (especially high-caloric prey) in the area of SSL population decline had become less abundant or diverse, this may have hindered female provisioning of pups. Poor nutrition can delay pup maturation and increase mortality. Female foraging success is therefore critically important for pup development and survival during the first year of life.

In this study, we examined the question: Do foraging trip durations of lactating females and pup growth rates differ between declining and stable populations in Alaska? Our null hypothesis was that there was no difference in these variables between the stable and declining populations. The alternative hypothesis was that there was a difference in attendance patterns and pup growth between the populations and that this difference may reflect relative foraging effort and prey availability or quality.

Materials and methods

Attendance patterns

Female attendance patterns were studied at four rookeries in Alaska (Fig. 1) during the first four to six weeks postpartum (Brandon 2000). The rookery on Lowrie Island (54º51'N, 133º32'W) in Southeast Alaska is in an area of stable population. Thirty-five transmitters were deployed on lactating females at Lowrie Island between 1993 and 1997, of which 28 produced usable data (7 in 1993; 9 in 1994; 5 in 1996; 7 in 1997). Four-

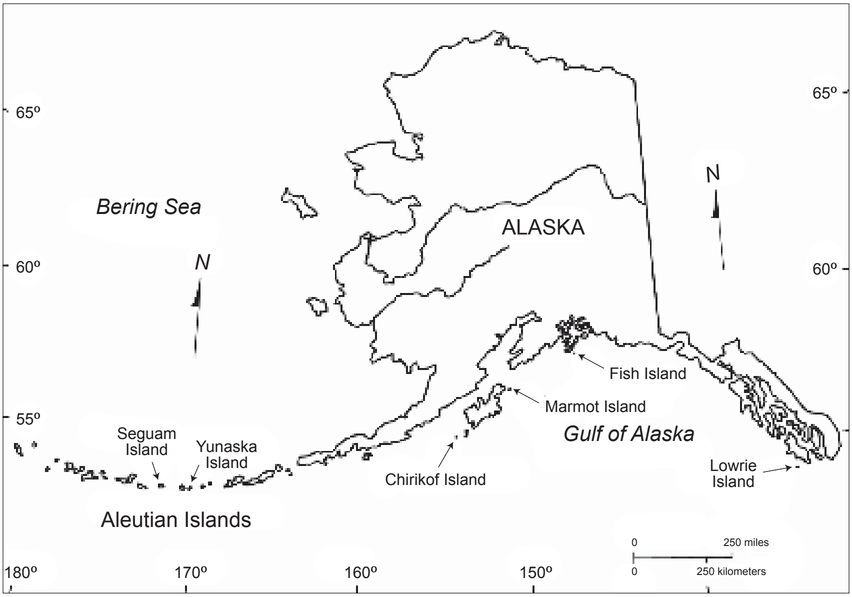


Figure 1. Study sites in Alaska. The Lowrie Island rookery in Southeast Alaska has a stable population of Steller sea lions. Rookeries at Marmot and Chirikof islands in the Gulf of Alaska and Yunaska and Seguam islands in the Aleutians are part of the declining population. The Fish Island rookery is located in a transitional area between the stable and declining populations.

teen transmitters were deployed in the area of declining population, of which seven produced usable data: four transmitters in 1993 at Chirikof Island (55°10'N, 155°8'W) in the central Gulf of Alaska and three transmitters in 1997 at Seguam Island (52°30'N, 172°30'W) in the eastern Aleutian Islands. Six transmitters were deployed on females in 1995 at Fish Island (59°53'N, 147°20'W) in the eastern Gulf of Alaska, of which four produced usable data. The number of SSL on Fish Island, which lies between the areas of stable and declining populations, has been growing slowly, and it is thus a transitional area between the two populations. Data from 28 females in the stable population, seven in the declining population, and four in the transitional area were used in the analyses. Data from some females were excluded because of (1) poor transmitter reception; (2) premature loss of the transmitter; or (3) only one foraging trip was recorded. The smaller sample size from the area of decline resulted from the remote locations of the rookeries and logistical constraints. All studies were performed in the summer, starting in early June and lasting for four to six weeks.

Adult females were darted with Telazol (Tiletamine HCl and Zolazepam HCl, Fort Dodge Laboratories, Fort Dodge, Iowa, USA: 2.0 mg per kg body mass), intubated, and anesthetized for about three hours with isoflurane using large-animal anesthesia and monitoring techniques (Heath et al. 1996). Each female was weighed in a sling attached to a tripod and an electronic scale (Rice Lake Weighing Systems, Rice Lake, Wisconsin; Ohaus I-20W, Ohaus, Pine Brook, New Jersey). Morphometric measurements included standard length (SL) and axillary girth (AG) (American Society of Mammalogists 1967). Radio transmitters (164-165 MHz, 150 g, Advanced Telemetry Systems, Isanti, Minnesota) were glued to the hair in the dorsal axillary area with epoxy. The transmitters fell off when the animals molted.

Radio signals from the transmitters were recorded on an automated data logger (DCC II, Advanced Telemetry Systems), set to scan each frequency for 20 seconds on a duty cycle of 15 minutes (30 minutes on Lowrie Island in 1994). The presence of a signal indicated that the female was on land or on the surface of the water near the rookery, while the lack of a signal indicated that the female was either at sea or the signal was blocked by a rock or other obstacle. Antennas were positioned to minimize the latter possibility. Transmitter range was estimated in the field to be two to four miles, depending on antenna location. When possible, absence or presence of the females on the rookery was verified by direct observation. When a signal was received for more than one hour, the female was assumed to be on land. The one hour minimum was used to reject spurious signals caused by background radio frequency noise. When a signal was not received for more than three hours, a female was assumed to be at sea. The three hour cutoff was chosen by performing a frequency distribution analysis of signal reception gaps, and finding the minimum in the distribution that separated the gaps into two groups (Boyd et al. 1991).

Any trips that started when the rookery was disturbed because of human presence were excluded. We found that interannual differences at Lowrie Island were not significantly different, so the data for all years at this rookery were combined. Results from Seguam and Chirikof were also not significantly different, so those locations were combined to represent the declining population. Data were analyzed using 1-way ANOVA and Tukey tests for multiple comparisons using Systat (SPSS, Chicago). Significance was determined using a $P \leq 0.05$.

Pup growth

From 1990 to 1997, SSL pups were studied at five locations in Southeast Alaska, the Gulf of Alaska, and the Aleutian Islands (Fig. 1). At Lowrie Island in Southeast Alaska, measurements were made in 1993, 1994, and

1997. In the Gulf of Alaska, measurements were made in 1990, 1991, and 1994 on Marmot Island (58º12'N, 151º50'W), in 1993 on Chirikof Island and in 1995 on Fish Island. On the Aleutian Islands of Seguam and Yunaska, pups were studied in 1997. Data from Seguam and Yunaska Islands were combined because the islands are geographically close and can be considered part of one rookery complex. The pup growth data was published previously in Brandon et al. (2005).

Only pups that had an attached umbilical cord or an unhealed umbilicus were selected for study and estimated to be 1-5 days in age (Davis and Brandon, unpubl. data). Choosing only pups with fresh umbilical cords minimized the age bias (Trites 1993) that occurs when capturing pups at different times and rookeries. Body mass (BM), standard length (SL), axillary girth (AG) (American Society of Mammalogists 1967), and body composition were measured for each pup. BM was measured to the nearest kilogram with a mechanical spring scale (Chatillon 160, Ametek, Florida) on Marmot Island in 1990 and 1991 and on Lowrie Island in 1993. BM of pups at all other sites and years was measured to the nearest tenth of a kilogram using an electronic scale (Rice Lake Weighing Systems, Rice Lake, Wisconsin; Ohaus I-20W, Ohaus, Pine Brook, New Jersey). SL was measured as a straight line from tip-of-nose to tip-of-tail, ventral surface down. Pups were restrained by hand and marked for later identification with hair bleach (Lady Clairol Maxi Blond, Clairol, Inc.) and with flipper tags attached in the axillary area of the fore-flippers.

Body composition was measured using the labeled water method (Nagy 1975, Nagy and Costa 1980, Costa 1987, Bowen and Iverson 1998). In this study, water labeled with a stable isotope of hydrogen (deuterium) was used to estimate total body water (TBW in kg and %TBW as a percentage of BM) and total body lipid (%TBL as a percentage of BM). Background concentration of deuterium was determined from blood samples taken from pups that were subsequently injected intramuscularly with 10 ml deuterium oxide (D_2O) (99% enriched, Cambridge Isotope Laboratories, Andover, Massachusetts). After a two-hour equilibration period (Costa 1987), blood samples were taken to determine the dilution of injected deuterium in total body water.

Pups were recaptured at approximately two-week intervals over periods ranging in length from 18-38 days (one to three recaptures over an average measurement period of 29.6 days) and were weighed and measured. Similar protocols were used on all rookeries except Marmot Island in 1990 and 1991, when only BM and SL were measured, and age of pups was not estimated. Therefore, no growth rates were obtained from those data.

Statistics were performed using Systat (Version 11, SPSS, Inc.), first treating each study site and year as a separate “location,” then combining data for multiple years at a location (e.g., Marmot Island and Lowrie Island) when no significant interannual differences were found. Significance

Table 1. Mean time onshore, time at sea, cycle time, and percentage of time onshore and at sea (mean ± standard deviation).

Location	n	Time onshore (hours)	Time at sea (hours)	Total cycle time (hours)	% of cycle time onshore	% of cycle time at sea
Area of stable population (S) Lowrie Is.	28	22.3 ± 9.22	25.6 ± 11.64	48.0 ± 22.86	48.9 ± 8.89	51.1 ± 8.89
Transitional area (T) Fish Is.	4	25.2 ± 7.31	19.4 ± 5.09	45.0 ± 6.35	53.1 ± 10.30	46.9 ± 10.31
Area of declining population (D) Chirikof Is. and Seguam Is.	7	20.9 ± 4.21	9.4 ± 3.32	31.2 ± 2.72	68.6 ± 9.99	31.4 ± 9.99
ANOVA		ns	$P = 0.0025$ S > D	ns	$P < 0.0001$ S < D T < D	$P < 0.0001$ S > D T > D

was determined at $P \leq 0.05$. Data were examined for heteroscedasticity (unequal variances) before analysis (Zar 1984). All post hoc pairwise comparisons were made using the Tukey multiple comparison test. Data from the first capture (1-5 days of age) were analyzed for comparison by location and sex using two-way ANOVA. Pup growth rate was estimated by performing a linear regression for each pup and extrapolating to $t = 0$ to estimate birth mass. Differences among means of pup growth rate and birth mass were then analyzed using two-way ANOVA to determine differences by location and sex.

Results

Female attendance

During the first four to six weeks postpartum, the time spent onshore by females did not differ significantly among rookeries, and averaged 22.5 h ± 8.26 SD (range = 21.9-25.2 h, Table 1). Average foraging trip duration was significantly different among rookeries ($P = 0.0025$) and ranged from 25.6 h ± 11.64 SD in the area of stable population (Lowrie Island) to 9.4 h ± 3.32 SD in the area of declining population (Chirikof and Seguam islands). Average foraging trip duration (19.4 h ± 5.09) for females in the transitional area (Fish Island) was twice the value for the declining population and 77% of the value for the stable population, but not significantly different from either. Overall, foraging trip duration

Table 2. Body mass (BM), standard length (SL), and axillary girth (AG) of neonatal (1-5 day old) pups in the stable (Lowrie Island) and declining (Marmot, Chirikof, Seguam, and Yunaska islands) populations (mean ± SD). Pups on Fish Island are in a transitional area between the stable and declining populations.

Location	*N*	BM (kg)		SL (cm)		AG (cm)	
		Male	Female	Male	Female	Male	Female
Lowrie Island (1993-1997)	39 M 41 F	22.14±2.206	19.54±1.667	98.3±4.56	94.1±3.96	64.9±3.33	64.3±5.01
Fish Island (1995)	11 M 9 F	22.62±1.695	19.20±2.388	**96.2**±26.76	**93.3**±6.39	68.5±2.96	64.0±4.00
Marmot Island (1994)	3 M 6 F	21.73±1.801	20.22±2.425	101.7±1.53	97.4±2.67	65.5±2.78	61.8±5.38
Chirikof Island (1993)	11 M 9 F	23.21±2.587	19.02±1.052	99.1±5.24	94.9±2.40	62.7±3.52	60.1±2.15
Seguam and Yunaska islands (1997)	7 M 9 F	24.17±1.971	20.51±1.883	**101.4**±4.29	**96.3**±2.55	67.7±3.50	63.9±3.66

Gray background indicates significant differences from all other sites, and bold type indicates a significant difference between two sites. SL on Fish Island was significantly different from SL on Seguam and Yunaska islands. AG on Chirikof Island was significantly different from AG at all other sites. In all cases, males were significantly larger than females. There were no significant interannual differences, so data from all years at Lowrie Island were combined.

among rookeries decreased in an east-to-west direction from the area of stable to declining population.

The average percentage of time spent onshore was significantly different among rookeries ($P < 0.0001$). Females in the area of population decline (Chirikof and Seguam islands) spent a significantly greater percentage (69%) of time onshore than did females in the area of stable population (49%) and area of transition (53%) ($P = 0.0001$) (Table 1). Consequently, the average percentage of time spent at sea was also significantly different among rookeries. Females in the area of decline spent a significantly smaller percentage (31%) of time at sea than did females in the area of stable population (51%) and area of transition (47%) ($P = 0.0001$) (Table 1). Overall, the percentage of time spent onshore increased and the percentage of time spent at sea decreased in an east-to-west direction.

Pup growth

There were no significant differences by rookery in pup mass at 1-5 days of age (Table 2) and no significant interaction between rookery and sex. The only significant difference in SL of 1-5 day old pups was that both genders were significantly longer on Seguam and Yunaska islands than on Fish Island ($P = 0.0395$). Pups on Chirikof Island had significantly smaller AG than pups on Lowrie, Fish, and Seguam and Yunaska islands ($P < 0.02$). Male and female pups were significantly different for all three morphometric measurements. Overall, male pups averaged 22.6 kg (± 2.21 SD, $n = 71$) and female pups averaged 19.6 kg (± 1.80 SD, $n = 74$) at first capture (1-5 days of age).

There was no significant difference by rookery or sex and no significant interaction between rookery and sex in %TBW or %TBL of pups at first capture. When all pups at all rookeries were combined ($n = 116$), %TBW was 72.1% of BM (± 3.17 SD) and %TBL was 5.6% of BM (± 2.68 SD). Male pups had a significantly greater absolute TBW than female pups ($P < 0.0001$), as would be expected because of the difference in BM at birth. There was a significant correlation between TBW and BM (Pearson $r = 0.945$, $P < 0.001$, $n = 116$; TBW (kg) = $0.6895 \times \text{BM} + 0.6618$).

Growth rates were treated as linear over the period monitored. Male and female pups on the same rookery grew at the same rate (in BM, SL, and AG) during the first six weeks postpartum. When compared by rookery, BM increased at a faster rate for pups on Chirikof Island ($P = 0.0005$) and on Seguam and Yunaska islands ($P = 0.0002$) than on Lowrie Island (Fig. 2 and Table 3). The increase in BM for pups on Fish Island did not differ significantly from that at other rookeries. Marmot Island pups grew significantly more slowly than pups on Seguam and Yunaska islands ($P = 0.0382$), but did not differ significantly from growth of pups at other rookeries.

SL increased at a faster rate for pups on Chirikof Island ($P = 0.0068$) and Seguam and Yunaska islands ($P = 0.0050$) than it did for pups on Low-

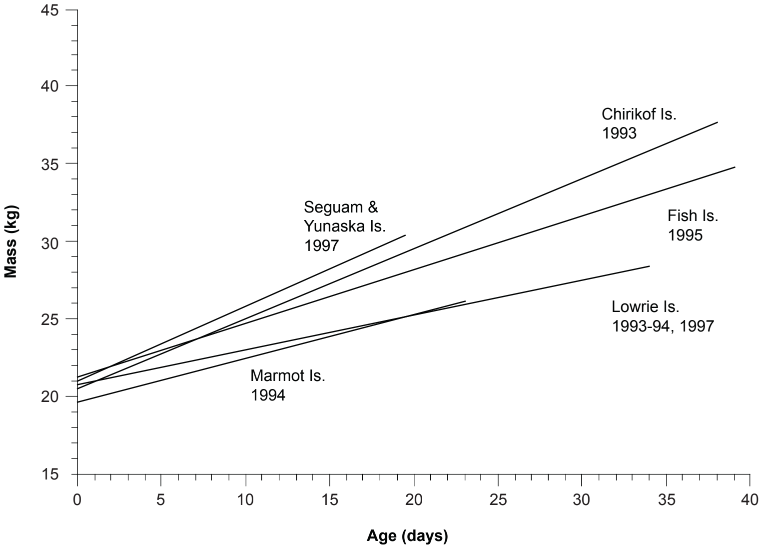


Figure 2. Summary of pup growth (body mass) during the first six weeks postpartum for all five rookeries. The length of each line indicates the length of the study period at that location. Pups from the Seguam, Yunaska, and Chirikof islands, in the declining population, grew significantly faster than pups from Lowrie Island, in the stable population. Pups from Seguam and Yunaska islands also grew significantly faster than pups from Marmot Island.

rie Island (Table 3). Growth in SL was also faster on Chirikof $P = 0.0383$) and Seguam and Yunaska islands ($P = 0.0230$) than on Fish Island, while the increase in SL on Marmot Island did not differ significantly from the other rookeries. The increase in AG was significantly greater on Seguam and Yunaska islands ($P = 0.0021$) and Marmot Island ($P = 0.0364$) than on Lowrie Island. There was no significant interaction between rookery and sex in the growth rate of BM, SL, and AG.

Body mass at birth extrapolated to $t = 0$ from growth rates did not differ by rookery. There was no significant interaction between rookery and sex, but extrapolated birth mass did differ by sex ($P < 0.0001$). Male pups at all rookeries averaged 22.4 kg (± 2.36 SD, $n = 39$), while female pups averaged 18.7 kg (± 2.08 SD, $n = 35$). These extrapolated birth masses were similar to the average BM measured on the rookery for male (22.6 kg) and female (19.6) pups 1-5 days old. There was no correlation between extrapolated birth mass and growth rate (Pearson $r = -0.09$, $P = 0.45$).

Table 3. Steller sea lion pup growth rates, 0-40 days of age (mean ± SD). There were no significant differences between male and female pups.

Location	*n*	BM growth rate (kg/day)	SL growth rate (cm/day)	AG growth rate (cm/day)
Lowrie Island (L)	26	0.23 ± 0.176	0.20 ± 0.322	0.25 ± 0.244
Fish Island (F)	13	0.35 ± 0.171	0.22 ± 0.183	0.41 ± 0.235
Marmot Island (M)	6	0.28 ± 0.141	0.22 ± 0.287	0.59 ± 0.510
Chirikof Island (C)	17	0.45 ± 0.126	0.47 ± 0.171	0.47 ± 0.187
Aleutian Islands (A) Seguam and Yunaska islands	12	0.48 ± 0.168	0.53 ± 0.163	0.59 ± 0.257
ANOVA results[a]		L M F C A	L F M C A	L F C M A

[a] Underlining indicates that there were no significant differences within an underlined grouping (e.g., for body mass growth rate, C was significantly different from L, and A was significantly different from M and L).

Discussion

We reject our null hypothesis that there is no difference in foraging trip duration between populations of SSL. Foraging trip durations of females in the stable population (25.6 h) and transitional area (19.4 h) were in the same range as foraging trips measured in previous studies. However, foraging trip durations (9.4 h) of females in the area of population decline were shorter than any previously reported for this species. In California, SSL were observed to make trips to sea of 22 h in 1973 (Hood and Ono 1997), 36 h in 1983 (Higgins et al. 1988), and 50 h in 1992 (Hood and Ono 1997). Using radio telemetry, Merrick and Loughlin (1997) reported trips to sea of 21 h for SSL in the central Gulf of Alaska and 25 h in the eastern Aleutian Islands from 1990 to 1993. A 1994-1995 observational study reported that SSL in the central Gulf of Alaska and in Southeast Alaska made trips averaging 22 h in length (Milette 1999), although trip lengths may have been overestimated due to the absence of observations at night. Based on these data, there appears to be a cline in time spent at sea, with decreasing trip lengths from east to west.

Although male and female pups differed significantly in size, there were no significant differences in pup size at birth among the rookeries studied. Rookery location should have less influence on pup size at birth than on neonatal growth because maternal foraging range is much greater during gestation than lactation (Merrick and Loughlin 1997). This reduces variation among rookeries in maternal size and feeding during gestation, both of which have been shown to influence pup birth mass in pinnipeds (Calambokidis and Gentry 1985; Kovacs and Lavigne 1986;

Trites 1991, 1992). In addition, gestation is less energetically expensive than early lactation, so differences in food availability would have less of an effect during gestation (Robbins and Robbins 1979, Albon et al. 1983, Oftedal 1984).

While most pup morphometrics at first capture did not differ among rookeries, growth parameters differed significantly (Fig. 2 and Table 3). Growth rates of pups on Seguam and Yunaska islands (0.48 kg day^{-1}) and on Lowrie Island (0.23 kg day^{-1}) represented the extremes, while growth rates of pups on Chirikof, Marmot, and Fish islands fell between these two extremes. In general, faster growth rates occurred in the west and slower growth rates in the east. In terms of mass, Seguam, Yunaska, and Chirikof Island pups grew two times faster than Lowrie Island pups.

Average %TBL of neonatal pups was low (5.6% BM) but in the range reported for other otariids. SSL pups are born with small energy stores and normally fast for short periods (ca. one day) while their mothers make foraging trips to sea. There have been few measurements of lipid content in otariid neonates. Jonker and Trites (2000) found a blubber content of 9.7% BM in five SSL pups in the first month postpartum. However, this measurement does not correspond directly to body fat content because they measured blubber content by weighing the sculp (skin plus blubber) and then calculating the fraction of sculp that was blubber by measuring skin and blubber thicknesses. Using the same labeled water method as in this study, Arnould et al. (1996a) found a %TBL of 9.4% BM in four Antarctic fur seal pups in the first month postpartum. In a similar study of one-day-old Antarctic fur seal pups, Arnould et al. (1996b) found a %TBL of 7.0% BM for female pups and 4.9% BM for male pups. Also using labeled water, Oftedal et al. (1987) found an average %TBL of 5% BM for neonatal California sea lion pups.

Females in the declining population did not make longer foraging trips than those in the area of stable population as might be predicted if prey had become less abundant or diverse. In addition, the results for pup size and growth gave no indication of food stress during early lactation. In fact, pups from the declining population on Seguam, Yunaska, and Chirikof islands grew faster than pups from the stable population on Lowrie Island during the first six weeks. Similar results were also found in a study of pup BM (Merrick et al. 1995), in which pups were weighed on rookeries from Oregon to the Aleutian Islands in late June and early July from 1987 to 1994. Although the pups' ages were unknown, weighing date was used as a covariate in the analysis. Merrick et al. (1995) found a continuous increase in pup BM from Oregon to Southeast Alaska and to the Aleutian Islands. These investigators also concluded that pup BM was on average greater in the declining population.

Considering the results for SSL pup growth in light of the population decline, we suggest three alternative hypotheses: (1) food availability was never a factor in the population decline; (2) food availability caused the overall decline, but lactating females and their pups were not affected during early lactation; or (3) this study was conducted when pups and lactating females were no longer experiencing decreased food availability.

Faster rates of pup growth may be normal for the Aleutian Islands and western Gulf of Alaska despite the population decline. The declining and stable populations are genetically distinct (Bickham et al. 1996), and perhaps the differences seen here are normal differences between the two populations. It is impossible to determine if growth and foraging behavior have changed over time, since historical data on maternal investment are sparse. Juveniles rather than neonates may be the affected age class in the declining population (Merrick et al. 1988), while lactating females are feeding on either different prey or age classes and not experiencing decreased food availability. York (1994) constructed a population model of SSL in Alaska and concluded that the current population decline could be accounted for by increased juvenile mortality.

Alternatively, because this study was performed late in the decline, the higher growth rates could be the result of lower population density and less competition for food in the declining population. Trites and Bigg (1992) reported larger body sizes in northern fur seal populations during a period of decline. The northern fur seal population in the Pribilof Islands in the Bering Sea increased from the early 1900s to the 1950s. During this period, adult body size decreased. From 1950 to the 1970s the population declined, with a concurrent increase in body size (Trites and Bigg 1992). Scheffer (1955) hypothesized that increased body size was due to decreased competition for food, which in turn would be due to the lower population density. It is possible the same density-dependent effects are occurring in the declining SSL population, since this study was performed late in the decline, after the original cause may have abated. However, the results must be treated with caution due to the small sample sizes over multiple years.

More information will be needed to determine the cause of the SSL decline and whether it is related to the availability of food, especially for different age classes and at different times of the year.

Acknowledgments

We thank T. Adams, R. Andrews, D. Bradley, J. Burns, M. Castellini, J.K. Chumbley, W. and S. Cunningham, J. Davis, F. Gulland, D. Gummeson, B. Heath, D. Johnson, S. Kanatous, D. Lidgard, R. Lindeman, R. Merrick, D. McAllister, L. Milette, K. Ono, L. Polasek, T. Porter, D. Rosen, J. Sease, T. Spraker, U. Swain, W. Taylor, A. Trites, D. van den Bosch, T. Williams, and the captain and crew of the R/V *Medeia* for assistance in the field. We thank K. Andrews for the map and D. Brandon for assistance in data collection and analysis. G. Worthy, A. Trites, T. Lacher, D. Owens, and M. Reynolds reviewed an early version of this manuscript. Funding and logistical support in the field were provided by the Alaska Department of Fish and Game, the National Marine Fisheries Service/National Marine Mammal Laboratory, Texas A&M University, and the Texas Institute of Oceanography. This research was conducted under Marine Mammal Permit No. 846 and 963.

References

Albon, S.D., T.H. Clutton-Brock, and R. Langvatn. 1992. Cohort variation in reproduction and survival: Implications for population demography. In: R.D. Brown (ed.), The biology of deer. Springer-Verlag, New York, pp. 15-21.

Albon, S.D., F.E. Guinness, and T.H. Clutton-Brock. 1983. The influence of climatic variation on the birth weights of red deer (*Cervus elaphus*). J. Zool. (Lond.) 203:295-298.

American Society of Mammalogists. 1967. Standard measurements of seals. J. Mammal. 48:459-462.

Andrews, R.D. 1999. Appendix B.9: Preliminary progress report of Steller sea lion (SSL) foraging ecology studies. In: A. Didier (ed.), Final Report on the Steller Sea Lion Feeding Ecology Workshop, held at Seattle, 11-12 February 1999. Pacific States Marine Fisheries Commission, Gladstone, Oregon, pp. 25-28.

Antonelis, G.A., B.S. Stewart, and W.F. Perryman. 1990. Foraging characteristics of female northern fur seals (*Callorhinus ursinus*) and California sea lions (*Zalophus californianus*). Can. J. Zool. 68:150-158.

Arnould, J.P.Y., I.L. Boyd, and J.R. Speakman. 1996a. Measuring the body composition of Antarctic fur seals (*Arctocephalus gazella*): Validation of hydrogen isotope dilution. Physiol. Zool. 69:93-116.

Arnould, J.P.Y., I.L. Boyd, and D.G. Socha. 1996b. Milk consumption and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups. Can. J. Zool. 74:254-266.

Baker, J.D., and C.W. Fowler. 1992. Pup weight and survival of northern fur seals *Callorhinus ursinus*. J. Zool. (Lond.) 227:231-238.

Bickham, J.W., J.C. Patton, and T.R. Loughlin. 1996. High variability for control-region sequences in a marine mammal: Implications for conservation and biogeography of Steller sea lions (*Eumetopias jubatus*). J. Mammal. 77:95-108.

Boltnev, A.I., A.E. York, and G.A. Antonelis. 1998. Northern fur seal young: Interrelationships among birth size, growth, and survival. Can. J. Zool. 76:843-854.

Bonner, W.N. 1984. Lactation strategies in pinnipeds: Problems for a marine mammalian group. Symp. Zool. Soc. Lond. 51:253-272.

Bowen, W.D., and S.J. Iverson. 1998. Estimation of total body water in pinnipeds using hydrogen-isotope dilution. Physiol. Zool. 71:329-332.

Boyd, I.L., N.J. Lunn, and T. Barton. 1991. Time budgets and foraging characteristics of lactating Antarctic fur seals. J. Anim. Ecol. 60:577-592.

Boyd, I.L., J.P.Y. Arnould, T. Barton, and J.P. Croxall. 1994. Foraging behavior of Antarctic fur seals during periods of contrasting prey abundance. J. Anim. Ecol. 63:703-713.

Braham, H.W., R.D. Everitt, and D.J. Rugh. (1980). Northern sea lion decline in the eastern Aleutian Islands. J. Wildl. Manag. 44:25-33.

Brandon, E.A.A. 2000. Maternal investment in Steller sea lions in Alaska. Ph.D. thesis, Texas A&M University, Galveston. 137 pp.

Brandon, E.A.A., D.G. Calkins, T.R. Loughlin, and R.W. Davis. 2005. Neonatal growth of Steller sea lion (*Eumetopias jubatus*) pups in Alaska. Fish. Bull. U.S. 103:246-257.

Bryden, M.M. 1968. Control of growth in two populations of elephant seals. Nature 217:1106-1108.

Burns, J.M. 1999. The development of diving behavior in juvenile Weddell seals: Pushing physiological limits in order survive. Can. J. Zool. 77:737-747.

Calambokidis, J., and R. Gentry. 1985. Mortality of northern fur seal pups in relation to growth and birth weights. J. Wildl. Dis. 21:327-330.

Costa, D.P. 1987. Isotopic methods for quantifying material and energy intake of free-ranging marine mammals. In: A.C. Huntley, D.P. Costa, G.A.J. Worthy, and M.A. Castellini (eds.). Marine mammal energetics. Soc. Mar. Mammal. Spec. Publ. 1:43-66.

Costa, D.P., J.P. Croxall, and C.D. Duck. 1989. Foraging energetics of Antarctic fur seals in relation to changes in prey availability. Ecology 70:596-606.

Feldkamp, S.D., R.L. DeLong, and G.A. Antonelis. 1991. Effects of El Niño 1983 on the foraging patterns of California sea lions (*Zalophus californianus*) near San Miguel Island, California. In: F. Trillmich and K. Ono (eds.), Pinnipeds and El Niño: Responses to environmental stress. Springer-Verlag, Berlin, pp. 146-155.

Francis, J., D. Boness, and H. Ochoa-Acuña. 1998. A protracted foraging and attendance cycle in female Juan Fernández fur seals. Mar. Mamm. Sci. 14:552-574.

Gaillard, J.-M., J.-M. Boutin, D. Delorme, G. Van Laere, P. Duncan, and J.-D. Lebreton. 1997. Early survival in roe deer: Causes and consequences of cohort variation in two contrasted populations. Oecologia 112:502-513.

Gentry, R.L. 1970. Social behavior of the Steller sea lion. Ph.D. thesis, University of California, Santa Cruz.

Georges, J.-Y., and C. Guinet. 2000. Maternal care in the subantarctic fur seals on Amsterdam Island. Ecology 81:295-308.

Heath, R.B., D. Calkins, D. McAllister, W. Taylor, and T. Spraker. 1996. Telazol and Isoflurane anesthesia in free ranging Steller sea lions. J. Zoo Wildl. Med. 27:35-43.

Higgins, L.V., D.P. Costa, A.C. Huntley, and B.J. Le Boeuf. 1988. Behavioral and physiological measurements of maternal investment in the Steller sea lion, *Eumetopias jubatus*. Mar. Mamm. Sci. 4:44-58.

Hood, W.R., and K.A. Ono. 1997. Variation in maternal attendance patterns and pup behaviour in a declining population of Steller sea lions (*Eumetopias jubatus*). Can. J. Zool. 75:1241-1246.

Innes, S., R.E.A. Stewart, and D.M. Lavigne. 1981. Growth in Northwest Atlantic harp seals *Phoca groenlandica*. J. Zool. (Lond.) 194:11-24.

Jonker, R.A.H., and A.W. Trites. 2000. The reliability of skinfold-calipers for measuring blubber thickness of Steller sea lion pups (*Eumetopias jubatus*). Mar. Mamm. Sci. 16:757-766.

Kovacs, K.M., and D.M. Lavigne. 1986. Maternal investment and neonatal growth in phocid seals. J. Anim. Ecol. 55:1035-1051.

Loughlin, T.R. 1998. The Steller sea lion: A declining species. Biosph. Conserv. 1:91-98.

Loughlin, T.R., A.S. Perlov, and W. Vladimirov. 1992. Rangewide survey and estimation of total number of Steller sea lions in 1989. Mar. Mamm. Sci. 83:220-239.

Merrick, R.L., and T.R. Loughlin. 1997. Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. Can. J. Zool. 75:776-786.

Merrick, R.L., R. Brown, D.G. Calkins, and T.R. Loughlin. 1995. A comparison of Steller sea lion, *Eumetopias jubatus*, pup masses between rookeries with increasing and decreasing populations. Fish. Bull. U.S. 93:753-758.

Merrick, R., P. Gearin, S. Osmet, and D. Withrow. 1988. Field studies of northern sea lions at Ugamak Island, Alaska, during the 1985 and 1986 breeding seasons. NOAA Tech. Memo. NMFS F/NWC-43. 60 pp.

Milette, L.L. 1999. Behaviour of lactating Steller sea lions (*Eumetopias jubatus*) during the breeding season: A comparison between a declining and stable population in Alaska. M.S. thesis, University of British Columbia, Vancouver.

Nagy, K.A. 1975. Water and energy budgets of free-living animals: Measurement using isotopically labeled water. In: N. Hadley (ed.), Environmental physiology of desert organisms. Dowden, Hutchinson, and Ross, Stroudsburg, Pennsylvania, pp. 227-245.

Nagy, K.A., and D.P. Costa. 1980. Water flux in animals: Analysis of potential errors in the tritiated water method. Am. J. Physiol. 238:R454-R465.

NMFS. 1995. Status review of the United States Steller sea lion (*Eumetopias jubatus*) population. Prepared by the National Marine Mammal Laboratory, National Marine Fisheries Service, Alaska Fisheries Science Center. 61 pp.

Oftedal, O.T. 1984. Body size and reproductive strategy as correlates of milk energy output in lactating mammals. Acta Zool. Fenn. 171:183-186.

Oftedal, O.T., S.J. Iverson, and D.J. Boness. 1987. Milk and energy intakes of suckling California sea lion *Zalophus californianus* pups in relation to sex, growth, and predicted maintenance requirements. Physiol. Zool. 60:560-575.

Ono, K.A. 1997. Presentation of current research. In: A. Didier (ed.), Final Report on the Steller Sea Lion Behavior/Rookery Studies Workshop, held at Seattle, 5-7 December 1997. Pacific States Marine Fisheries Commission, Gladstone, Oregon.

Ono, K.A., D.J. Boness, and O.T. Oftedal. 1987. The effect of a natural environmental disturbance on maternal investment and pup behavior in the California sea lion. Behav. Ecol. Sociobiol. 21:109-118.

Porter, B. 1997. Winter ecology of Steller sea lions (*Eumetopias jubatus*) in Alaska. M.S. thesis, University of British Columbia, Vancouver.

Robbins, C.H., and B.L. Robbins. 1979. Fetal and neonatal growth patterns and maternal reproductive efforts in ungulates and subungulates. Am. Nat. 114:101-116.

Sandegren, F.E. 1970. Breeding and maternal behavior of the Steller sea lion (*Eumetopias jubatus*) in Alaska. M.S. thesis, University of Alaska.

Scheffer, V.B. 1955. Body size with relation to population density in mammals. J. Mammal. 39:493-515.

Swain, U.G. 1996. Foraging behaviour of female Steller sea lions in Southeast Alaska and the Eastern Gulf of Alaska. In: Steller sea lion recovery investigations in Alaska, 1992-1994. Alaska Department of Fish and Game, Division of Wildlife Conservation, Wildlife Technical Bulletin 13, pp. 135-166.

Trillmich, F., and D. Limberger. 1985. Drastic effects of El Niño on Galapagos pinnipeds. Oecologia 67:19-22.

Trites, A.W. 1991. Fetal growth of northern fur seals: Life-history strategy and sources of variation. Can. J. Zool. 69:2608-2617.

Trites, A.W. 1992. Fetal growth and the condition of pregnant northern fur seals off western North America from 1958 to 1972. Can. J. Zool. 70:2125-2131.

Trites, A.W. 1993. Biased estimates of fur seal pup mass: Origins and implications. J. Zool. (Lond.) 229:515-525.

Trites, A.W., and M.A. Bigg. 1992. Changes in body growth of northern fur seals from 1958 to 1974: Density effects or changes in the ecosystem? Fish. Oceanogr. 1:127-136.

Tveraa, T., B.-E. Sæther, R. Aanes, and K.E. Erikstad. 1998. Body mass and parental decisions in the Antarctic petrel *Thalassioca antarctica*: How long should the parents guard the chick? Behav. Ecol. Sociobiol. 43:73-79.

York, A.E. 1994. The population dynamics of northern sea lions, 1975-1985. Mar. Mamm. Sci. 10:38-51.

Oxygen Stores of California Sea Lion Pups: Implications for Diving Ability

Carey E. Kuhn
University of California, Department of Ecology and Evolutionary Biology, Santa Cruz, California

David Aurioles-Gamboa
Centro Interdisciplinario de Ciencias Marinas-Instituto Politécnico, Departamento de Biologia Marina y Pesquerias, La Paz, Baja California Sur, México

Michael J. Weise and Daniel P. Costa
University of California, Department of Ecology and Evolutionary Biology, Santa Cruz, California

Abstract

Diving mammals are faced with the challenge of locating and catching prey while also breath-holding. The most efficient way to maximize total time under water is to use aerobic metabolism, relying on the oxygen stored in the blood, muscle, and lungs. While oxygen stores have been measured in adult animals, there are few reports on the development of oxygen stores in young pinnipeds as they transition to independence. This study examined the total body oxygen stores of California sea lion pups (*Zalophus californianus*) at or near weaning in April 2003 at Los Islotes, Mexico (24º35'N, 110º23'W). We measured mass, plasma volume, blood volume, hematocrit, hemoglobin, and muscle myoglobin content. These values were used to estimate total oxygen available to pups in the blood, muscle, and lungs.

Pup mass ranged from 26.4 to 42.4 kg (mean 33.0 ± 4.7 kg). Mean plasma volume was 1.6 ± 0.1 L and total blood volume was 9.9% of mass. Mean hematocrit, hemoglobin, and myoglobin concentration were 52.4 ± 0.9%, 22.9 ± 2.8 g per 100 ml, and 2.3 ± 0.6 g per 100 g muscle, respectively. Based on these values, mass specific oxygen stores were estimated to be 34.5 ± 2.2 ml O_2 per kg. At or near weaning, California sea lion pups at Los Islotes have only 53% of adult female oxygen stores and therefore will not be able to forage on the deep prey resources exploited by adults in this population.

Introduction

Transition to nutritional independence is a vital stage in the life of young mammals and plays a key role for recruitment into the population (Eberhardt and Siniff 1977). For marine mammals, being nutritionally independent means developing the ability to locate and capture prey while diving. Physiological capacity ultimately sets a limit that diving animals must operate within (Elsner and Gooden 1983; Castellini et al. 1985; Kooyman 1985, 1989; Ponganis et al. 1993, 1997). A critical component of this physiological capacity is the oxygen stored in the blood, muscle, and lung that is available to support aerobic metabolism while diving. These oxygen stores and the rate at which these resources are used determine an animal's aerobic diving ability (Kooyman 1989). Relying on aerobic metabolism allows the animal to maximize total accumulated dive time, and therefore foraging time, by minimizing the interdive interval (Kooyman et al. 1980, Kooyman 1989, Ydenberg and Clark 1989, Costa et al. 1998). As physiology sets a limit on diving, the variation in total body oxygen stores has been reported for adults across a range of pinniped species (e.g., Lenfant et al. 1970; Kooyman 1989; Ponganis et al. 1993; Costa et al. 2001, 2004; Costa and Sinervo 2004).

Studies of the development of oxygen stores in young pinnipeds have focused mostly on young phocids (true seals) and have found that total oxygen stores are often not fully developed at the age of weaning. For northern elephant seals (*Mirounga angustirostris*) and gray seals (*Halichoerus grypus)* total body oxygen stores increase rapidly from the time of birth to the first trip to sea; however, mass specific oxygen stores are only 73.5% and 67%, respectively, of adult values at the start of the first foraging trip (Thorson and Le Boeuf 1994, Noren et al. 2005). Studies with Weddell seal (*Leptonychotes weddellii*) and harbor seal (*Phoca vitulina*) pups also found that development of total body oxygen stores is not complete by the age of weaning (Burns and Castellini 1996, Jorgensen et al. 2001, Burns et al. 2005). For the Weddell seal, yearlings were still only at 65% of the mass specific oxygen stores of adult females, eight or more months after weaning (Burns and Castellini 1996).

Given the importance of the transition to nutritional independence and the limit physiological development may place on foraging, it is surprising that few studies have been published on the total body oxygen stores of young otariids (fur seals and sea lions; Lenfant et al. 1970, Ponganis et al.1997, Costa et al. 1998, Arnould et al. 2003, Richmond 2004). With the extremely abbreviated (4 to 50 days) lactation interval of phocid seals we might expect pups to be physiologically less developed at weaning (Costa 1991). In contrast, we might expect the considerably longer (4 months to 3 years) lactation period of otariids to allow pups to be weaned with a physiological capacity closer to adults (Costa 1991).

Research examining only blood oxygen stores of Galapagos fur seals (*Arctocephalus galapagoensis*) found at weaning many blood parameters reached adult levels (Horning and Trillmich 1997). Costa et al. (1998) also found for juvenile New Zealand sea lions (*Phocarctos hookeri*) blood oxygen stores matched those of adult females. However, research on the development of total body oxygen stores in pups of the Steller sea lion (*Eumetopias jubatus)*, Australian fur seal (*Arctocephalus pusillus*), and Australian seal lion (*Neophoca cirenea*) suggests physiological development is not complete at the age of weaning (Richmond 2004, Archer and Arnould, Deacon Univ., Australia, unpubl.; Fowler and Costa, Univ. of California, Santa Cruz, unpubl.). For the Steller sea lion blood oxygen stores are similar to adult values at 9 months (Richmond 2004). However, due to the lagging development of muscle oxygen stores, total body oxygen stores take up to 21 months to reach adult values (Richmond 2004).

For the California sea lion (*Zalophus californianus*), an abundant predator along the western coast of the United States and Mexico, little information is available on total body oxygen stores as pups transition to nutritional independence. Measurements of diving behavior of female sea lions in California populations found females often make short dives feeding at relatively shallow depths (mean duration 2.1 minutes, mean depth <65m; Antonelis et al. 1984; Feldkamp et al. 1989, 1991). More recent studies have found that female California sea lions at Los Islotes, Mexico, dive regularly to depths over 200 meters, with over 50% of dive durations greater than 4 minutes and dives lasting over 9 minutes (Kuhn, Aurioles, and Costa unpubl.). In comparison to the short, shallow dives of females in California populations, the longer, deeper dives of females at Los Islotes requires the use of a greater amount of oxygen stores. If pups are foraging on a similar prey resource, this presents a challenge as pups are not only inexperienced but also still developing physiologically.

This study examined if pups at Los Islotes have the physiological capabilities to forage on the same prey resources as adult females. Specifically, we measured the total body oxygen stores of California sea lion pups to examine their physiological development at or near the age of weaning. In addition, we compared these finding to data available on the oxygen stores of adult females to examine how pups differ at this important life stage.

Methods

Field sampling

Research was conducted from April 8 through April 27, 2003, at Los Islotes, Baja California Sur, Mexico (24º35'N, 110º23'W), a 250 m^2 island breeding colony in the Bay of La Paz. Pups were estimated to be 9 to 10 months of age, and at or near weaning (based on peak pupping data from 2002, Aurioles-Gamboa unpubl.). A total of nine pups were captured on the rocks with modified hoop nets (Furhman Diversified, Texas, USA). Animals were weighed using a 250 kg capacity digital scale (± 0.2 kg, Dyna-Link, Measurement Systems International, Washington, USA), given an intramuscular dose of Midazolam HCl (0.2 mg per kg, Hoffman-La Roche, New Jersey, USA), and then manually restrained for the remaining procedures. Under Midazolam, the sedation levels of the pups ranged from unresponsive to no sign of sedation.

Standard measurements were taken including mass, and standard and curvilinear length. An initial blood sample was taken from the caudal gluteal vein into a syringe and transferred into a green (lithium heparin) vacutainer. Plasma volume (PV) was determined by injecting approximately 0.6 mg per kg of Evan's blue dye (EB) into the caudal gluteal (El-Sayed et al. 1995). Syringes of EB were weighed prior to injection and flushed post injection to ensure all material contained in the syringe was injected. EB injections were considered successful if three complete flushes of the syringe were obtained. Three samples were taken at approximately 10 minute intervals up to 40 minutes post injection. All blood samples were collected by syringe and transferred to lithium heparin vacutainers. Blood samples were stored on ice until processed, within 10 hours.

Muscle myoglobin content was determined in muscle biopsies taken from the main locomotor muscle, the supraspinatous and tricep complex. A 4 ml dose of Lidocaine was injected into the sample area approximately 5 minutes prior to biopsy. Using a histocut biopsy needle (14 GA × 16 cm) muscle samples were collected, frozen in the field, and stored at –80ºC until analyzed.

Animals were held until there were no remaining signs of sedation and then released into the water. Each animal received a unique alphanumeric symbol that was clipped into the dorsal pelage. All animals except one were resighted on the rookery within one to seven days.

Lab analysis

Using duplicate samples, hematocrit (HCT) was determined from the initial blood samples using microcentrifugation. All blood was then centrifuged at 3,000 rpm for 15 minutes and the plasma was frozen until further analysis. Hemoglobin (Hb) was determined using the cyanomethemoglobin photometric method (Sigma kit 525, St. Louis, Missouri, USA).

Mean corpuscular hemoglobin content (MCHC) was calculated using the equation: MCHC = (Hb/HCT) × 100.

Plasma volume (PV) was determined following the techniques of El-Sayed et al. (1995) and Foldager and Blomqvist (1991). All plasma samples were thawed and 1 ml was centrifuged for 5 minutes before analysis. Blood volume (BV) was calculated using the equation: BV = PV/[(100 – HCT)/100]. Total blood oxygen stores were calculated assuming arterial stores of 33%, venous stores of 67%, and an oxygen combining capacity of 1.34 ml O_2 per g Hb (Kooyman 1989, Davis and Kanatous 1999).

Following the methods of Reynafarje (1963), myoglobin content was determined for all muscle samples. Muscle oxygen stores were calculated using the equations from Lenfant et al. (1970), assuming a muscle mass of 37% of body mass (Ponganis et al. 1997). Lung oxygen stores were estimated using the equations from Gentry and Kooyman (1986), assuming an oxygen content of 15% and a diving lung volume of 50% (Kooyman et al. 1971). Total body oxygen was calculated as the sum of blood, muscle and lung oxygen stores. For data presented for seven adult females from Los Islotes (Weise and Costa unpubl.) samples were collected and analyzed following the methods described above.

Statistics

Means are presented ± SD, unless otherwise noted. The difference between two means was tested using a two-sample *t*-test (SYSTAT 10.0, SPPSS Inc. 2000). Differences between sexes were tested using a two-sample *t*-test and data were combined when no significant differences were found. To test for relationships a linear regression analysis was performed. Significance was determined at $P < 0.05$.

Results

Mass ranged from 26.4 to 42.4 kg with a mean of 33.0 ± 4.7 kg. Mean HCT, Hb, and MCHC were 52.4 ± 0.9%, 22.9 ± 2.8 g per 100 ml, and 45.2 ± 4.4 g per 100 ml, respectively (N = 9). There was no relationship between mass and HCT, Hb, or MCHC (Fig. 1). In addition, there was no difference between males (N = 3) and females (N = 6) for mass, HCT, Hb, or MCHC (Fig. 1).

Plasma volume was calculated for four animals (based on successful EB injections) and ranged from 1.5 to 1.7 L (mean 1.6 ± 0.1 L). Mean mass specific plasma volume was 47.2 ± 1.9 ml per kg, or 4.7% of mass. Mean blood volume was 3.3 ± 0.2 L and mean mass specific blood volume was 99.2 ± 6.7 ml per kg (range 95.7 – 109.3 ml per kg), or 9.9% of mass. This resulted in a calculated mean total blood oxygen of 0.53 ± 0.03 L. Mass specific blood oxygen and other mass specific parameters are summarized in Table 1.

Table 1. Summary of mass specific blood, muscle, and lung oxygen stores for California sea lion pups at Los Islotes, Mexico. Both blood oxygen stores and total body oxygen stores were only calculated for pups with successful plasma volume measurements.

	Blood O_2 (ml per kg)	Muscle O_2 (ml per kg)	Lung O_2 (ml per kg)	Total O_2 (ml per kg)
Mean (± SD)	16.0 (1.1)	10.8 (2.6)	8.5 (0.1)	34.5 (2.2)
Range	15.5-17.7	8.3-16.0	8.4-8.6	32.5-37.7
N	4	8	9	4

Between 4 and 20 mg of muscle per animal was collected for myoglobin analysis (N = 8). Myoglobin concentration ranged from 1.76 to 3.37 g per 100 g muscle (mean 2.3 ± 0.6 g per 100 g muscle) and mean total muscle oxygen was 0.35 ± 0.08 L. There was no relationship between myoglobin concentration and sample mass, pup mass, or pup sex. We estimated mean lung oxygen stores to be 0.28 ± 0.04 L (mass specific values presented in Table 1).

Total body oxygen was only calculated for animals with measured plasma volume (N = 4). Mean total body oxygen was 1.1 ± 0.1 L. Out of the three oxygen stores, blood accounts for the largest proportion available to a pup at 45%, followed by muscle at 31%, and the lungs at 24%.

Discussion

At weaning young animals are often forced to find food in an unfamiliar environment. For diving animals this means not only locating prey, but also having the physiological abilities to chase and capture prey while breath-holding. California sea lion pups are weaned between 10 to 12 months of age; however, studies have found foraging can begin as early as 7 months (Aurioles-Gamboa 1988, Heath 1989, Boness et al. 1991). This study found that at 9 to 10 months of age, when most pups are at or near the age of weaning, they do not have the physiological capacity of adult females. As oxygen stores in the blood, muscle, and lungs are the support for aerobic metabolism while diving, the amount of oxygen available is closely linked to the time an animal can spend underwater foraging (Costa 1993). Ultimately, the lower oxygen stores of pups relates to a decreased amount of time available to spend foraging at depth. In addition to the lack of physiological development, young animals are also faced with the challenges of foraging inexperience and a higher metabolic rate, or more rapid use of the available oxygen stores (Rea and Costa 1992, Ponganis et al. 1993, Thorson and Le Boeuf 1994). All of these

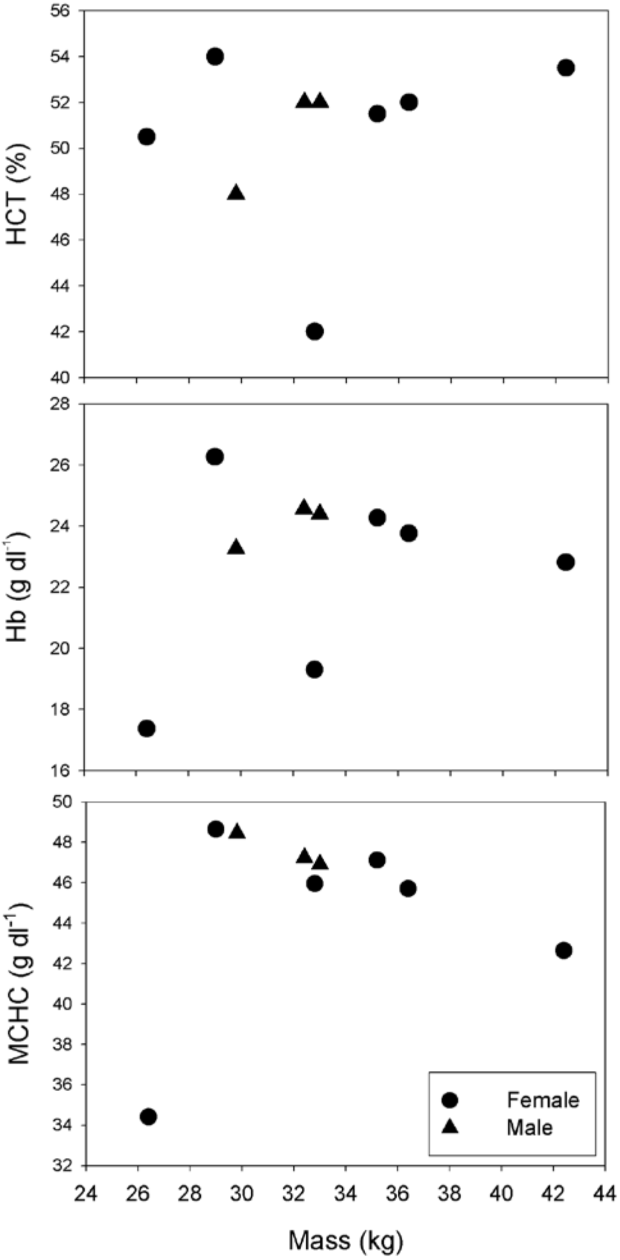


Figure 1. HCT, Hb, and MCHC for California sea lion pups at Los Islotes plotted against pup mass. Each point represents one individual. There is no relationship between mass and HCT, Hb, or MCHC. There were also no differences between sexes for the parameters measured.

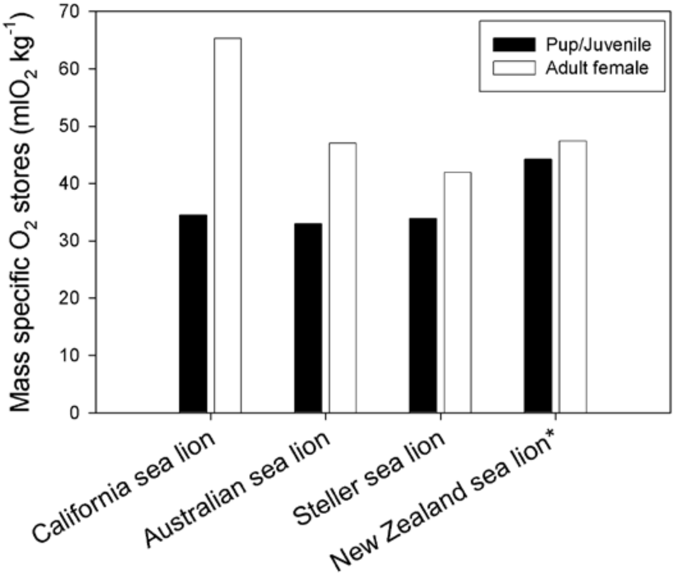


Figure 2. **Comparison of mass specific oxygen stores between adult females and young sea lions near the age of weaning. California sea lion pups at Los Islotes have only 53% of adult female oxygen stores (Weise and Costa unpubl.). Australian sea lion pups (15 months, Fowler and Costa unpubl.) have approximately 70% of adult oxygen stores only a few months prior to weaning (Costa et al. 2001). Data for Steller sea lions pups at 9 months and adult females from Richmond 2004. New Zealand sea lion values are for juveniles of unknown age (denoted by *, Costa et al. 1998). Note the similar value of mass specific oxygen stores for all 3 pups at or near weaning (California, Australian, and Steller sea lions). However, the greatest difference between adult and young oxygen stores is found in the California sea lions from Los Islotes.**

factors may play a role in the ability of young sea lions to complete this vital stage and reach maturity.

This study found that mass specific oxygen stores of California sea lion pups at or near the age of nutritional independence are comparable to those published for other young animals in the family Otariidae (sea lions and fur seals, Fig. 2). Richmond (2004) found for Steller sea lions of the same age mass specific total oxygen stores of 33.9 ml O_2 per kg. For California sea lions ranging in age from one to three years (N = 3), Ponganis et al. (1997) found average mass specific total body oxygen of 39.7 ± 3.0 ml O_2 per kg. In both of these studies the mass specific total oxygen stores were below those measured for adults, suggesting that the extended dependency period of the family Otariidae in comparison to the phocids is still not long enough for pups to complete physiological development.

Due to the importance of the blood as a large oxygen storage site, other studies on the diving capabilities of young pinnipeds have focused specifically on measuring blood oxygen stores. In comparison to mass specific blood oxygen stores for juveniles of the deepest diving otariid, the New Zealand sea lion, California sea lion pup oxygen stores are 22% lower (Costa et al. 1998). In contrast, when compared to pups of the much smaller Antarctic (*Arctocephalus gazella)* and subantarctic fur seal (*A. tropicalis*), the sea lion pups in this study have mass specific blood volumes that fall between those measured for the two species well before weaning (Arnould et al. 2003). When specifically looking at hematocrit and hemoglobin development, the variation between species in the family Otariidae is extensive. For the Galapagos fur seal, the species with the longest lactation period in the family Otariidae, pups do not reach adult hematocrit and hemoglobin levels until 1.5 years (Horning and Trillmich 1997). By 15 months Australian sea lion pups have developed hematocrit and hemoglobin values similar to adults (Fowler and Costa unpubl.). In contrast, Steller and California sea lion pups have developed adult hematocrit and hemoglobin by 5 and 9 months of age, respectively (Richmond 2004). As both of these species are weaned near one year of age compared to the longer lactation intervals of the Australian sea lion and Galapagos fur seal, this suggests development of hematocrit and hemoglobin may be related to pressures experienced near weaning when pups are expanding their exploitation of the marine environment. The range of developmental time for these parameters from 5 months to 1.5 years within this family indicates development may be closely linked with lactation duration but requires further examination once these blood parameters are measured in a greater number of young otariids.

Finally, although the mean value for pup myoglobin concentration was slightly lower, there was no significant difference between our values and those measured by Ponganis et al. (1997) for three juvenile California sea lions ($P = 0.56$). For Steller sea lions at 9 months of age myoglobin concentration in another major locomotor muscle, the pectoralis, was comparable to the values for California sea lion pups (Richmond 2004). All of these values are only slightly lower than concentrations measured for adult Steller sea lions and Northern fur seals (*Callorhinus ursinus*; Kanatous et al. 1999). However, mean pup myoglobin values were almost three times lower than those measured for seven adult female sea lions at Los Islotes (Weise and Costa unpubl.). This results in pups requiring a longer developmental period to reach the adult values measured for this population. Future research examining post weaning oxygen stores of pups at Los Islotes can help elucidate when this developmental stage is reached.

The drastic disparity in myoglobin values between pups and adults results in a difference in the proportional division of oxygen stores between the blood, muscle, and lungs. For California sea lion pups blood is the largest oxygen store available (45%) at or near weaning (Table1). This is in contrast to the division of oxygen stores in adult female sea lions at Los Islotes where myoglobin is the largest oxygen store at 47% (Weise and Costa unpubl.). Many studies have shown muscle myoglobin can be the slowest of all of the oxygen stores to develop (Thorson and Le Boeuf 1994, Noren et al. 2001, Burns et al. 2005). However, Noren et al. (2001) found for multiple species of marine mammals, the last stage of myoglobin development occurs at the start of independent foraging. For these sea lion pups, myoglobin values were drastically lower than adult females at the stage of independent foraging (Weise and Costa unpubl.). This limits the amount of absolute oxygen available for diving and will constrain both time under water and the habitat (by depth) available to pups for foraging.

The physiology measured in this study, although interesting when compared to other species, is most important when put into a behavioral context. At Los Islotes, studies have found that female California sea lions dive deeper and longer than previously reported for this species (Kuhn, Aurioles-Gamboa, and Costa unpubl.; Feldkamp et al. 1989). This results in females using a greater amount of oxygen stores to remain submerged for longer dive durations as they reach deep prey resources. A recent physiological study at Los Islotes measured the mass specific oxygen stores of seven adult females and found a mean of 65.3 ± 3.7 ml O_2 per kg (Weise and Costa unpubl.). In comparison to females from this population, pups have approximately 53% of the oxygen stores (Fig. 2). This value is lower than that measured for both Australian and Steller sea lion pups where oxygen stores are approximately 70% and 80%, respectively, near the age of weaning (Fig. 2; Australian sea lion females: Costa et al. 2001; Australian sea lion pups: Fowler and Costa unpubl.; Steller sea lions: Richmond 2004). As California sea lion pups fall within the range of percentage of adult oxygen stores measured for other pinniped species, this study provides added support to the hypothesis of both Richmond (2004) and Noren et al. (2005), that all pinniped species must develop a minimum level of adult oxygen stores in order to survive at the stage of nutritional independence.

Although pups require further development to reach adult physiology, the lower absolute energetic requirements conferred by smaller body size may allow pups to forage on alternate prey resources not sufficient for adult animals (Peters 1983, Millar and Hickling 1990, Costa 1993). In fact, research at another breeding colony of California sea lions found pups and juveniles from 8 to 21 months feed primarily on crustaceans.

Adults at this sample population, similar to Los Islotes, are instead feeding on schooling and deep-water fish (Aurioles-Gamboa et al. 1984, 2003; Aurioles-Gamboa 1988). Although pups are able to find a sufficient prey resources to survive, restricted diving, and hence foraging ability, may limit the available options for pups if prey resources change. This can result in pups being more vulnerable to environmental fluctuations (Trillmich and Ono 1991, Horning and Trillmich 1999). Research examining animals as they develop may help elucidate when these California sea lions finally achieve adult oxygen stores. In addition, data on the diving and foraging of pups and juveniles may provide insight into the alternative strategies used by pups to survive until physiological development is complete.

Acknowledgments

This work was supported by grants from UC Mexus Program SC-03-15 and the Office of Naval Research grant N00014-02-1-1012. We thank J. Alvarez, C. Ansta, M. Higuera, C. Mcknight, M. Rutishauser, S. Simmons, Y. Tremblay, and M. Zamarron for their assistance in the field. All research was approved by the University of California IACUC. Samples were collected under permit No. SGPA/DGVS.–0575 from Dirección General de Vida Silvestre (SEMERNAT) and supported by project 1230 by Consejo Nacional de Ciencia y Tecnología-SEMARNAT.

References

Antonelis, G.A, C.H. Fiscus, and R.L. Delong. 1984. Spring and summer prey of California sea lions, *Zalophus californianus*, at San Miguel Island, California, 1978-79. Fish. Bull. U.S. 82:67-76.

Arnould, J.P.Y., S.P. Luque, C. Guinet, D.P. Costa, J. Kingston, and S.A. Shaffer. 2003. The comparative energetics and growth strategies of sympatric antarctic and subantarctic fur seal pups at Iles Crozet. J. Exp. Biol. 206:4497-4506.

Aurioles-Gamboa, D. 1988. Behavioral ecology of California sea lions in the Gulf of California. Ph.D. thesis, University of California, Santa Cruz.

Aurioles-Gamboa, D., C. Fox, F. Sinsel, and G. Tanos. 1984. Prey of the California sea lion (*Zalophus californianus*) in the Bay of La Paz, Baja California Sur, Mexico. J. Mamm. 65(3):519-521.

Aurioles-Gamboa, D., F. Garcia-Rodriguez, M. Ramirez-Rodriguez, and C. Hernandez-Camcho. 2003. Interaction between the California sea lion and the artisanal fishery in the La Paz Bay, Gulf of California, Mexico. Ciencias Marinas 29(3):357-370.

Boness, D.J., O.T. Oftedal, and K.A. Ono. 1991. The effect of El Niño on pup development in the California sea lion (*Zalophus californianus*). I. Early postnatal growth. In: Pinnipeds and El Niño: Responses to environmental stress. Springer-Verlag.

Burns, J.M., and M.A. Castellini. 1996. Physiological and behavioral determinants of the aerobic dive limit in Weddell seal (*Leptonychotes weddellii*) pups. J. Comp. Physiol. B 166:473-483.

Burns, J.M., D.P. Costa, K. Frost, and J.T. Harvey. 2005. Development of oxygen stores in harbor seals: Effects of age, mass, and body composition. Phys. Biochem. Zool. 78:1057-1068.

Castellini, M.A., B.J. Murphy, M. Fedak, K. Ronald, N.J. Gofton, and P.W. Hochachka. 1985. Potentially conflicting demands of apnea and exercise in seals. J. Appl. Zool. 58:392-399.

Costa, D.P. 1991. Reproductive and foraging energetics of pinnipeds: Implications for life history patterns. In: D. Renouf (ed.), Behaviour of pinnipeds. Chapman and Hall, London.

Costa, D.P. 1993. The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. Symp. Zool. Soc. Lond. 66:293-314.

Costa, D.P., and B. Sinervo. 2004. Field physiology: Physiological insights from animals in nature. Ann. Rev. Phys. 66:209-238.

Costa, D.P., N.J. Gales, and D.E. Crocker. 1998. Blood volume and diving ability of the New Zealand sea lion, *Phocarctos hookeri*. Phys. Zool. 71(2):208-213.

Costa, D.P., N.J. Gales, and M.E. Goebel. 2001. Aerobic dive limit: How often does it occur in nature? Comp. Biochem. Phys. Part A 129A:771-783.

Costa, D.P., C.E. Kuhn, M.J. Weise, S.A. Shaffer, and J.P.Y. Arnould. 2004. When does physiology limit the foraging behaviour of freely diving mammals? Inter. Con. Ser. 1275:359-366.

Davis, R., and S. Kanatous. 1999. Convective oxygen transport and tissue oxygen consumption in Weddell seals during aerobic dives. J. Exp. Biol. 202:1091-1113.

Eberhardt, L.L., and D.B. Sinnif. 1977. Population dynamics and marine mammal management policies. J. Fish. Res. Board Can. 34:183-190.

El-Sayed, H., S.R. Goodall, and R. Hainsworth. 1995. Re-evaluation of Evans blue dye dilution method of plasma volume measurement. Clin. Lab. Haematol. 17:189-194.

Elsner, R., and G. Gooden. 1983. Diving and asphyxia. Cambridge University Press.

Feldkamp, S.D., R.L. Delong, and G.A. Antonelis. 1989. Diving patterns of California sea lions, *Zalophus californianus*. Can. J. Zool. 67:872-883.

Feldkamp, S.D., R.L. Delong, and G.A. Antonelis. 1991. Effects of El Niño 1983 on the foraging patterns of California sea lions (*Zalophus californianus*) near San Miguel Island, California. In: Pinnipeds and El Niño: Responses to environmental stress. Springer-Verlag.

Foldager, N., and C.G. Blomqvist. 1991. Repeated plasma volume determination with the Evans blue dye dilution technique: The method and the computer program. Comp. Biol. Med. 21:35-41.

Gentry, R.L., and G.L. Kooyman. 1986. Fur seals: Maternal strategies on land and at sea. Princeton University Press.

Heath, C.B. 1989. The behavioral ecology of the California sea lion, *Zalophus californianus*. Ph.D. thesis, University of California, Santa Cruz. 255 pp.

Horning, M., and F. Trillmich. 1997. Development of hemoglobin, hematocrit, and erythrocyte values in Galapagos fur seals. Mar. Mamm. Sci. 13(1):100-113.

Horning, M., and F. Trillmich 1999. Lunar cycles in diel prey migrations exert a stronger effect on the diving of juvenile than adult Galapagos fur seals. Proc. R. Soc. Lond. B. 266:1127-1132.

Jorgensen, C., C. Lydersen, O. Brix, and K.M. Kovacs. 2001. Diving development in nursing harbour seal pups. J. Exp. Biol. 204:3993-4004.

Kanatous, S.B., L.V. DiMichele, D.F. Cowan, and R.W. Davis. 1999. High aerobic capacities in the skeletal muscles of pinnipeds: Adaptations to diving hypoxia. J. Appl. Phys. 86:1247-1256.

Kooyman, G.L. 1985. Physiology without restraint in diving mammals. Mar. Mamm. Sci. 1:166-178.

Kooyman, G.L. 1989. Diverse divers: Physiology and behavior. Springer-Verlag, Berlin.

Kooyman, G.L., D.H. Kerem, W.B. Campbell, and J.J. Wright. 1971. Pulmonary function in freely diving Weddell seals (*Leptonychotes weddellii*). Resp. Physiol. 12:271-282.

Kooyman, G.L., E.A. Wahrenbrock, M.A. Castellini, R.W. Davis, and E.E. Sinnett. 1980. Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: Evidence of preferred pathways from blood chemistry and behavior. J. Comp. Physiol. 138:335-346.

Lenfant, C., K. Johansen, and J.D. Torrance. 1970. Gas transport and oxygen storage capacity in some pinnipeds and the sea otter. Respir. Physiol. 9:227-286.

Millar, J.S., and G.J. Hickling. 1990. Fasting endurance and the evolution of mammalian body size. Funct. Ecol. 4:5-12.

Noren, S.R., S.J. Iverson, and D.J. Boness. 2005. Development of the blood and muscle oxygen stores in gray seals (*Halichoerus grypus)*: Implications for juvenile diving capacity and the necessity of a terrestrial postweaning fast. Phys. Biochem. Zool. 78(4):482-490.

Noren, S.R., T.M. Williams, D.A. Pabst, W.A. McLellan, and J.L. Dearolf. 2001. The development of diving in marine endotherms: Preparing the skeletal muscles of dolphins, penguins, and seals for activity during submergence. J. Comp. Physiol. B 171:127-134.

Peters, R.H. 1983. The ecological implications of body size. Cambridge University Press.

Ponganis, P.J., G.L. Kooyman, and M.A. Castellini. 1993. Determinants of the aerobic dive limit of Weddell seals: Analysis of diving metabolic rates, postdive end tidal PO_2s and blood and muscle oxygen stores. Phys. Zool. 66:732-749.

Ponganis, P.J., G.L. Kooyman, L.M. Winter, and L.N. Starke. 1997. Heart rate and plasma lactate responses during submerged swimming and trained diving in California sea lions, *Zalophus californianus*. J. Comp. Physiol. B 167:9-16.

Rea, L.D., and D.P. Costa. 1992. Changes in standard metabolism during long-term fasting in northern elephant seal pups (*Mirounga angustirostris*). Phys. Zool. 65:97-111.

Reynafarje, B. 1963. Simplified method for the determination of myoglobin. J. Lab. Clin. Med. 61:138-145.

Richmond, J.P. 2004. Ontogeny of total body oxygen stores and aerobic dive potential in the Steller sea lion (*Eumetopias jubatus*). Master's thesis, University of Alaska Anchorage.

Thorson, P.H., and B.J. Le Boeuf. 1994. Developmental aspects of diving in northern elephant seal pups. In: B.J. Le Boeuf, and R.M. Laws, Elephant seals: Population ecology, behavior, and physiology. University of California Press, Berkeley.

Trillmich, F., and K. Ono. 1991. Pinnipeds and El Niño: Response to environmental stress. Springer-Verlag, Berlin.

Ydenberg, R.C., and C. Clark. 1989. Aerobiosis and anaerobiosis during diving by western grebes: An optimal foraging approach. J. Theor. Biol. 139:437-449.

Heavy Metal Distribution in Southern Sea Lions (*Otaria flavescens*) from Argentina

Marcela Gerpe and Diego Rodríguez
Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Universidad Nacional de Mar del Plata, Facultad de Ciencias Exactas y Naturales, Departamento de Ciencias Marinas, Mar del Plata, Argentina

Jorge Moreno
Universidad Nacional de Mar del Plata, Facultad de Ciencias Exactas y Naturales, Departamento de Ciencias Marinas, Mar del Plata, Argentina

Ricardo Bastida
Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Universidad Nacional de Mar del Plata, Facultad de Ciencias Exactas y Naturales, Departamento de Ciencias Marinas, Mar del Plata, Argentina

Julia Aizpún
Universidad Nacional de Mar del Plata, Facultad de Ciencias Exactas y Naturales, Departamento de Ciencias Marinas, Mar del Plata, Argentina

Abstract

Marine mammals accumulate heavy metals in their tissues and organs, and diet is the major intake of contaminants in these top predators. In the present study, heavy metal analyses were performed in muscle, liver, and kidney of three adults and one juvenile southern sea lion of both sexes (1.2-2.3 m) found dead on beaches of northern Argentina. We studied both essential (copper and zinc) and non-essential (total mercury and cadmium) heavy metals. Atomic absorption spectrophotometry was used for determination, using cold vapor for mercury and air/acetylene flame techniques for the rest. In both methods, previous acid digestion was made with nitric/sulfuric (Hg) and perchloric/nitric (Cd, Zn, Cu) mixtures. The method's quality was checked with a Certified Reference Material, and the detection limit was 0.05 µg per g. Mercury concentrations were highest in liver, whereas cadmium mainly concentrates in kidney. Juveniles and adults presented the same tissue distribution pattern for essential and non-essential heavy metals. Hepatic mercury concentrations ranged from 47.6 µg per g (adult male) to 23.3 µg per g (juvenile female), with renal cadmium concentrations between 5.7 µg per g and 0.8 µg per g, respectively. Although a limited number of sea lions were analyzed, there is a tendency to accumulate essential and non-essential metals with age in *O. flavescens*.

Introduction

Marine coastal environments are highly impacted by human activities, with some areas of high urban and industrial development turning into “hot spots” of pollution. Pollutants are both organics, such as polychlorinated biphenyls (PCBs) and polychlorinated pesticides, and inorganic, principally heavy metals. The latter ones are classified as essential and non-essential metals, based on presence or absence of a known physiological function; such is the case of zinc and copper, and mercury and cadmium, respectively. Furthermore, cadmium and mercury are very toxic and dangerous to the biota, even at low levels (Goyer and Clarkson 2001).

Marine sources of heavy metals are natural, such as volcanism and weathering, or anthropogenic, like mining and industrial/urban wastes; the human contribution is significantly higher than natural ones (Förstner and Wittmann 1983). Both environmental and metal characteristics determine their speciation or physical-chemical forms. Moreover, these metal species are directly related with their bioavailability, the fraction that is available to be assimilated by organisms.

Diet plays an important role as the main metal source, particularly in marine mammals, and prey preferences can influence the heavy metal contents of predators. Cephalopods and fish are natural accumulators of cadmium (Miramand and Bently 1992, Caurant and Amiard-Triquet 1995, Gerpe et al. 2000), and mercury (Zhang et al. 2001) respectively, resulting in cephalopod-consuming and piscivorous marine mammals being selectively exposed to these heavy metals. Marine mammals, as top predators of marine food webs, generally present high levels of heavy metals in their organs, even in muscle where the lowest levels are usually found (Law 1995, Gerpe et al. 2002). This characteristic, coupled with their longevity and diverse foraging ecology, places marine mammals as an interesting group to study heavy metals. Selected cetacean and pinniped species have been studied for several years, but heavy metal studies in the South American sea lion (*Otaria flavescens*) are scarce (Peña et al. 1988, Gerpe 1996).

The aim of the present paper was to study levels and distribution of cadmium (Cd), zinc (Zn), copper (Cu), and total mercury (Hg) in liver,

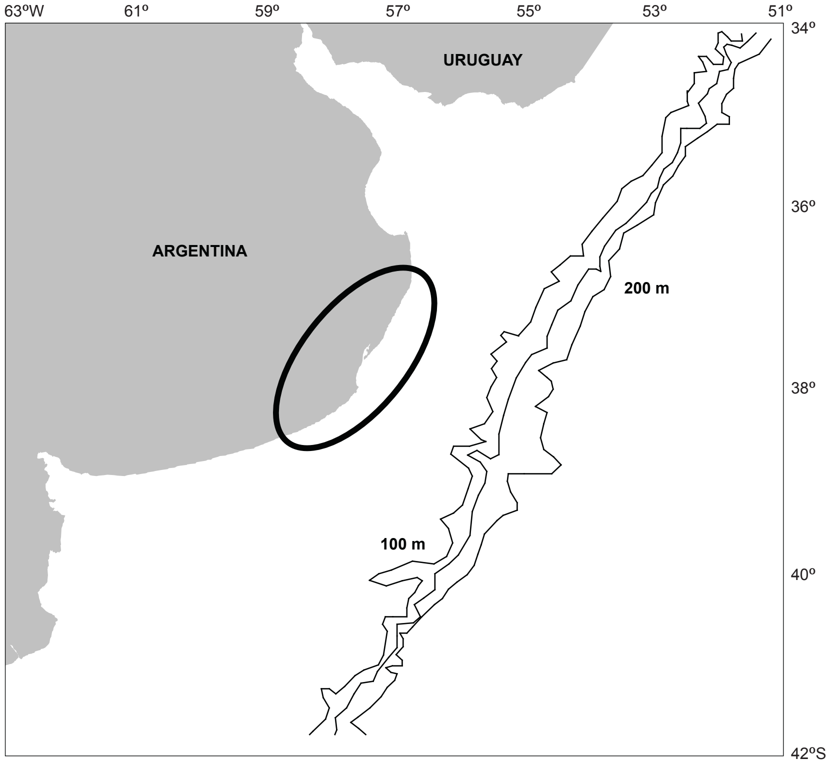


Figure 1. Sampling areas of *Otaria flavescens*, Buenos Aires province (36º14'S, 38º32'S), Argentina.

kidney, and muscle of juvenile and adult southern sea lions from Argentina.

Material and methods

Southern sea lions were obtained from beaches of Buenos Aires Province (36º14'S, 38º32'S), Argentina (Fig. 1). Total length and weight, sex, and age class were determined for each specimen (Table 1). Liver, muscle, and kidney samples were taken to analyze total mercury, zinc, copper, and cadmium in fresh tissue. Only very fresh carcasses were sampled to prevent further biases in analytical procedures due to post-mortem decomposition.

Cadmium, copper, and zinc concentrations were determined by atomic absorption spectrophotometry (AAS) with air-acetylene flame, us-

Table 1. Biological data of four southern sea lions.

Specimen no.	Total length (cm)	Total weight (kg)	Sex	Age class
1	146	67	Female	Adult
2	230	300	Male	Adult
3	137	ND	Female	Adult
4	121	ND	Female	Juvenile

ND = not determined.

ing a deuterium lamp for background correction. Samples were digested with perchloric and nitric acids (1:3) according to the method described by FAO/SIDA (1983). Total mercury was performed following the method of Moreno et al. (1984). Mineralization was made with sulfuric and nitric acids (4:1) in thermostatic bath (<60ºC); the oxidation was completed with potassium permanganate and hydrogen peroxide. Both determinations were made with a Shimadzu AA-640-13 spectrophotometer. Analytical grade reagents were used to prepare samples, blanks, and calibration curves. In order to assure quality control, a Certified Reference Material Number 6 (mussel) from the National Institute for Environmental Studies (NIES, Tsukuba, Japan), Japan Environmental Agency, was analyzed with the samples. The values obtained were in agreement with the certified concentrations ($P < 0.05$). The detection limit of the method was 0.05 µg per g wet weight. Metal concentrations were expressed in micrograms per gram (wet weight) and determinations were by duplicates.

Statistical differences were tested by parametric (*t*-test and one-way ANOVA) or nonparametric (Mann Whitney *U* test and Kruskall Wallis ANOVA) procedures, with an initial test of homoscedasticity (Levene test; $p < 0.05$). Post-hoc comparisons were performed by Scheffé test. Statistical analyses were performed using Statistica (1999) software.

Results

Heavy metal concentrations found in *Otaria flavescens* are presented in Table 2. No significant differences in concentrations were found between tissues for both zinc (ANOVA $F = 0.064$; df = 2, 9; $p = 0.939$) and copper (ANOVA $F = 0.669$; df = 2, 9; $p = 0.536$). In contrast, significant differences in concentrations between tissues were found in both cadmium (Kruskall Wallis ANOVA $H = 7.138$ [2; $n = 8$]; $p = 0.028$) and mercury (ANOVA $F = 42.093$; df = 2, 9; $p < 0.001$). Liver presented the highest levels of mercury (Scheffé test, $p < 0.001$), whereas cadmium was mainly concentrated in kidney. Although limited by the small sample size, the distributional

Table 2. Heavy metal concentrations in muscle, liver, and kidney of *Otaria flavescens*.

Tissue	Mercury	Cadmium	Zinc	Copper
Muscle	1.42 ± 0.53	0.12 ± 0.21	7.74 ± 5.74	0.83 ± 0.50
Liver	33.90 ± 10.09	0.63 ± 0.47	8.31 ± 9.05	1.26 ± 0.57
Kidney	0.75 ± 0.47	2.16 ± 2.39	6.45 ± 7.47	0.92 ± 0.57

μg per g wet weight, mean ± standard deviation.

Table 3. Range of heavy metal concentrations found in juvenile and adult southern sea lions.

	Mercury		Cadmium		Zinc		Copper	
Tissue	Juvenile	Adults	Juvenile	Adults	Juvenile	Adults	Juvenile	Adults
Muscle	0.85	0.99-2.09	ND	ND-0.43	3.54	4.24-16.03	0.37	0.79-1.54
Liver	23.26	32.31-47.59	0.27	0.30-1.27	4.12	1.89-21.69	1.00	0.79-2.09
Kidney	0.47	0.42-1.43	0.75	0.93-5.73	3.97	2.62-17.57	0.64	0.42-1.73

μg per g wet weight. ND = not detectable (<0.05 μg per g).

pattern for Hg (liver > muscle > kidney) and cadmium (kidney > liver > muscle) seem to be consistent in juveniles and adults, also with lower values in younger animals (Table 3).

Comparing non-essential metal concentrations within each organ, mean mercury concentrations were significantly higher than cadmium ones in muscle (Mann Whitney $U = 0.00$; $p = 0.02$) and liver (t-test, $t = 6.588$; df = 6; $p < 0.01$), whereas no significant differences were found in kidney (t-test, $t = -1.158$; df = 6; $p = 0.290$). Comparing essential metal concentrations within each organ, mean zinc concentrations were significantly higher than copper ones in liver (Mann Whitney $U = 1.00$; $p = 0.043$) and kidney (Mann Whitney $U = 1.00$; $p = 0.043$), whereas no significant differences were found in muscle (t-test, $t = 2.397$; df = 6; $p = 0.053$).

The resulting distributions of heavy metals in each organ of all specimens were: liver (Cd < Cu < Zn < Hg), kidney (Cu = Hg < Cd < Zn), and muscle (Cd < Cu < Hg < Zn).

Liver-muscle ([L]/[M]) rate was above 1 for all heavy metals, with the exception of zinc in a single animal (Table 4). Kidney-muscle [K]/[M] rate was above 1 for cadmium and below 1 for mercury, with fluctuating values for zinc and copper (Table 4). This pattern was consistent in both the juvenile and adults.

Table 4. Liver/muscle and kidney/muscle rates found in *Otaria flavescens.*

Rate	Mercury	Cadmium	Zinc	Copper
Liver/muscle	18.74-32.64	2.95-68.00	0.26-1.35	1.00-2.70
Kidney/muscle	0.39-0.68	13.33-122.00	0.23-1.12	0.53-1.73

Comparing non-essential heavy metal concentrations between the southern sea lions and their known prey (Rivero et al. 1999, Koen Alonso et al. 2000, Naya et al. 2000), we found that mercury concentrations were higher in sea lions than in fish and invertebrates, but for cadmium the situation was the opposite, because prey presented higher levels in key organs as hepatopancreas or liver (Table 5).

Discussion

Liver and kidney are the target organs for mercury and cadmium, respectively, with the major relationship being mercury-liver and cadmium-kidney. This trend was confirmed in other pinniped species from different areas (Law et al. 1991, 1992; Malcolm et al. 1994; Szefer et al. 1994; Sydeman and Jarman 1998; Woshner et al. 2001; Riget et al. 2005). This characteristic metal accumulation in these organs is in concordance to their physiology, as both play an important role in body depuration—even in the case of contaminants—and they contain high levels of metallothioneins, a group of proteins that bind metals (Roesijadi 1992, 1996; Das et al. 2002). These proteins present high affinity for divalent metals, such as those studied here, and the sulfydryl groups are responsible for that binding. Metallothioneins regulate the homeostasis of some essential metals, like copper and zinc, and they can be induced by non-essential metals, like cadmium and mercury (Roesijadi 1992). This natural function is also a detoxifying mechanism for toxic and dangerous metals (Roesijadi 1996). Unfortunately, metallothionein information on marine mammals is scarce, and absent for sea lions. Tohyama et al. (1986) reported a correlation between these proteins with age in *Phoca vitulina*, and Das et al. (2000, 2002) found high cadmium and mercury levels in liver and kidney related to metallothioneins in marine mammals, particularly for *Lagenorhynchus acutus*. So, the high levels of non-essential metals found in liver and kidney of *O. flavescens* could be associated with the presence of those proteins.

Metal accumulation in liver and kidney of marine mammals could be evaluated by [L]/[M] and [K]/[M] rates. These rates establish the relation between target organs and muscle levels, usually considered the background levels. They could be used as good indicators to measure the

Table 5. Cadmium and mercury concentrations in prey species of *Otaria flavescens*.

Prey species	Tissue	Mercury	Cadmium	Reference
Cynoscion guatucupa (striped weakfish)	Muscle	0.23-0.42	NA	Pérez et al. (1986)
	Muscle	0.14±0.08	NA	Marcovecchio et al. (1989)
	Liver	0.16±0.07	NA	
Micropogonias furnieri (whitemouth croaker)	Muscle	<0.05-0.25	NA	Pérez et al. (1986)
	Muscle	0.11±0.04	NA	Marcovecchio et al. (1989)
	Liver	0.13±0.04	NA	
Conger orbignyanus (Argentine conger)	Muscle	0.29±0.07	0.22±0.07	Marcovecchio et al. (1989)
	Liver	0.34±0.11	2.16±0.66	
Loligo brasiliensis (longfin inshore squid)	Hepatopancreas	0.06±0.02	NA	Marcovecchio et al. (1988)
Illex argentinus (shortfin Argentine squid)	Muscle	<0.05-0.41	NA	Pérez et al. (1986)
	Muscle	ND	0.03-0.18	Gerpe et al. (2000)
	Hepatopancreas	ND	142-363	
	Gonads	ND	0.06-0.25	
Pleoticus muelleri (red Argentine shrimp)	Muscle	NA	ND	Jeckel et al. (1996)
	Hepatopancreas	NA	3-11.8	
	Gonads	NA	0.08-1.1	

µg per g wet weight. ND = not detectable, NA = not analyzed.

accumulation of non-essential metals in liver and kidney. Some of the [K]/[M] rates found in *O. flavescens* for cadmium are mercury reflect the high capacity to accumulate metals from environment.

As in all marine mammals, the principal source of metals in southern sea lions is food, and particular prey can determinate the contribution of specific metals. Southern sea lions prey on fish, crustaceans, and cephalopods (Vaz Ferreira 1982, Rivero et al. 1999, Koen Alonso et al. 2000, Naya et al. 2000). The specimens analyzed here could belong to Patagonian or Buenos Aires province populations, and both groups may have different prey preferences. In Patagonia sea lions frequently prey on fish (frequency of occurrence, FO = 3.8-72.7%) and cephalopods (squid and octopuses FO = 3.8-54.5%; Koen Alonso et al. 2000), whereas in Buenos Aires province fish are more frequently preyed upon (FO = 100%) than cephalopods (octopus only; FO = 23%; Rivero et al. 1999). The higher level of mercury compared with cadmium found in the studied specimens strongly suggests that they belong to the Buenos Aires province stock. Sea lions have higher exposure to mercury than cadmium via food, because fish are good accumulators of that metal (Zhang et al. 2001, Jewett et al. 2003). Fish accumulate mercury as a methylated form, and this organic species presents higher bioavailability and toxicity than inorganic mercury for predators. Southern sea lions accumulate mercury from food at a high rate, surpassing concentrations reported in fish, revealing a biomagnification process. In contrast no biomagnification occurred with cadmium; the levels in southern sea lions were lower than those reported in their prey. Crustaceans and, mainly, cephalopods (Miramand and Bently 1992, Gerpe et al. 2000) are natural accumulators of cadmium which is transferred to top predators (Bustamante et al. 1998), but in the case of the studied southern sea lions these items could have been preyed at a low frequency.

Zinc and copper are essential biochemical components in marine mammals, and it is difficult to evaluate their accumulation processes and establish the level above the normal physiological concentrations. Based on [L]/[M] and [K]/[M] rates, we suggest that the concentrations found are around the background concentrations, because they are slightly fluctuating above and below 1. Essential metals are under metabolic homeostatic control, which usually maintains them at physiological levels. Metallothioneins are also involved in these mechanisms, allowing to take or to release zinc and copper based on their needs. Both zinc and copper act as cofactors of several enzymes; the higher metabolic requirements of zinc (Förstner and Wittmann 1983) could explain the higher concentrations of this metal.

Our results, although with a limited number of animals, showed a tendency to accumulate mercury and cadmium with age, suggesting that southern sea lions have physiological mechanisms allowing its concentration throughout life. Bioaccumulation of these toxic metals could affect the survival or behavior of southern sea lions but, unfortunately, related literature is null. Levels found here were below the maximum hepatic levels of tolerance informed by Wagemann and Muir (1984) for mercury (100-400 µg per g wet weight) and Law et al. (1996) for cadmium (20-200 µg per g wet weight). So, levels in *O. flavescens* likely do not represent a severe problem for its health, made more convincing by the presence of high levels (natural and/or induced) of metallothioneins, detoxifying both toxic metals.

Mercury and cadmium in *O. flavescens* were previously studied only by Peña et al. (1988). Although no body length or age class was given, we found a similar distributional pattern with highest mercury levels in liver and cadmium in kidney. Hepatic concentrations were slightly higher (47.0 µg per g wet weight) and renal cadmium levels were significantly higher (1.40-8.60 µg per g). Southern sea lions studied by Peña et al (1988) come from a male haul-out located inside the Mar del Plata harbor. The sea lions from this colony feed mainly on discarded fish and squid (Baldás et al. 1987, Rodríguez et al. 1992, Chaijale 1999), with a high frequency of squid in their diet. As mentioned above, squid may have contributed to higher cadmium levels found by Peña et al. (1988).

Finally, southern sea lions could be considered as a potential biomonitor of its environment. Top predator information could provide valuable information about bioavailability of metals (principally toxic ones), bioaccumulation processes, and biomagnification through marine food webs.

Acknowledgments

The authors thank Lic. Sergio Moron for his invaluable help during sampling.

References

Baldás, M.I., R. Bastida, and H.P. Castello. 1987. Características generales del apostadero de lobos marinos de un pelo, *Otaria flavescens*, del puerto de Mar del Plata (Argentina). Abstracts Reun. Trab. Espec. Mamíferos Acuat. América del Sur, pp. 111-112.

Bustamante, P., F. Caurant, S.W. Fowler, and P. Miramand. 1998. Cephalopods as a vector for the transfer to top marine predator in the North-East Atlantic ocean. Sci. Total Environ. 220:71-80.

Caurant, F.C., and C. Amiard-Triquet. 1995. Cadmium contamination in pilot whale *Globicephala melas*: Source and potential hazard to the species. Mar. Pollut. Bull. 3:207-210.

Chaijale, N. 1999. Feeding ecology of southern sea lions in Mar del Plata Harbour. Undergraduate thesis, Facultad de Ciencias Exactas, Fisicas y Naturales, Universidad Nacional de Cordoba. 99 pp. (In Spanish.)

Das, K., V. Jacob, and J.M. Bouquegneau. 2002. White-sided dolphin metallothioneins: Purification, characterization and potential role. Comp. Biochem. Physiol. 131C:245-251.

Das. K., V. Jacob, V. Debacker, G. Mellerioux, R. Biondo, N. Gerardin, and J.M. Bouquegneau. 2000. Characterization and potential role of metallothioneins in marine mammals. Comp. Biochem. Physiol. 126A:37-42.

FAO/SIDA. 1983. Manual de métodos de investigación del medio ambiente acuático. Parte 9. Análisis de presencia de metales y organoclorados en los peces. FAO Doc. Téc. Pesca 212. 35 pp.

Förstner, U., and G.T.W. Wittmann. 1983. Metal pollution in the aquatic environment. Springer-Verlag.

Gerpe, M.S. 1996. Distribución y dinámica de metales pesados en mamíferos marinos. Ph.D. thesis, Mar del Plata University, Argentina. 342 pp.

Gerpe, M.S., J.E.A. de Moreno, V.J. Moreno, and M.L. Patat. 2000. Cadmium, zinc and copper accumulation in the squid *Illex argentinus* from the southern Atlantic Ocean. Mar. Biol. 136(6):1039-1044.

Gerpe, M.S., D.H. Rodríguez, V.J. Moreno, R.O. Bastida, and J.E. Aizpún de Moreno. 2002. Accumulation of heavy metals in the Franciscana (*Pontoporia blainvillei*) from Buenos Aires Province, Argentina. Lat. American J. Aquat. Mamm. 1:95-106.

Goyer, R.A., and T.W. Clarkson. 2001. Toxic effects of metals. In: C.D. Klaassen (ed.), Casarett and Doull's toxicology: The basic science of poisons. 6th edn. McGraw-Hill, pp. 811-868.

Jeckel, W.H., R.R. Roth, and L. Ricci. 1996. Patterns of trace-metal distribution in tissues of *Pleoticus muelleri* (Crustacea: Decapoda: Solenoceridae). Mar. Biol. 125(2):297-306.

Jewett, S.C., X. Zhang, A.S. Naidu, J.J. Kelley, D. Dasher, and L.K. Duffy. 2003. Comparison of mercury and methylmercury in northern pike and Arctic grayling from Western Alaska rivers. Chemosphere 50(3):383-392.

Koen Alonso, M., E.A. Crespo, S.N. Pedraza, N.A. García, and M.A. Coscarella. 2000. Food habits of the South American sea lion, *Otaria flavescens*, off Patagonia, Argentina. Fish. Bull. U.S. 98:250-263.

Law, J.R. 1995. Metals in marine mammals. In: Environmental contaminants in wildlife. Chapter 15. British Crown, pp. 357-376.

Law, R.J., R.L. Stringer, R. Allchin, and B.R. Jones. 1996 Metals and organochlorines in sperm whales (*Physeter macrocephalus*) stranded around the North Sea during the 1994/1995 winter. Mar. Pollut. Bull. 32(1):72-77.

Law, R.J., B.R. Jones, J.R. Baker, S. Kennedy, R. Milne, and R.J. Morris. 1992. Trace metal in the livers of marine mammals from the Welsh coast and the Irish sea. Mar. Pollut. Bull. 24(6):296-304.

Law, R.J., C.E. Fileman, A.D. Hopkins, J.R. Baker, J. Harwood, D.B. Jackson, S. Kennedy, A.R. Martin, and R.J. Morris. 1991. Concentrations of trace metals in the livers of marine mammals (seals, porpoises and dolphins) from waters around the British Isles. Mar. Pollut. Bull. 22(4):183-191.

Malcolm, H.M., I.L. Boyd, D. Osborn, M.C. French, and P. Freestone. 1994. Trace metals in Antarctic fur seal (*Arctocephalus gazella*) livers from Bird Island, South Georgia. Mar. Pollut. Bull. 28(6):375-380.

Marcovecchio, J.E., V.J. Moreno, and A. Pérez. 1988. Determination of heavy metals concentrations in biota of Bahia Blanca. Sci. Total Environ. 75:181-190.

Marcovecchio, J.E., V.J. Moreno, and A. Pérez. 1989. Cadmium, zinc and total mercury distribution in organisms from Samborombon Bay (La Plata River estuary). In: J.P. Vernet (ed.), Heavy metals in the environment. Vol. 1, pp. 366-369.

Miramand, P., and D. Bently. 1992. Concentration and distribution of heavy metals in tissues of two cephalopods, *Eledone cirrhosa* and *Sepia officinalis*, from the French coast of the English Channel. Mar. Biol. 114-407-414.

Moreno, V.J., A. Pérez, R. Bastida, J.E.A. de Moreno, and A.M. Malaspina. 1984. Distribución de mercurio total en los tejidos de un delfín nariz de botella (*Tursiops gephyreus*, Lahille, 1908) de la Provincia de Buenos Aires (Argentina). Rev. Invest. Des. Pesq. 4:93-102.

Naya, D.E., R. Vargas, and M. Arim. 2000. Preliminary analysis of southern sea lion (*Otaria flavescens*) diet in Isla de Lobos, Uruguay. Boletin de la Sociedad Zoologica del Uruguay (2da Epoca) 12:14-21. (In Spanish.)

Peña, N.I., V.J. Moreno, J.E. Marcovecchio, and A. Pérez. 1988. Total mercury, cadmium and lead distribution in tissues of the southern sea lion (*Otaria flavescens*) in the ecosystem of Mar del Plata, Argentina. In: U. Seelinger, L.D. de Lacerda, and S.R. Patchineelam (eds.), Metals in coastal environments of Latin America. Springer-Verlag, pp. 140-146.

Pérez, A., V.J. Moreno, J.E.A. de Moreno, and A. Malaspina. 1986. Distribución del mercurio total en pescados y mariscos del Mar Argentino. Rev. Invest. Des. Pesq. 6:103-115.

Riget, F., D. Muir, M. Kwan, T. Savinova, M. Nyman, V. Woshner, and T. O'Hara. 2005. Circumpolar pattern of mercury and cadmium in ringed seals. Sci. Total Environ. 351-352:312-322.

Rivero, L., R. Bastida, D. Rodriguez, and G. Westergaard. 1999. Southern sea lion feeding habits in Puerto Quequen, Argentina. Resúmenes Expandidos del VIII Congreso Latinoamericano de Ciencias del Mar I:265-266. (In Spanish.)

Roesijadi, G. 1992. Metallothioneins in metal regulation and toxicity in aquatic animals. Aquat. Toxicol. 22:81-114.

Roesijadi, G. 1996. Metallothionein and its role in toxic metal regulation. Comp. Biochem. Physiol. 113C:117-123.

Sydeman, W.J., and W.M. Jarman. 1998. Trace metals in seabirds, Steller sea lions, and forage fish and zooplankton from Central California. Mar. Pollut. Bull. 36:828-832.

Szefer, P., M. Malinga, K. Skora, and J. Pempkowiak. 1994. Heavy metals in harbour porpoises from the Puck Bay in the Baltic Sea. Mar. Pollut. Bull. 28(9):570-571.

Tohyama, C., S-I. Himeno, C. Watanabe, T. Suzuki, and M. Morita. 1986. The relationship of the increased level of metallothionein with heavy metal levels in the tissues of the harbour seal (*Phoca vitulina*). Ecotoxicol. Environ. Safety 12:85-94.

Vaz Ferreira, R. 1982. *Otaria flavescens* (Shaw), South American sea lion. Mammals in the seas. Vol. 4. FAO Fish. Ser. 5, pp. 477-496.

Wagemann, R., and D.C.G. Muir. 1984. Concentrations of heavy metals and organochlorines in marine mammals of northern waters: Overview and evaluation. Can. Tech. Rep. Fish. Aquat. Sci. 1279:1-97.

Woshner, V.M., T. O'Hara, G.R. Bratton, and V.R. Beasley. 2001. Concentrations and interactions of selected essential and non-essential elements in ringed seals and polar bears of Arctic Alaska. J. Wildl. Dis. 37:711-721.

Zhang, X., A.S. Naidu, J.J. Kelley, S.C. Jewett, D. Dasher, and L.K. Duffy. 2001. Baseline concentrations of total mercury and methyl-mercury in salmon returning via Bering Sea (1999-2000). Mar. Pollut. Bull. 42:993-997.

Chromium Cytotoxicity in Steller Sea Lion Lung, Skin, and Testes Cells

John Pierce Wise Sr.
University of Southern Maine, Wise Laboratory of Environmental and Genetic Toxicology, Maine Center for Toxicology and Environmental Health, Portland, Maine; and Alaska SeaLife Center, Seward, Alaska

Caroline E.C. Goertz[1]
University of Southern Maine, Wise Laboratory of Environmental and Genetic Toxicology, Portland, Maine

Sandra S. Wise
University of Southern Maine, Wise Laboratory of Environmental and Genetic Toxicology, Maine Center for Toxicology and Environmental Health, Portland, Maine

Andrew T. Morin
University of Southern Maine, Wise Laboratory of Environmental and Genetic Toxicology, Portland, Maine

J. Lawrence Dunn
Mystic Aquarium, Mystic, Connecticut

Frances M.D. Gulland
The Marine Mammal Center, Sausalito, California

Mary Bozza and Shannon Atkinson
Alaska SeaLife Center, Seward, Alaska

W. Douglas Thompson
University of Southern Maine, Maine Center for Toxicology and Environmental Health, Department of Applied Medical Sciences, Portland, Maine

---

[1] Currently at the Alaska SeaLife Center, Seward, Alaska.

Abstract

The western population of Steller sea lions is endangered, and several hypotheses have been proposed to explain its decline. We are investigating the hypothesis that metals might be a factor in this decline. We found that chromium induced a concentration-dependent cytotoxicity in an organ-specific manner in Steller sea lion cells. Testicular cells were the most sensitive, and skin cells the most resistant. Lung cells were of intermediate sensitivity. Chromium uptake, measured by ICP-AES, increased with concentration in a cell-specific manner. When exposed to the same concentrations of sodium chromate, testicular cells accumulated greater intracellular concentrations of chromium ions than skin or lung cells did. This difference in chromium ion uptake may account for part of the differences in cytotoxicity among cell types. Tissue samples obtained opportunistically from pups were analyzed using inductively coupled plasma mass spectrometry (ICP-MS). Most pups had undetectable levels of chromium; however, in those where chromium was detected, its concentration was similar to that causing 50% cytotoxicity in culture. This finding suggests chromium may be a significant risk factor for Steller sea lions. These data were determined from a small number of samples from pre-weaned pups, and thus may not reflect adult exposure levels. However, given that chromium is known to accumulate and persist in human tissues, it is likely that adult exposures will prove to be much higher than pup levels. Further research is aimed at identifying chromium levels in adult tissues, determining genotoxic levels and investigating effects of other metals on Steller sea lion cells.

Introduction

Currently, the western population of Alaska Steller sea lions is in crisis, having declined 70% over the last 30 years, yet the reasons for this decline are uncertain (Trites and Larkin 1996). The fact that the decline may be limited to the western population and not the eastern Steller sea lion population in Alaska strongly suggests that an environmental factor such as environmental contamination is involved. Steller sea lions are exposed to a variety of contaminants, including metals, through their environment and diet, and indeed, preliminary studies indicate that Steller sea lions bioaccumulate aluminum, copper, mercury, vanadium, and silver (Sydeman and Jarman 1998; Saeki et al. 1999, 2001).

However, while these studies clearly show that Steller sea lions are exposed to metals, they don't identify either the consequences or extent of exposure. Data are limited either by the number of metals considered or the number of organs considered. For example, some studies looked at several metals, but only in one organ system (Sydeman and Jarman 1998, Saeki et al 2001). Another study examined many organs, but only three metals (Saeki et al. 1999) As a result, our understanding of metal toxicity and bioaccumulation in Steller sea lions is uncertain. It is very possible that some metals are at toxic levels in untested organs. For example, in bowhead whales (*Baelaena mysticetus*) cadmium levels in the liver appear to be relatively normal at 11 ppm, but reach levels in the kidney of 64 ppm, which are even higher (200-300 ppm) in the kidney cortex (Bratton et al. 1997).

In humans and rodents, metals have well-established toxic effects on many of the major systems of the body including the respiratory, neurologic, immunologic, reproductive, and endocrine systems (reviewed in Chang 1996, Amdur et al. 1996). The inference is that similar events will occur in sea lions at potentially toxic doses extrapolated from data in terrestrial species. Any extrapolations to much more divergent species such as Steller sea lions would be tentative at best (reviewed in Chang 1996, Amdur et al. 1996). Furthermore, it has been shown with marine mammals in particular that there are such significant differences in potency among species that a level that is highly toxic to one species may not be toxic to another. For example, the concentrations of cadmium in the kidney cortex of a bowhead would kill most land-dwelling animals, but the bowheads seem unaffected (Amdur et al. 1996, Bratton et al. 1997). To fully understand the effects on these animals, it is essential that we begin to determine the dose-related toxicological effects of these metals.

The main reason the toxic effects and doses of metals have not been determined in Steller sea lions is the lack of adequate and appropriate models. Specifically, these types of mechanistic investigations require exposing either the sea lions themselves or a cell line derived from them to metals and studying effects. However, exposing sea lions has legal, ethical, and logistical difficulties, and no Steller sea lion cell lines have been reported. A few cell lines express Steller sea lion immunoglobulins, but these are rodent cell hybrids and while useful for producing antibodies, they are not useful for mechanistic studies of toxicology or cellular physiology. Thus to study the toxicity of metals in Steller sea lions, cell lines are needed from multiple organs as metals have been shown to be toxic to some organs and not others (reviewed in Chang 1996, Amdur et al. 1996).

Accordingly, this report begins to address this need by establishing cell lines from Steller sea lions and investigating the toxicity of chromium, a common environmental contaminant. We consider the cytotoxic effects of chromium in cell lines that we developed from three major organs from Steller sea lions, to understand different responses to metal exposure in these organs.

Materials and methods

Chemicals and reagents

Sodium chromate, colcemid, and potassium chloride were purchased from Sigma/Aldrich. Giemsa stain was purchased from Biomedical Specialties Inc. (Santa Monica, California). Gurr's buffer, trypsin/EDTA, L-15, sodium pyruvate, penicillin/streptomycin, and L-glutamine were purchased from Invitrogen Corporation (Grand Island, New York). Crystal violet, methanol, and acetone were purchased from J.T. Baker (Phillipsburg, New Jersey). A 50:50 mixture of Dulbecco's minimal essential medium and Ham's F-12 (DMEM/F-12) was purchased from Mediatech Inc. (Herndon, Virginia). Cosmic calf serum (CCS) was purchased from Hyclone, (Logan, Utah). Tissue culture dishes, flasks, and plasticware were purchased from Corning Inc. (Acton, Massachusetts).

Cells and cell culture

Steller sea lion fibroblasts were isolated from tissue explants obtained during necropsy of free-ranging animals found dead, or euthanized stranded animals, and from skin biopsies of captive animals. Tissue explants and biopsies were placed in L-15 with pen/strep and gentamicin, then shipped with cold packs to the Wise Laboratory. Explants were rinsed several times in phosphate-buffered saline (PBS) with pen/strep and gentamicin. Tissues were sliced into small pieces with a scalpel, rinsed repeatedly, and placed into T-25 flasks with complete culture media consisting of DMEM/F-12 supplemented with 15% cosmic calf serum, 2 mM L-glutamine, 100 U per ml penicillin, 100 μg per ml streptomycin, and 0.1 mM sodium pyruvate, and placed in a 37ºC humidified incubator with 5% CO_2. When near confluence, cells were subcultured using 0.25% trypsin in 1 mM EDTA solution, resuspended in media containing 10% dimethyl sulfoxide in cryopreservation vials, and stored in liquid nitrogen until use. When thawed, cells were rinsed with complete media prior to being resuspended in fresh complete media and placed in flasks. Cells were maintained as adherent subconfluent monolayers by feeding at least twice weekly and subculturing at least once a week using 0.25% trypsin in 1 mM EDTA solution. All experiments were conducted on logarithmically growing cells.

Preparation of chemicals

Sodium chromate (CAS #7775-11-3, ACS reagent minimum 98% purity) was used as a model of soluble Cr(VI) and was administered as previously described (Wise et al. 2002).

Cytotoxicity assays

Cytotoxicity was determined by a clonogenic assay measuring the reduction in plating efficiency in treatment groups relative to controls as previously described (Wise et al. 2002). There were four dishes per treatment group and each experiment was repeated at least three times.

Cell preparation for determination of intracellular chromium ion levels

Cells were prepared for determination of intracellular Pb and Cr levels as previously described (Wise et al. 2002). Briefly, a monolayer of cells was treated for 24 hours with varying concentrations of sodium chromate. The cells were harvested and treated with a hypotonic solution followed by 2% SDS. This solution was sheered through a needle seven times and filtered through a 0.2 μm filter into a vial. Cr ion concentrations of the samples were then measured by inductively coupled plasma atomic emission spectrometry (ICP-AES) as described below.

Determination of intracellular chromium ion levels in cultured cells

Intracellular Cr levels were measured with a Perkin Elmer Optima 2000 ICP-AES, equipped with a gem cone low flow nebulizer (Wise et al. 2004b, Holmes et al. 2005). Cr was measured at an emission wavelength of 267.716 with a minimum detection limit of 2 ppb. Yttrium (Y) was used as an internal standard for both ions. Intracellular concentrations were converted from measured μg per L to μM by dividing by the atomic weight of the element, volume of the sample, the number of cells in the sample, and the average cell volume (measured at 1.125 pl by a Beckman Coulter Multisizer 3).

Determination of chromium ion levels in tissues from free-ranging animals

Tissues were obtained opportunistically from free-ranging animals found dead by field researchers investigating other aspects of Steller sea lion life history and physiology or were provided by Native subsistence hunters from animals obtained during legally authorized harvests. Between 5 and 15 grams of tissue were placed in plastic vials and stored at –70ºC until analysis. Location, gender, and estimated age were recorded for each animal. Thawed tissues were homogenized and diluted in nitric acid. Levels of Cr in tissues were determined by sector field ICP-MS. A VG Axiom MC instrument, equipped with a CETAC U5000AT ultrasonic nebulizer, was used in all studies. Solutions were introduced to the ultrasonic nebulizer using a peristaltic pump operating at 500-1,000 μL per min. Cr was determined using the ^{52}Cr isotope at a resolving power of 6000 (R = m per Δm); this cleanly separates the $^{52}Cr^+$ peak from $^{40}Ar^{12}C^+$ and $^{35}Cl^{16}O^1H^+$ peaks. ^{51}V was used as an internal standard for Cr determination.

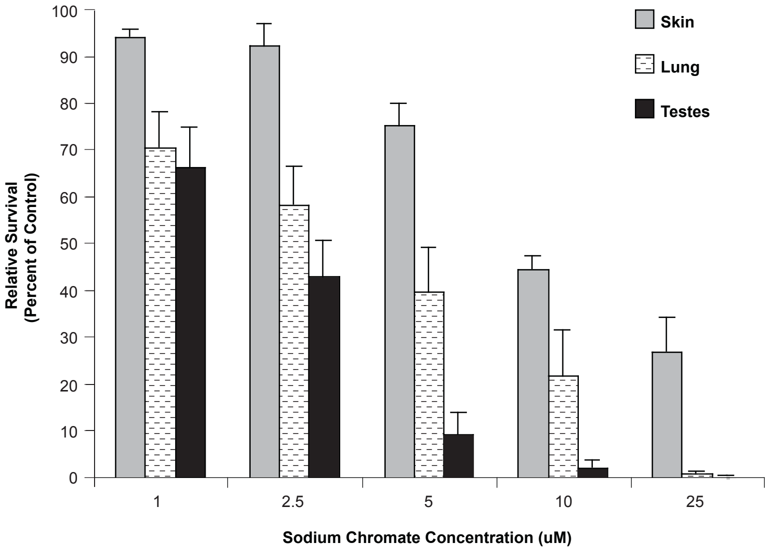


Figure 1. Cytotoxicity of chromium in Steller sea lion cells. Sodium chromate induces cytotoxicity in Steller sea lion cells in a concentration-dependent manner. Skin is most resistant to chromium. Testes cells are most sensitive to chromium treatment. In skin only concentrations greater than 5 μM were significantly more toxic than the control, $p < 0.004$. In lung and testes all concentrations were significantly more toxic than controls, $p < 0.03$. Error bars = standard error of the mean. Data are representative of a minimum of three replicates.

Statistical analysis

The Student's *t*-test was used to calculate *p*-values to determine the statistical significance of the difference in means. No adjustment was made for multiple comparisons. Interval estimates of differences are 95% confidence intervals, based also on Student's *t* distribution.

Results

Cytotoxicity of sodium chromate in Steller sea lion cells

Steller sea lion lung, skin, and testes cells exposed to sodium chromate for 24 h induced a concentration-dependent cytotoxicity (Fig. 1). The relative survival of skin cells was 94, 92, 75, 44, and 27% after exposure to 1, 2.5, 5, 10, and 25 μM of sodium chromate, respectively. All concentrations greater than 5 μM were statistically different from control, $p < 0.004$. The

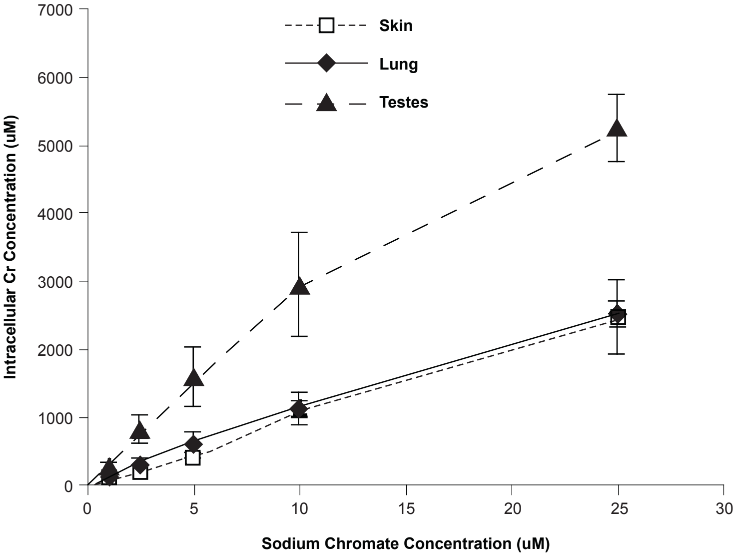


Figure 2. Uptake of chromium ions in Steller sea lion cells. Chromium ions are taken into Steller sea lion cells in a concentration-dependent manner. Cells from the testes take up the most chromium. Lung and skin have the lowest uptake. All concentration in all cell lines were significantly higher than controls, $p < 0.04$. Error bars = standard error of the mean. Data are representative of a minimum of three replicates.

relative survival of lung cells was 70, 58, 39, 21, and 0% after exposure to 1, 2.5, 5, 10, and 25 μM of sodium chromate, respectively. The relative survival of testes cells was 66, 43, 9, 2, and 0% after exposure to 1, 2.5, 5, 10, and 25 μM of sodium chromate, respectively. All concentrations in the lung and testes cells were significantly different from the control, $p < 0.03$.

Intracellular chromium ion levels in cultured cells

Sodium chromate induced concentration-dependent increases in intracellular Cr ion levels in Steller sea lion cells after a 24 h exposure (Fig. 2). Concentrations of 1, 2.5, 5, 10, and 25 μM produced intracellular Cr concentrations of 70, 196, 423, 1110, and 2457 μM in skin cells; 88, 316, 615, 1114, and 2507 μM in lung cells; and 264, 804, 1582, 2929, and 5241 μM in testes cells respectively. All concentrations in all cell lines were significantly higher than controls, $p < 0.04$.

Table 1. Tissue residues of chromium in Steller sea lion pups.

Tissue	Number of samples[a]	Tissue concentration (ppb wet weight)[b]	Tissue molarity (μM)[c]	Cell culture LC 50 (μM)
Skin	(3/4)	274 ± 336	5.27	10
Lung	(3/17)	216 ± 289	4.15	2.5
Testes	(2/12)	151 ± 96	2.89	2.5

[a] Number of samples with detectable Cr levels per total samples tested.
[b] ± standard deviation.
[c] Data reflect mean tissue concentration of Cr.

Intracellular chromium ion levels in tissues from free-ranging animals

Tissue levels of Cr were measured by ICP-MS (Table 1). The concentrations as measured were 274, 216, and 151 ppb in skin, lung, and testes respectively. Tissue molarity was calculated by dividing by the atomic mass of the metal and assuming a tissue density close to 1 mg per ml. Concentrations producing a 50% reduction in cell survival in culture are listed for comparison. The preliminary data indicate that levels of chromium in these tissues are on the order of concentrations shown to cause a 50% reduction in cell survival following a 24 hour exposure in cell culture. All measurements were done in Steller sea lion pups.

Discussion

This is the first report of the successful culture of Steller sea lion lung, skin, and testes cells. It is also the first determination of the cytotoxicity of hexavalent chromium in Steller sea lion cells. We find that chromium is cytotoxic to cell lines from all three organs tested in a concentration-dependent and tissue-specific manner. Skin cells were the most resistant suggesting a possible protective barrier from environmental chromium. Lung cells were of intermediate susceptibility and cells from testes were the most sensitive.

This study showed that lung and skin cells internalized the same amount of chromium, and that skin cells are much more resistant to the cytotoxic effects of chromium suggesting that skin cells respond differently to chromium than lung cells or that the deleterious effects of chromium are more easily repaired in skin cells than in other types of cells. These observations are consistent with the fact that chromate induces lung cancer, but not skin cancer, in humans (IARC 1990). Testes cells internalized much more chromium than the somatic tissues and these cells were the most sensitive to its toxicity. Thus it is likely that the increased sensitivity of the testes cells was a result of higher intracellular concentrations of chromium.

Comparing tissue loads to the uptake and cytotoxicity data indicates that Steller sea lion pups are exposed to potentially highly cytotoxic concentrations of chromium. The data indicate that chromium concentrations reached cytotoxic levels in the lung, skin, and testes of the pups. Chromium is a well-established lung and skin toxicant (ATSDR 2000). Increased cell death and turnover in these tissues is likely to lead to scarring and fibrosis, potentially resulting in lung disease and decreased performance of skin as an effective environmental barrier (Amdur et al. 1996). It would be premature to conclude that the sea lions are experiencing these effects; however, the results suggest that the potential for such events exists, and could contribute to adverse effects on the health of these animals.

Chromium is also a reproductive toxicant (ATSDR 2000). The cytotoxic effects of chromium on testicular cells can have important implications for the overall reproductive success of the animals. Damage to the testes can interfere with the ability to produce viable sperm and may alter reproductive behaviors thus reducing overall reproductive fitness. In rodent studies, chromium has been shown to accumulate in the testes indicating that it can readily cross the blood-testis barrier and that the testes are a target organ in rodent species (Witmer et al. 1989, 1991). Rodents exposed to chromium were found to have reduced testicular weights, degeneration of seminiferous tubules, decreased sperm counts, and alterations in reproductive behaviors (Chowdhury and Mitra 1995, Bataineh et al. 1997, Al-Hamood et al. 1998). Our observations that the sea lion testes are exposed to cytotoxic concentrations of chromium suggest that these potential outcomes are possible and indicate that more study of testicular morphology and function in sea lions is needed.

Our data are also consistent with results from studies of human lung and skin cells showing that chromium induced a concentration-dependent increase in cytotoxicity (Pritchard et al. 2001; Wise et al. 2002, 2003, 2004a,b; Holmes et al. 2005); however, they also suggest that sea lions may be more resistant to the cytotoxic effects of chromium. For example, in human skin fibroblasts 1, 2, 3, and 4 μM sodium chromate induced 30, 15, 2, and less than 1% relative survival respectively; by contrast we found greater than 40% survival in sea lion cells at 10 μM (Pritchard et al. 2001). Similarly, sea lion lung cells are also more resistant to chromium. Previously, it was shown that 2.5, 5, and 10 μM sodium chromate induced 39, 3, and 0% relative survival respectively in human lung cells. By contrast, 21% of the sea lion lung cells still survived at 10 μM. It is uncertain why sea lion cells might be more resistant and may reflect novel protective mechanisms that have evolved in the sea lion.

Considered together, our data suggest that chromium may pose a meaningful risk for the health of Steller sea lions. Full interpretation of the data is limited by the small number of tissue samples that were available from free ranging Steller sea lions to determine chromium levels, and more samples are needed to assess the true extent of such exposure. Additionally, interpretation of the chromium tissue levels is complicated by the age of the animals; all were pups and thus the exact exposure levels of adults are uncertain, but likely higher, as chromium levels are known to accumulate and persist and the testis is a major site of accumulation (Witmer et al. 1989, 1991; Ishikawa et al. 1994). In addition, these pups are from the eastern stock of animals and thus reflect exposure levels to that population. It is unknown if chromium levels in the western stock are similar. Future research is aimed at assessing the levels of chromium in western stock animals and in adults of both populations as well as assessing the levels and effects of other contaminants.

Acknowledgments

The authors acknowledge David St. Aubin for his efforts and enthusiasm in helping to start this project. Tissue collection was done by several individuals from the following organizations covered by the listed permits: Alaska Department of Fish and Game (NMFS Permit No. 158-364); Alaska SeaLife Center (NMFS Permit #881-1443-04); Mystic Aquarium (NMFS LOA 23 Dec 1980, USDA Research Permit #16-R-031); and The Marine Mammal Center (NMFS LOA #1514-10, California Department of Fish and Game, Live Marine Mammal Permit # 76-6). In particular, thanks go to Jen Burns, Tom Gelatt, Millie Gray, Kendal Mashburn, Jo-Ann Mellish, Natalie Noll, Lorrie Rea, Julie Richmond, Carol Stephens, Pam Tuomi, Jason Waite, Denise Greig, Amie Holmes, Nishad Jayasundara, and Jennifer Little. The authors would also like to thank Phillip Zavadil and the Tribal Government of St. Paul for the collection of Steller sea lion samples. Marine mammal cell line development and use by the Wise Laboratory for Environmental and Genetic Toxicology is performed under NMFS Permit 1008-1637-00. The analysis of tissues for metal content was performed by Robert Taylor at the Trace Element Research Laboratory, Texas A&M. Support for this research was provided by NOAA grant NA16FX1412.

References

Al-Hamood, M.H., A. Elbetieha, and H. Bataineh. 1998. Sexual maturation and fertility of male and female mice exposed prenatally and postnatally to trivalent and hexavalent chromium compounds. Reprod. Fert. Dev. 10:179-183.

Amdur, M.O., J. Doull, and C.D. Klaassen (eds.). 1996. Casarett and Doull's toxicology: The basic science of poisons. Pergamon Press, New York.

ATSDR. 2000. Toxicological profile for chromium. U.S. Department of Health and Human Services, Public Health Service, Agency for Toxic Substances and Disease Registry (ATSDR), Atlanta, Georgia.

Bataineh, H., M.H. Al-Hamood, A. Elbetieha, et al. 1997. Effect of long-term ingestion of chromium compounds on aggression, sex behavior and fertility in adult male rat. Drug Chem. Toxicol, 20(3):133-149.

Bratton, G.R., W. Flory, C.B. Spainhour, and E.M. Haubold. 1997. Assessment of selected heavy metals in liver, kidney, muscle, blubber and visceral fat of Eskimo harvested bowhead whales *Balaena mysticetus* from Alaska's north coast. Report to the Alaska North Slope Borough, Department of Wildlife Management.

Chang, L.W. (ed.). 1996. Toxicology of metals. CRC Press, Boca Raton, Florida.

Chowdhury, A.R, and C. Mitra. 1995. Spermatogenic and steroidogenic impairment after chromium treatment in rats. Indian J. Exp. Biol. 33:480-484.

Holmes, A.L., S.S. Wise, H. Xie, N. Gordon, W.D. Thompson, and J.P. Wise Sr. 2005. Lead ions do not cause human lung cells to escape chromate-induced cytotoxicity. Toxicol. Appl. Pharmacol. 203(2):167-176.

IARC. 1990. Chromium, nickel and welding. Monographs on the evaluations of carcinogenic risk to humans. International Agency for Research on Cancer (IARC), Lyon, France. 648 pp.

Ishikawa, Y., K. Nakagawa, Y. Satoh, T. Kitagawa, H. Sugano, T. Hirano, and E. Tsuchiya. 1994 "Hot spots" of chromium accumulation at bifurcations of chromate workers' bronchi. Cancer Res. 54:2342-2346.

Pritchard, D.E., S. Ceryak, L. Ha, J.L. Fornsaglio, S.K. Hartman, T.J. O'Brien, and S.R. Patierno. 2001. Mechanism of apoptosis and determination of cellular fate in chromium. VI. Exposed populations of telomerase-immortalized human fibroblasts. Cell Growth Differ. 12:487-496.

Saeki, K., M. Nakajima, T.R. Loughlin, D.C Calkins, N. Baba, M. Kiyota, and R. Tatsukawa. 2001. Accumulation of silver in the liver of three species of pinnipeds. Environ. Pollut. 112:19-25.

Saeki, K., M. Nakajima, K. Noda, T.R. Loughlin, N. Baba, M. Kiyota, R. Tatsukawa, and D.G. Calkins. 1999. Vanadium accumulation in pinnipeds. Arch. Environ. Contam. Toxicol. 36:81-86.

Sydeman, W.J., and W.M. Jarman. 1998. Trace metals in seabirds, Steller sea lion and forage fish and zooplankton from central California. Mar. Pollut. Bull. 36:828-832.

Trites, A.W., and P.A. Larkin. 1996. Changes in abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: How many were there? Aquat. Mammal. 22:153-166.

Wise Sr., J.P., S.S. Wise, and J.E. Little. 2002. The cytotoxicity and genotoxicity of particulate and soluble hexavalent chromium in human lung cells. Mutat. Res. 517:221-229.

Wise, S.S., J.H.C. Schuler, S.P. Katsifis, and J.P. Wise Sr. 2003. Barium chromate is cytotoxic and genotoxic to human lung cells. Environ. Mol. Mutagen. 42:274-278.

Wise, S.S., L.W. Elmore, S.E. Holt, J.E. Little, B.H. Bryant, and J.P. Wise Sr. 2004a. Telomerase-mediated lifespan extension of human bronchial cells does not affect hexavalent chromium–induced cytotoxicity or genotoxicity. Mol. Cell. Biochem. 255:103-111.

Wise, S.S., A.L. Holmes, M.E. Ketterer, W.J. Hartsock, E. Fomchenko, S. Katsifis, W.D. Thompson, and J.P. Wise Sr. 2004b. Chromium is the proximate clastogenic species for lead chromate–induced clastogenicity in human bronchial cells. Mutat. Res. 560:79-89.

Witmer, C.M., R. Harris, and S.I. Shupack. 1991. Oral bioavailability of chromium from a specific site. Environ. Health Perspect. 92:105-110.

Witmer, C.M., H-S. Park, and S.I. Shupack. 1989. Mutagenicity and disposition of chromium. Sci. Total Environ. 86:131-148.

Predictability of Prey Available to Steller Sea Lions in Southeastern Alaska

Scott M. Gende
National Park Service, Coastal Program, Glacier Bay Field Station, Juneau, Alaska

Michael F. Sigler
NOAA Fisheries, Alaska Fisheries Science Center, Auke Bay Lab, Juneau, Alaska

Abstract

The ability to predict the distribution of prey in space and time can influence foraging efficiency for marine vertebrates: search efforts can be concentrated in a specific area at a specific time of year, reducing energy expended randomly searching for prey. We examined the predictability of pelagic fish distributions during 24 months of surveys in Lynn Canal, Southeast Alaska. The spatial distribution of available prey (measured as energy density) during a given month was examined to determine if it was an accurate indicator of prey distribution during the following month (monthly time scale) or during the same month the following year (annual time scale). We also examined how predictability varied among seasons and across several spatial scales. Pacific herring (*Clupea pallasii*) dominated the prey energy available to Steller sea lions (*Eumetopias jubatus*), often occurring at densities several orders of magnitude greater than walleye pollock (*Theragra chalcogramma*), particularly during the winter months. Prey distribution in one month was a good indicator of prey distribution the same month the following year, but mostly during the winter months. This was due to the formation of large schools of herring in consistent locations during both winters. The distribution of prey in one winter month was also a good indicator of the distribution of prey the following month. However, significant month-to-month correlations were less frequent than at annual time scales due to a southerly movement of herring aggregations as the winter progressed. High densities

and predictable distributions of high-energy prey, such as herring, at relatively small spatial scales may facilitate efficient foraging by Steller sea lions and play a central role in the nutritional health of the stable or increasing populations in this area.

Introduction

The ability to predict the distribution of prey is an important component of foraging behavior of predators (Webb and Marcotte 1984, Grand and Grant 1994), and this is particularly relevant for air-breathing vertebrates that forage at sea. Faced with physiological and energetic constraints in acquiring prey that may be ephemerally available in time and patchily distributed in a three-dimensional water space, predictable distributions of prey allow foraging marine mammals and birds to concentrate search efforts in specific areas at specific times of the year, facilitating efficient foraging (Irons 1998, Davoren et al. 2003). The value of predicting the distribution of prey is especially high for marine mammals, such as Steller sea lions (*Eumetopias jubatus*), which must acquire information about the distribution and abundance of prey by swimming through the water column visually searching for fish (Schusterman 1981).

Despite the general agreement that predictability is an important attribute of prey, and relevant to the fitness and foraging ecology of marine mammals (e.g., Sinclair and Zepplin 2002) and seabirds (e.g., Skov et al. 2000), very few studies have quantified prey predictability for marine predators, particularly across large time scales (months, years). Here we examine the spatial and temporal predictability of pelagic prey available to free-ranging Steller sea lions across two years in Lynn Canal, southeastern Alaska. For this study we sought to quantify (1) the predictability of prey from month to month or within months from one year to the next; and (2) changes in predictability among species or at varying spatial scales.

Materials and methods

Acoustic surveys were conducted in Favorite Channel, upper Lynn Canal, southeastern Alaska, between Tee Harbor (58º43'N, 134º77'W) and Vanderbilt Reef (58º58'N, 134º97'W) on a monthly basis between June 2001 and May 2003. This area was chosen because it is relatively sheltered, facilitating year-round surveys using small, cost-effective vessels, and because it encompasses a variety of habitats (depth range between 5 and 305 m; average depth = 60 m), typical of areas used by foraging sea lions in southeastern Alaska. It also includes a site (Benjamin Island) used as a seasonal haul-out, where up to 800 sea lions are present from October until April.

To estimate prey available to Steller sea lions, we used a portable 38 kHz Simrad echo-integration system with a 12° beam angle, towed beside the F/V *Williwaw* at 11 km per hr. We simultaneously collected location data using a Garmin global positioning system with a location accuracy of ≤10 meters. From June 2001 to May 2002, acoustic surveys followed a path that ran parallel to the mainland or offshore islands or perpendicular between the two. Thereafter, surveys followed a zigzag path across the same area. Differences in survey paths allowed us to encompass as much habitat as possible within the study area, although the blocking method during analysis (see below) allowed us to compare areas despite slight deviations in survey path. We chose to sample during the daylight hours (between 0900 and 1700) because it facilitated observations of foraging sea lions while collecting acoustic data.

Length, weight, and species classification data, necessary complements to acoustic data, were collected quarterly with mid-water trawls deployed from the 18 m F/V *Solstice* from September 2001 to March 2002 and the 31 m F/V *Viking Storm* from May 2002 to May 2003. Two mid-water trawls were used, a 164 Nordic rope trawl with 1.5 m^2 alloy doors, 7 m height and 17 m width with a 19 mm mesh codend liner and a mesh wing 25/21/64 trawl with 3.0 m^2 alloy doors, 11 m height and 29 m width with a 32 mm mesh codend liner. The larger mid-water trawl was used with the larger vessel to match its larger trawl-handling equipment.

An echo integrator summed the returning echoes from fish observed beneath the vessel. The acoustic data were classified by species, integrated for 0.183-km length intervals and 10 m depth intervals, and corrected for instrument calibration using the echo-integration software SonarData Echoview. The output of acoustic scattering (NASC: Nautical Area Scattering Coefficient) is proportional to fish density (MacLennan and Simmonds 1992). To convert NASC to fish density in numbers, estimates of acoustic reflectivity for single fish were needed by species. Target strength (TS) refers to the acoustic reflectivity of a single echo or fish and depends on length (L in cm), $TS = 20 \log_{10} L + b$ (MacLennan and Simmonds 1992). For pollock, $b = -66$ (Traynor 1996) and for herring, $b = -65.4$ (Ona 2003). In addition, NASC and TS values for herring were adjusted for depth compression of the air bladder (Ona 2003) and acoustic shadowing (Zhao and Ona 2003). Target strength is transformed to backscattering cross-section, $\sigma_{bs} = 4\pi 10^{TS/10}$. Fish density in numbers was computed by dividing NASC by σ_{bs}. Fish density in weight equals density in number multiplied by average weight and is expressed in units of kg km^{-2}.

Fish density in weight was then converted to nutritional energy using season-, size-, and species-specific energy conversions determined in a companion study (Vollenweider 2005). Whereas variability in mass-specific energy content of walleye pollock (hereafter “pollock”) and herring was approximately twofold (7.7 kJ g^{-1} vs. 4.3 kJ g^{-1} respectively), biomass density in an area could vary by several orders of magnitude.

Therefore, the variation in prey energy density was due mostly to variation in biomass present of a given species, rather than differences in mass-specific energy content. Monthly biomass and energy estimates were highly related (pollock: $r^2 = 0.97$; herring $r^2 = 0.99$), and thus we report results only in terms of nutritional energy. Nutritional energy is expressed in units of millions of kJ km^{-2} by species, 0.183 km transect, and 10 m depth interval.

We integrated each transect's data across 10 m depth intervals, such that each transect had an estimate of prey energy density (in millions of kJ km^{-2}). The transect data were then grouped into blocks, where each block encompassed a latitudinal minute (e.g., 58º25'N to 58º26'N, a distance of 1.83 km; see also Fauchald et al. 2000, Davoren et al. 2003). We then computed means (and standard errors) using the energy density estimates from transects as data points for each 1-minute block (each block contained at least six transects). As a result of this blocking procedure, the study area had a maximum of 16 latitudinal blocks (for each month surveyed), each with an average energy density.

Predictability

We define predictability as the degree to which prey energy density in an area predicts the energy density available in that same area at a different time period. We examined predictability using two different time periods (annual and monthly), and area was defined using four different spatial scales. For the annual time period, we asked the question of whether the distribution and relative quantity of prey in the study area in one month during the first year of surveys was an accurate indicator of the distribution and relative quantity of prey during the same month the following year. We used the coefficient of determination of linear regression to serve as a measure of predictability: the greater amount of variation explained, the more predictable the prey resources occur across the study area. For example, in November 2001 the prey density was calculated for each latitudinal block and was regressed against the density estimates in the same blocks in November 2002. Analyzing the data in this manner thus provides equal weight to areas where prey are consistently present and to areas where prey are consistently absent. In other words, we assume it is equally important for a sea lion to be able to predict where they should forage (consistent high density prey patches), as being able to predict where not to forage (where prey are consistently absent). A slope that is significantly different from zero indicates predictability. This analysis was repeated for all months.

For the monthly time period, we used the same regression techniques but asked whether the distribution and relative quantity of prey within the study period during one month was an accurate indicator of the distribution and quantity of prey the following month, repeated for all consecutive month combinations.

Finally, for each of these time periods, we examined how predictability varied with incremental increases in spatial scale. For example, the smallest spatial scale corresponded to the study area divided into 1-minute latitudinal blocks (1.83 km), the next spatial scale into 2-minute blocks (3.66 km), and the third spatial scale divided the study area into 3-minute blocks (5.49 km). At the 3-minute scale, the study area was divided into 5 blocks, which we considered to be the lowest number of data points that could be used to calculate meaningful regressions. Consequently at the smallest spatial scale, there were more blocks but fewer transects in each block, whereas at the larger scales the study area contained fewer blocks but more transects per block.

As many correlation coefficients were generated from the same data, we controlled the Type I error rate in our multiple comparisons by Bonferroni-correcting the p-values, i.e., the family-wise error rate was divided by the total number of tests each data set was used to generate.

Results

A total of 22 acoustic surveys were conducted between June 2001 and May 2003. No data were collected in June and July 2002 due to equipment failure.

At the study-wide spatial scale, prey energy available to foraging sea lions varied dramatically among months and among species (Fig. 1). For herring, energy density ranged between 1 (June 2001) and 5,998 (December 2001) million kJ km^{-2}. In both years, energy peaked in December and January due to the presence of multiple, large schools of herring. In contrast, the average energy densities of pollock were generally an order of magnitude less than herring, varying between 0.2 (February 2002) and 58 (September 2001) million kJ km^{-2}.

Consequently, herring constituted most of the energy available to sea lions in most months. Averaged across all months, herring represented 82% of the pelagic prey energy available to sea lions, compared to 17% for pollock. Pacific hake (*Merluccius productus*) contributed the remaining 1% in several months. However, the disparity in energy attributed to herring was even greater during the winter months. Between November and February, herring constituted an average of 99% of the available energy, compared to less than 1% for pollock.

Predictability of prey from one year to the next

Whether the distribution of prey in a given month was a good predictor of the distribution of prey the same month the following year varied among seasons for both herring and pollock (Table 1). For herring, 5 (of 10 possible) months were found to be good indicators of prey the same month the following year with 4 of 5 (80%) of these months during the winter, November-February. For example, averaged across all spatial scales, over

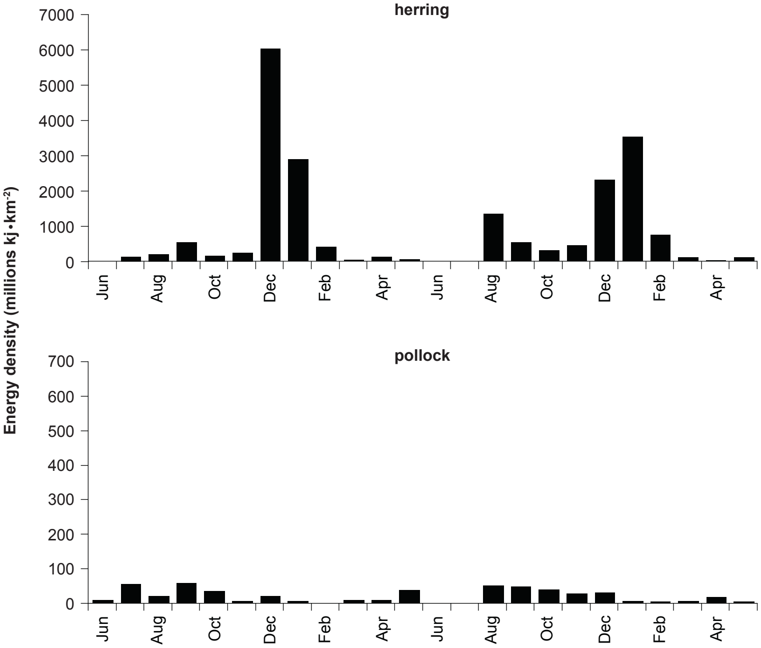


Figure 1. Energy densities of herring and pollock, June 2001-May 2003, Lynn Canal, southeastern Alaska. Note the difference in scale for herring vs. pollock.

93% of the variation in the distribution of herring in November 2002 was explained by the distribution of herring in November 2001 (Fig. 2). This pattern was consistent for most of the winter months: over 50% of the variation in the distribution of herring in January 2003 was explained by the distribution and abundance of herring in January 2002. In contrast, herring were not as predictable during the non-winter months (March-October), mostly because schools were quite small and ephemerally located, and the locations of these small schools were not consistent from year to year (Fig. 3). One exception was that a few small herring schools were consistently found near Tee Harbor during August.

Pollock were also predictable, mostly during the winter months (Table 1), albeit in much lower densities compared to herring. For example, November and January distributions of pollock were predictable regardless of spatial scale and comparable in predictability to herring. However, the densities of pollock in these months were often several orders of magnitude less than that for herring.

Table 1. Predictability (R^2 values of linear regressions of energy in one year regressed against energy in the same area the next year of herring and pollock). (----) indicates statistically insignificant linear regressions following Bonferroni corrections of Type I error rate.

	Herring			Pollock		
Spatial scale (size of blocks in km^2)	1.83	3.66	5.49	1.83	3.66	5.49
Aug 01-Aug 02	0.77	0.63	0.88	----	----	----
Sep 01-Sep 02	----	----	----	----	----	----
Oct 01-Oct 02	----	----	----	----	----	----
Nov 01-Nov 02	0.89	0.95	0.94	0.55	0.83	0.61
Dec 01-Dec 02	0.24	----	----	----	----	----
Jan 02-Jan 03	----	0.50	0.50	0.58	----	----
Feb 02-Feb 03	----	0.53	0.41	----	----	----
Mar 02-Mar 03	----	----	----	----	----	----
Apr 02-Apr 03	----	----	----	----	----	----
May 02-May 03	----	----	----	----	----	----

Predictability of prey in consecutive months

Similar to the annual time scales, the distribution of prey from one month to the next was predictable mostly during the winter months. The distribution and relative quantity of herring were predictable based on the previous month's distribution and quantity in a total of only 4 (of a possible 20) consecutive-month combinations, although 3 of 4 (75%) of these significant regressions included one of the winter months (Table 2). For example, the distribution of herring in October 2001 explained between 70% and 94% of the variation in the distribution of herring in November 2001, depending upon spatial scale. Likewise, up to 83% of the variation in herring distribution in February 2002 was explained by the distribution of herring in January 2002. However, significant results were found across multiple spatial scales for only 2 month-to-month combinations (Oct 01-Nov 01 and Jan 02-Feb 02).

Similar results were found for pollock (Table 2). The distribution and density of pollock in a month was predicted by the previous month's distribution for 5 different monthly combinations. Of these, 4 (80%) included winter months.

Predictability of herring from month to month appeared to be independent of the spatial scale of analysis (Table 2). In some cases, herring were more predictable at larger spatial scales (e.g., October-November

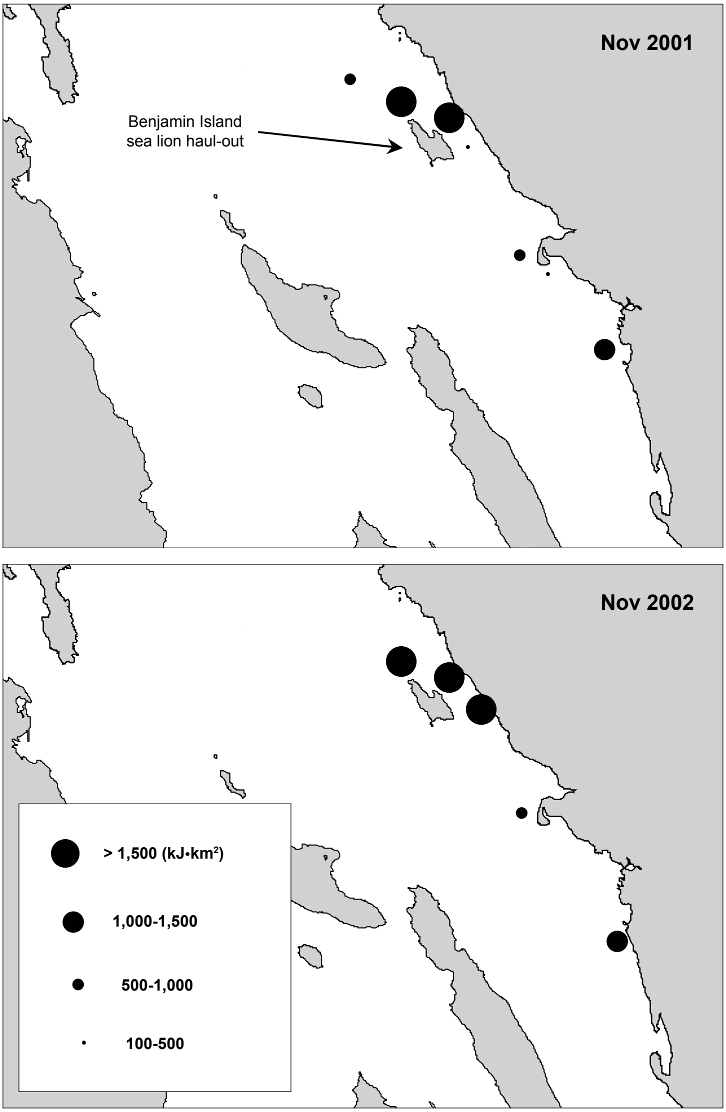


Figure 2. Distribution of prey energy in Lynn Canal, November 2001 and November 2002.

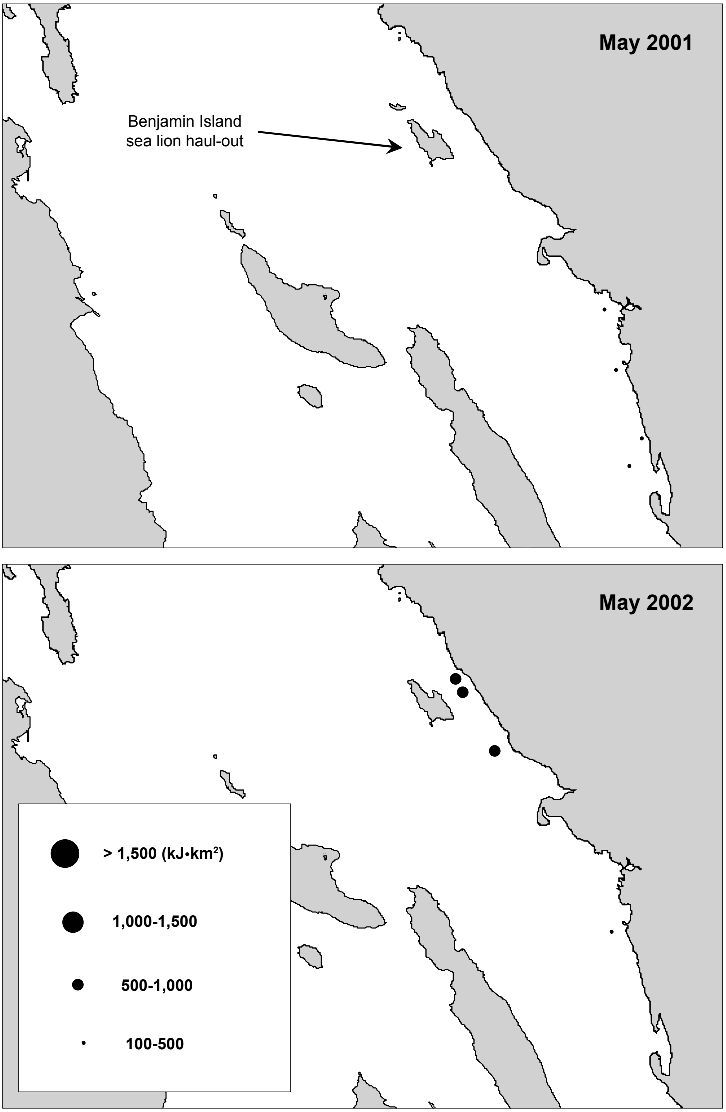


Figure 3. Distribution of prey energy in Lynn Canal, May 2001 and May 2002.

Table 2. Predictability (R^2 values of linear regressions of energy in one month regressed against energy in the same area the next month of herring and pollock). (----) indicates statistically insignificant linear regressions following Bonferroni corrections of Type I error rate.

		Herring			Pollock		
Spatial scale (size of latitudinal blocks in km^2)		1.83	3.66	5.49	1.83	3.66	5.49
	Jun 01-Jul 01	----	----	----	----	----	----
	Jul 01-Aug 01	----	0.77	----	----	----	----
	Aug 01-Sep 01	----	----	----	----	----	----
	Sep 01-Oct 01	----	----	----	----	----	----
Year 1	Oct 01-Nov 01	0.70	0.86	0.94	----	----	----
	Nov 01-Dec 01	----	----	-----	----	0.57	0.58
	Dec 01-Jan 02	----	----	----	0.51	0.59	0.67
	Jan 02-Feb 02	0.83	0.83	0.76	----	----	----
	Feb 02-Mar 02	----	----	----	----	----	----
	Mar 02-Apr 02	----	----	----	----	----	----
	Apr 02-May 02	----	----	----	----	----	----
	Aug 02-Sep 02	----	----	----	----	----	----
	Sep 02-Oct 02	----	----	----	----	----	----
	Oct 02-Nov 02	----	----	----	----	0.76	0.78
Year 2	Nov 02-Dec 02	----	----	0.72	----	0.61	0.66
	Dec 02-Jan 03	----	----	----	----	----	
	Jan 03-Feb 03	----	----	----	----	----	0.69
	Feb 03-Mar 03	----	----	----	----	----	----
	Mar 03-Apr 03	----	----	----	----	----	----
	Apr 03-May 03	----	----	----	----	----	----

2002) whereas in other cases predictability decreased with increasing spatial scale (January-February 2002). Results of the monthly predictability of pollock differed from herring in that a general trend of increasing predictability occurred with increasing spatial scale. For example, 51% of the variation in pollock distribution in January 2002 was explained by the distribution of pollock the previous month when data were analyzed at a scale of 1 latitudinal block, but predictability increased almost linearly to 67% at a scale of 3 latitudinal blocks.

Discussion

Large schools of herring, which were largely absent in other months, began to form in the study area beginning November and were still present until February during both survey years. Consequently, the total pelagic prey energy available to sea lions was considerably higher during the winter months, and was dominated by herring. Perhaps more importantly for foraging sea lions is that these schools formed in the same locations during the same months in subsequent years. Coupled with the consistent absence of medium or even small schools of herring in many other areas, the distribution of prey was highly predictable on an annual basis.

For example, in November of both years, large schools of herring were found in the same locations east and north of Benjamin Island, but were largely absent from the rest of the study area. As the winter progressed, the large schools were still present but had shifted from the northern part of the study area (between latitude 58º58'N and 58º55'N) to the more southern portion by February (between latitude 58º47'N and 58º48'N). These shifts occurred during both years of surveys. This explains why predictability of herring was actually better using the same month the previous year, as opposed to the previous month's distribution.

The only exception to the significant winter correlations was that a relationship was found in August. Small schools of herring were consistently found near Tee Harbor in August in both years. Herring appear to aggregate to feed near Tee Harbor in August, and salmon are often captured while feeding on herring in this area during this month.

Herring tend to follow the same migration paths and utilize the same overwintering areas elsewhere as well (e.g., Hay and McCarter 1997, Corten 2002). For example, in the summer, herring form small, dynamic feeding schools, which tend to move extensively to utilize relatively ephemeral aggregations of copepods (Kvamme et al. 2000). In the late fall copepod densities are reduced, and herring begin to aggregate into large schools and migrate to overwintering areas. Once in the overwintering areas, herring movements are minimized, as feeding is reduced and energy conservation is necessary.

Given that locations of herring concentrations can be highly predictable, sea lions clearly have the opportunity to respond to this predictability to maximize foraging efficiency. In fact, during our surveys aggregations of sea lions were consistently associated with large schools of herring in the study area (see also Hay and McCarter 1997, Gende and Sigler 2006). Although sea lions were able to locate these large schools during the winter months, their search efficiency remains unclear. Further studies that couple prey distributions and sea lion movements at time scales that more closely match foraging bout frequency (e.g., days or weeks) will help determine whether sea lions are actually responding to the predictability of prey, i.e., the absence of clues to the location of prey, or if they embark on random walks and simply select herring schools that are the largest.

Alternatively, sea lions have demonstrated the ability to remember long-term visual, audio, and spatial cues years after exposed to those stimuli (Schusterman 1981), and coupled with evidence that individuals can exhibit long-term fidelity to winter haul-out sites, suggests they can remember information on the distribution of fish during one year to direct foraging efforts in the following year. Photoperiod or water temperature may serve as proximate cues for sea lions to begin foraging in certain areas, although which cues are most optimal to follow will depend upon how closely they track prey resources (predictive power) and the costs of having followed a cue that falsely predicts food. Sea lions may also utilize the presence of other animals (including sea lions) as a cue of productive foraging areas.

It is important to consider that knowing of even the general location of herring schools can reduce significant search time and thus potentially increase foraging efficiency. Our results demonstrated that predictability can occur at both larger and smaller spatial scales, although it is unclear how this might influence search strategies of sea lions. Sea lions may utilize information of prey distributions at large spatial scales to travel to a certain areas, before invoking more random search strategies once in these areas.

Acknowledgments

We thank Peter Ord of the F/V *Williwaw* for boat support; and David Csepp, Yumi Arimitsu, and Jennifer Mondragon for technical support. Comments from Mary Willson improved the manuscript. Reference to trade names does not imply endorsement by the U.S. government.

References

Corten, A. 2002. The role of "conservatism" in herring migrations. Rev. Fish Biol. Fish. 11:339-361.

Davoren, G.K., W.A. Montevecchi, and J.T. Anderson. 2003. Search strategies of a pursuit-diving marine bird and the persistence of prey patches. Ecol. Monogr. 73:463-481.

Fauchald, P., K.E. Erikstad, and H. Skarsfjord. 2000. Scale-dependent predator-prey interactions: The hierarchical spatial distribution of seabirds and prey. Ecology 81:773-783.

Gende, S.M., and M.F. Sigler. 2006. Persistence of forage fish 'hot spots' and its association with foraging Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska. Deep-Sea Research II 53:1-14.

Grand, T.C., and J.W. Grant. 1994. Spatial predictability of food influences its monopolization and defense by juvenile convict cichlids. Anim. Behav. 47:91-100.

Hay, D.E., and P.B. McCarter. 1997. Continental shelf area and distribution, abundance, and habitat of herring in the North Pacific. In: Forage fishes in marine ecosystems. Alaska Sea Grant College Program , University of Alaska Fairbanks, pp. 559-572.

Irons, D.B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. Ecology 79:647-655.

Kvamme, C., L. Nottestad, A. Ferno, O.A. Misund, A. Dommasnes, and B.E. Axelsen. 2000. A sonar study of the migration pattern of Norwegian spring-spawning herring (*Clupea harengus* L.) in July. ICES CM2000, pp. 1-24.

MacLennan, D.N., and E. J. Simmonds. 1992. Fisheries acoustics. Chapman and Hall, New York. 325 pp.

Ona, E. 2003. An expanded target-strength relationship for herring. ICES J. Mar. Sci. 60: 493-499.

Schusterman, R.J. 1981. Behavioral capabilities of seals and sea lions: A review of their hearing, visual, learning and diving skills. Psych. Rec. 31:125-143.

Sinclair, E.H., and T.K. Zepplin. 2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). J. Mamm. 83:973-990.

Skov, H., J. Durinck, and P. Andell. 2000. Associations between wintering avian predators and schooling fish in the Skagerrak-Kattegat suggest reliance on predictable aggregations of herring *Clupea harengus*. J. Avian Biol. 31:135-143.

Traynor, J.J. 1996. Target-strength measurements for walleye pollock (*Theragra chalcogramma*) and Pacific whiting (*Merluccius productus*). ICES J. Mar. Sci. 53:253-258.

Vollenweider, J.J. 2005. Variability in Steller sea lion (*Eumetopias jubatus*) prey quality in southeastern Alaska. M.S. thesis, University of Alaska Fairbanks. 87 pp.

Webb, D.G., and B.M. Marcotte. 1984. Resource predictability and reproductive strategy in *Tisbe cucumariae* Humes (Copepoda: Harpacticoida). J. Exp. Mar. Biol. Ecol. 77:1-10.

Zhao, X., and E. Ona. 2003. Estimation and compensation models for the shadowing effect in dense fish aggregations. ICES J. Mar. Sci. 60:155-163.

The Diet of *Otaria flavescens* in Chile: What Do We Know?

L.A. Hückstädt
University of California Santa Cruz, Ocean Sciences Program, Long Marine Lab, Santa Cruz, California; and Universidad de Concepción, Departamento de Oceanografía, Concepción, Chile

T. Antezana
Universidad de Concepción, Departamento de Oceanografía, Concepción, Chile

Abstract

The southern sea lion *Otaria flavescens* has been described as a generalist and opportunistic predator; however, few studies have been conducted in Chilean waters focusing on diet. Here we review information on the diet of *O. flavescens* along the Chilean coast. Most of the information comes from studies conducted approximately 20 years ago in south-central Chile, with one exception in northern Chile. We found that *O. flavescens* exhibits important dissimilarities in its diet among locations, especially between north and south-central Chile. In general, prey diversity was regionally low; hence niche breadth analysis indicated it as a specialist (as opposed to graphic analysis, which describes it as a generalist predator when data from all locations were pooled together). We concluded that the species features plastic trophic habits with a diet determined by prey abundance at the locality and period of feeding. The results showed a slight niche overlap between small-scale fishing fleets and *O. flavescens*. Arica, where the referred overlap reaches 99%, proved the only exception with both sea lions and the fishery concentrating on anchovy (*Engraulis ringens*). Potential competition expressed as niche overlap with small-scale fisheries varied according to the regional catch level, and was less in those locations where the fishing effort was greatest.

Introduction

The southern sea lion (*Otaria flavescens*) inhabits both coasts of the South American subcontinent from ca. 5ºS along the Peruvian and Chilean coasts to Cape Horn on the Pacific, and along the Argentinean, Uruguayan, and Brazilian coasts (ca. 23ºS), including the Falkland Islands on the Atlantic (Aguayo and Maturana 1973, Vaz-Ferreira 1979, Jefferson et al. 1993).

The rangewide population is unknown, though some have estimated it at 300,000 individuals (Vaz-Ferreira 1979, Sielfeld et al. 1977, Werner and Campagna 1995). In Chile, the sea lion has been considered a relatively abundant species (Sielfeld 1983), with an estimated population reaching 100,000 individuals (Sielfeld et al. 1997, Aguayo-Lobo et al. 1998, Oporto et al. 1999).

The sea lion is considered an opportunistic predator, with a wide diet spectrum that includes invertebrates (cephalopods), fish, and even birds and calves of other species of pinnipeds (Aguayo and Maturana 1973, Vaz-Ferreira 1979, George-Nascimento et al. 1985, Jefferson et al. 1993, Harcourt 1993, Thompson et al. 1998), though diet varies by area. Like other pinnipeds, the sea lion has been considered a potential competitor for fisheries occurring in the same spatial range. If fisheries extend their exploitation range to include other sea lion prey, competition could be intensified (FAO 1978, Northridge 1985, Oporto et al. 1991, Wickens 1995).

Chile has experienced an accelerated and sustained development in commercial fishing during the last 30 years, reaching catches of up to 5 million tons per year (SERNAPESCA 2000). Thus, it is highly likely that interactions will continue to develop between fishing and the southern sea lion (e.g., Oporto et al. 1991, Oliva 1984, Sepúlveda 1998, Hückstädt and Antezana 2003).

Our objective was to evaluate the existing information on the diet composition of the sea lion along the Chilean coast, using both published and unpublished scientific sources. An evaluation of the existence and magnitude of competition between the southern sea lion and small-scale fisheries (those conducted by boats under 18 m long, according to Chilean legislation) is presented, and the effects of this interaction on both the sea lion and the small-scale fisheries are estimated.

Materials and methods

Compilation of information

We reviewed all available published and unpublished sources on the diet of southern sea lion in Chile. The existing information consisted of six diet studies based on stomach contents from collections or carcasses found on shore between 1972 and 1997 (Appendix 1), and included information from eight different locations between Arica (18º30'S) and Isla

Mocha (39º18'S) (Fig. 1). Since the available data are not presented with a common nomenclature, the information was re-interpreted and reorganized, following the criteria proposed by Hyslop (1980). We calculated frequency of occurrence (*%O*) (number of stomachs with a given prey item divided by total number of stomachs examined), dominance percentage (*%D*) (number of individuals of given prey item divided by total individuals of all prey items), and gravimetric percentage (*%G*) (sum weight of individuals of a given prey item divided by the total weight of all prey items). The data from the different sources (Appendix 1) were reorganized and split as follows: Oliva (1984) data were split into three locations; George-Nascimento et al. (1985) included four different sampling sites but was considered as only one location, named as Region VIII; both Habitat Consultores Ltda. (1981) and Oliva (1984) considered information from "Cabo Carranza," and although both sources present data on the same years, there are differences between them, so we distinguished them by using Cabo Carranza-1 and Cabo Carranza-2, respectively.

The fisheries information was also analyzed for the corresponding years in which diet analyses of sea lion were carried out (1972-1973, 1979-1981, and 1995-1997).

Regional variation

We used a cluster analysis (single linkage) and the index of binary similarity of Jaccard (*Sj*) (Krebs 1999) to examine the relationship between the different locations and sea lion diet:

$$S_j = \frac{a}{a+b+c}$$

where,

S_j = index of similarity of Jaccard

a = number of prey items in the sample (locality) A and sample (locality) B

b = number of prey items in the sample (locality) B but not in sample (locality) A

c = number of prey items in the sample (locality) A but not in sample (locality) B

Diet composition

Most of the data available for this study did not include *%G*, but did include the parameters *%O* and *%D*, which made it possible to perform a graphic analysis of the feeding strategy, according to Costello (1990, "Costello graphic analysis" [CGA]). CGA allows a description of the relative

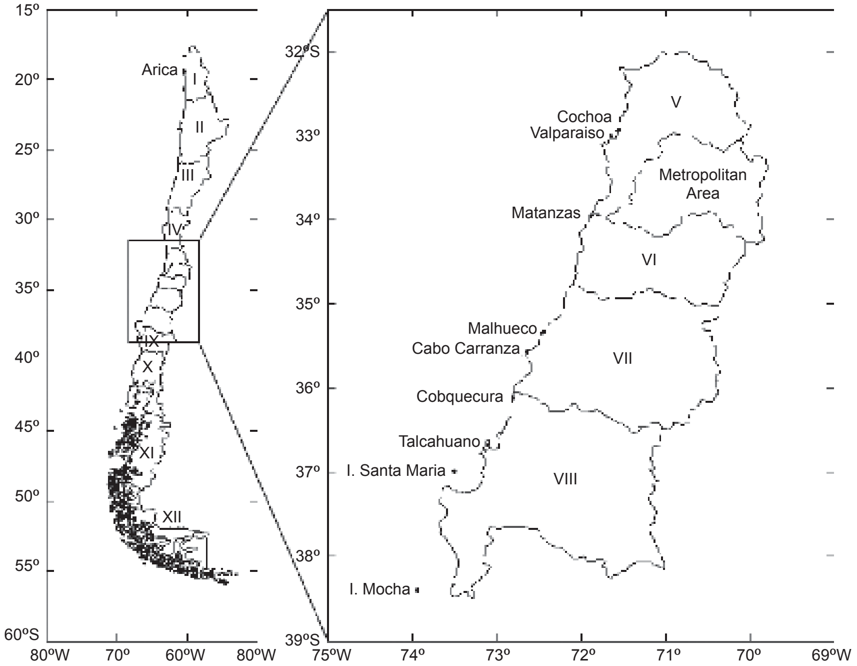


Figure 1. Location of haul-outs of *Otaria flavescens* included in this study along the Chilean coast. The map also shows political divisions of Chilean National Territory.

importance of a prey item (i.e., if the item is dominant or rare in the diet). This method determines the homogeneity of the predator's prey selection, based on the analysis of the graph of %*D* vs. %*O*, where each point represents the occurrence and dominance for a given prey, and where prey with high %*D* and %*O* are considered dominant in the diet; high %*O* and low %*D* can be interpreted as a generalized diet; and low %*O* and high %*D* indicate a specialized diet (Costello 1990). CGA was performed for general data and for each specific area.

Niche breadth

Niche breadth is understood to be the degree of specialization of a species (Krebs 1999). We used Levin's standardized index (B_A) (Labropoulou et al. 1999) to estimate niche breadth:

$$B_A = \frac{1}{n-1}\left(\frac{1}{\sum_j p_{ij}^{2}} - 1\right)$$

where,

B_A = Levin's standardized index for predator *i*

p_{ij} = proportion of diet of predator *i* that is made up of prey *j*

n = number of prey categories

B_A ranges from 0 to 1, with lower values indicating a specialized diet (few prey items dominating) and higher values indicating a generalized diet (Krebs 1999, Labropoulou et al. 1999). We used the Jackknife technique to calculate confidence intervals for B_A (Manly 1997, Krebs 1999).

Niche overlap

We used the Morisita-Horn index (Krebs 1999, C_H) to estimate the amount of overlap between the catches of the small-scale fisheries and the diet of sea lions. This method uses proportions rather than numeric data, and avoids using an abundance of environmental resources (prey items):

$$C_H = \frac{2\sum p_{ij} p_{ik}}{\sum p_{ij}^2 + \sum p_{ik}^2}$$

where,

C_H = Morisita-Horn index of overlap between species *j* and *k* (in this study, *j* corresponds to sea lion and *k* to small-scale fisheries)

p_{ij}, p_{ik} = proportions of predator *j* and *k* with prey *i* in their stomachs/catches ($i = 1, 2, 3, \ldots, n$)

n = Total number of resources (prey items)

C_H ranges fall between 0 and 1, where 0 indicates no overlap among predators and 1 indicates maximum overlap among predators. We used the Jackknife technique to calculate confidence intervals for C_H (Manly 1997, Krebs 1999).

Potential competition with small-scale fisheries

Since not all of the available sources included in this study discriminated among prey species, and the parameter %*G* was not always present when analyzing the diet of sea lion, total consumption was estimated without distinguishing among prey species. Analysis was carried out according to the political divisions of the Chilean territory, in accordance with the available fishing data (Fig. 1).

We used the most recent estimates of the sea lion population in calculations of consumption (Sielfeld et al. 1997, Aguayo-Lobo et al. 1998, Oporto et al. 1999). For the southernmost area of Chile, recent estimates of the population size of sea lion were not available when this study was conducted. We accounted for sex and body size differences by separating the population into three sex age classes (juveniles, adult females, and adult males) to estimate annual consumption. Calves were not included in this analysis because they rely exclusively on mother's milk until 5 months of age (Kastelein et al. 1995).

Annual consumption for the population of sea lion was estimated according to:

$$Cp = \sum dr_i \times n_i \times 330$$

where,

Cp = annual consumption for the population (kg per year)

dr = daily ration of class i (kg per day per ind)

n_i = number of individuals in class i (ind)

In this calculation, we assumed that adults feed during a period of ca. 330 days per year. Feeding activity decreases during the four week breeding period (austral summer) when the animals stay in colonies (Habitat Consultores Ltda. 1981, Oliva 1984).

Daily ration (*dr*) for both adult classes was obtained from Kastelein et al. (1995). For juveniles, *dr* was estimated using the relationship between corporal mass and *dr* (Innes et al. 1987). Mass for each age, was estimated from corporal length following criteria by Trites and Pauly (1998):

$$\ln M_i = a + b \ln X$$

where,

M_i = corporal mass for age i

a and b = linear regression coefficients (see Trites and Pauly 1998)

X = corporal length for age i

Daily ration (*dr*) stabilizes at 8 years for juvenile males and at 4 years for females (Kastelein et al. 1995), so average lengths were estimated for animals between 1 year and the age of stabilization of *dr* for each sex. Since no data were available for females in Chilean waters, Von-Bertalanffy's growth parameters were taken from Rosas et al. (1993) for Brazilian waters. For juvenile males, Von-Bertalanffy's growth parameters were taken from Sielfeld et al. (1997) for Chilean waters, which are highly consistent with those reported by Rosas et al. (1993).

Results

Five out of the six sources in this study corresponded to south-central Chile, and one corresponded to the northern area. However, information on the feeding behavior of southern sea lion from north-central Chile was not available. There was a linear relationship between the number of samples analyzed in each study and the number of prey items found per sample (analyzed stomachs), ($R^2 = 0.874$, $p < 0.05$).

Regional variation

Sea lions from Cochoa had the lowest diversity of prey (4), while animals from Cabo Carranza-2 included 13 prey items in their diet. Similarity analysis denoted marked differences in diet composition among the distinct locations (Fig. 2). The similarities ranged from approximately 15%-50% with the greatest similarities found between Cochoa and Malhueco and the least between Valparaiso and the rest of the sites (Fig. 2). When analyzing all information, the greatest overall dissimilarity between prey items was found, as expected, between Arica (north) and the cluster formed by the south-central locations.

Diet composition

The CGA for the general data (Fig. 3a) supported previous work that sea lions are generalist predators, with relatively few dominant prey items in their diet. However, when analyzing CGA by location (Fig. 3b-g), we found variations in feeding strategy (either generalists or specialists), and relative dominance of prey items. For instance, the CGA for Arica (Fig. 3b) indicated a specialization on anchovy (*Engraulis ringens*), and the CGAs for Malhueco (Fig. 3d), Cabo Carranza (Fig. 3e-f), and Region VIII (Fig. 3g) showed a moderate dominance of elephant fish (*Callorhynchus callorhynchus*), hake (*Merluccius gayi*), and whip-tale hake (*Macruronus magellanicus*), respectively.

Niche breadth and niche overlap

Although the overall CGA indicated a generalist diet, the niche breadth analysis suggested a specialized diet at each site in this study, with B_A values between 0.061 (Arica) and 0.413. Only Cochoa had a generalized diet with a B_A of 0.614, (Table 1). Niche overlap between sea lions and small-scale fisheries varied regionally (Table 2) with Arica having the highest degree of overlap ($C_H = 0.98$) and Region VIII the lowest ($C_H = 0.074$).

Potential competition with small-scale fisheries

Comparisons between landings and estimated consumption of fishes by sea lions are presented in Fig. 4. For Regions VI, IX, and XI, fish consumption by sea lions was estimated to be between 4.6 and 8.7 times that of small-scale fisheries. In Regions VII and X, fish consumption was only

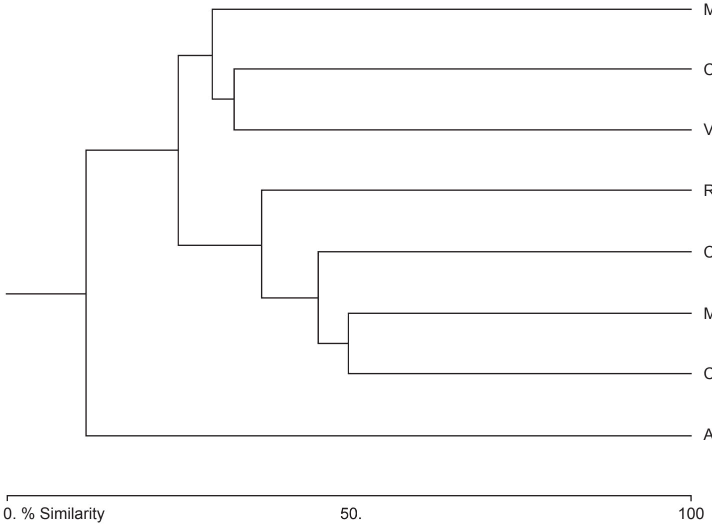


Figure 2. **Cluster analysis (single linkage) of the diet of *Otaria flavescens* among different locations in Chile. Similarity was computed using the index of binary similarity of Jaccard (*Sj*).**

slightly less than the catch by small-scale fisheries. The situation changed for the rest of the country, with small-scale fishing fleets reporting elevated harvested biomasses of fish, much greater than sea lion consumption, especially in Regions IV and VIII, with landings between 8 to 30 times the biomass consumed by sea lions, respectively.

Discussion

Pinnipeds are top predators capable of modifying the structure and dynamics of ecosystems (FAO 1978, Beverton 1985, Trites 1997). The southern sea lion has been described as a generalist predator with a wide diet spectrum determined by the ecosystem (Aguayo and Maturana 1973, Torres 1979, Vaz-Ferreira 1979, Jefferson et al. 1993), which is partially consistent with the results here shown.

In Chile, information on the diet of sea lions is limited and lacks uniformity, which is an impediment to the comparison of data from different years and/or locations. Sources used in this study included information on the parameters *%O* and *%D*, but authors grouped species into categories (e.g., fishes) instead of more detailed information (i.e., Aguayo and Maturana 1973, Aguayo-Lobo et al. 1998). Gravimetric information was not considered in most sources, which restricts the use of an index of

Table 1. Niche breadth of *Otaria flavescens* according to location. B_A corresponds to Levin's standardized index.

Location	B_A	Confidence limits	*d.f.*
Arica	0.061	−0.0236 ± 2.306(0.1014)	8
Cochoa	0.614	0.5766 ± 2.776(0.2213)	4
Malhueco	0.413	0.3681 ± 2.571(0.1951)	5
Cabo Carranza-1	0.162	−0.0917 ± 2.447(0.2807)	6
Cabo Carranza-2	0.181	0.1959 ± 2.160(0.0908)	13
Region VIII	0.197	0.0473 ± 2.201(0.1993)	11

relative importance (IRI), considered as an estimate of the importance of an item in the predator's diet, and thus impedes obtaining a more accurate analysis of the predator's diet (Hyslop 1980).

Sample size was limited due to its dependence on authorization to sacrifice a limited number of animals or the opportunistic finding of a carcass. Our work suggests that a greater number of samples is needed to reach more precise conclusions on the trophic ecology of the sea lion. The correlation between number of prey items in the stomachs and the number of samples (stomachs) reflects the bias associated with the small sample size in each study.

Along the Chilean coast, sea lions appeared to feed on a lower diversity of prey items compared with diet reports for the species from other locations and countries (e.g., Thompson et al. 1998, Paredes and Arias 1999).

Cubillos et al. (1998) proposed a subdivision of the Humboldt Current System (HCS) into three distinct subsystems: (a) North; (b) Central-North; and (c) Central-South. The rest of the country does not correspond to this system, but can be referred to as South. These subsystems imply differences in sea lion diet considering its dependence on the local prey resources (Aguayo and Maturana 1973). None of the locations showed similarity above 50%, and Arica (North), showed the greatest dissimilarity of all the locations. Locations that are geographically close (e.g., Cabo Carranza and Malhueco) had large dissimilarities between them, possibly associated with seasonal changes in available food among studies. In addition, the available data did not always consider factors such as weight contribution and quantity of prey items to sea lion diet, and varied in sample size. Each of these factors likely contributed to the results as reported.

Our results supported the notion that sea lions are a generalist species, but when we were analyzing for each location, CGA highlighted differences between trophic habits (e.g., specialist in Arica, with domi-

Table 2. Niche overlap between *Otaria flavescens* and the small-scale fishing fleet. C_H corresponds to the Morisita-Horn index of overlap.

Location	C_H	Confidence limits	*d.f.*
Arica	0.985	1.9260 ± 2.052(0.9456)	27
Cochoa	0.431	0.3767 ± 2.026(0.2399)	37
Malhueco	0.241	0.4164 ± 2.101(0.1766)	18
Cabo Carranza-1	0.182	1.0013 ± 2.101(0.1080)	18
Cabo Carranza-2	0.210	0.1772 ± 2.074(0.1363)	22
Region VIII	0.074	–0.1555 ± 2.019(0.2161)	41

nant prey items in Malhueco and Cabo Carranza-1, generalist in other locations). Since the niche breadth measurement employed does not consider food availability (Krebs 1999), the results could be misleading. Niche breadth analysis indicated that the southern sea lion is a specialist predator in most locations, with the exceptions of Cochoa and Malhueco, which could be associated with the environmental dominance of some resources instead of predator's preference.

Between 7 and 43% of prey overlapped with small-scale fisheries, except for Arica, where overlap reaches up to 99%. Sea lions had a highly specialized diet in this location and also the highest overlap with small-scale fisheries along the coast, which could be associated with the presumed dominance of *E. ringens.* On the other hand, the lowest overlap was found in Region VIII, where small-scale fisheries landings are 30 times the consumption of prey by sea lion, and hence competition was considered low. Sea lion consumption rises up to 8.8 times the landings of the small-scale fishing fleet in some regions (e.g., IX and XI), but effects have not been evaluated.

Pinnipeds play a major role in the ecosystem as moderators of the prey populations that comprise their diet (Trites 1997, Bax 1998). It is necessary to re-evaluate the actual trophic habits of the sea lion and to describe what the relationships are, if any, with coastal fisheries.

According to the results of this study, the highest overlap between fisheries and sea lions occurred at Arica (see Sielfeld et al. 1997). Since marine mammals show temporal variability in their trophic habits (Beverton 1985), changes in the diet composition are likely to occur in response to environmental conditions (including fishing activities), so it could be expected that a more important relationship may be developing between sea lions and the fishing sector at present, with both concentrating on those more abundant species and thus focusing the potential competition (see Northridge 1985, Wickens 1995).

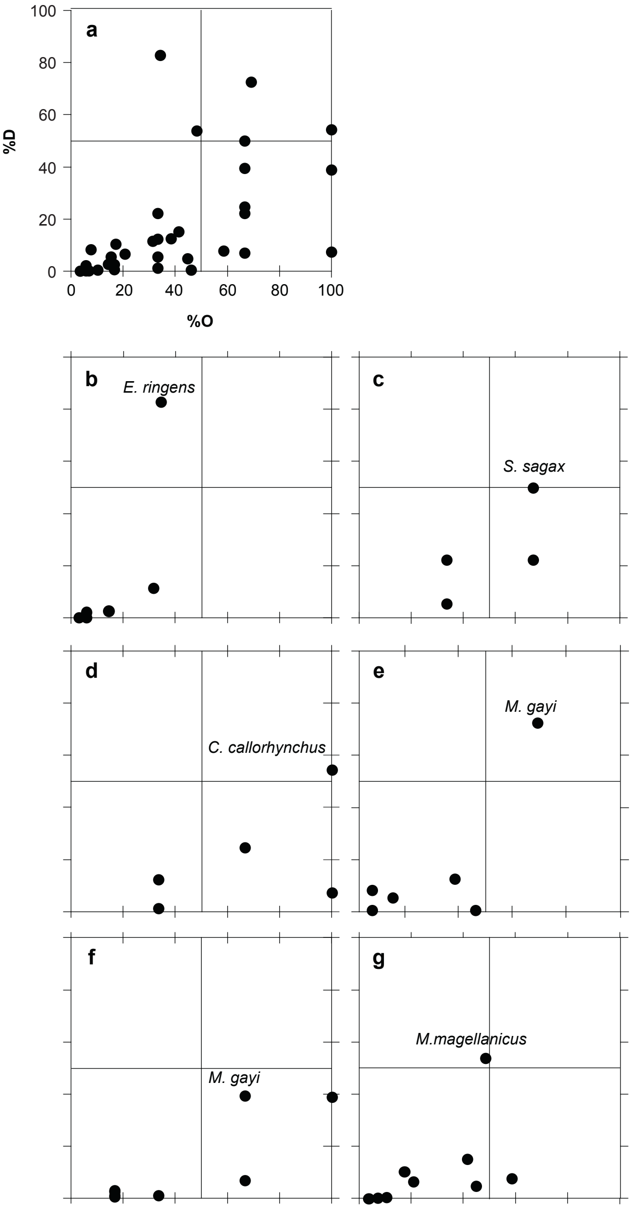


Figure 3. Costello's graphic analysis (CGA) of the feeding strategy of *Otaria flavescens*. (a) CGA for the entire data, (b) CGA for Arica, (c) CGA for Cochoa, (d) CGA for Malhueco, (e) CGA for Cabo Carranza-1, (f) CGA for Cabo Carranza-2, and, (g) CGA for Region VIII.

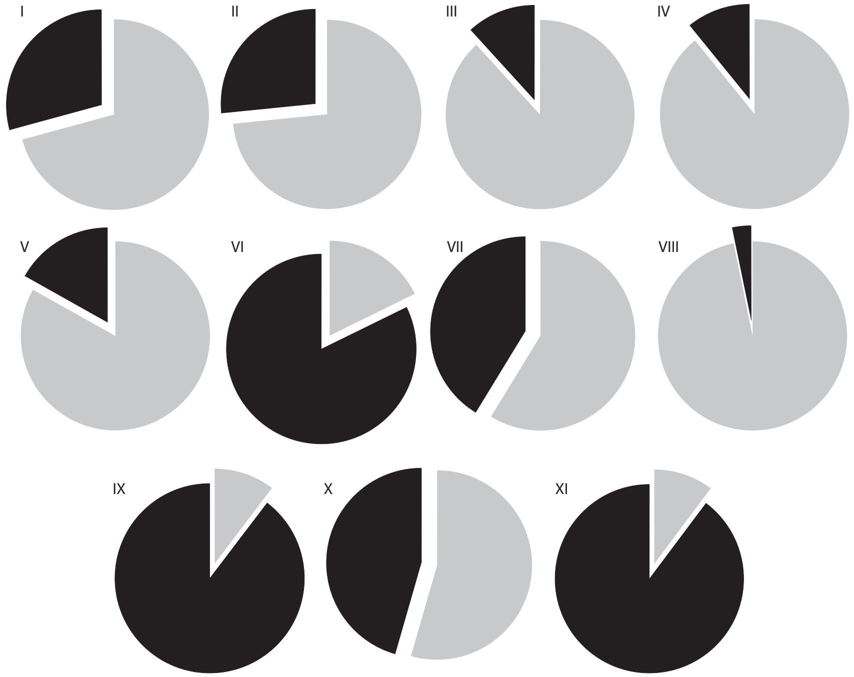


Figure 4. Comparisons of total consumption by *Otaria flavescens* population (black), and small-scale fishing fleet (gray) for Regions I to XI, Chile.

Acknowledgments

The authors would like to acknowledge L. Duarte, S. Purca, B. Yannicelli, R. Vögler, D. Oliva, and M. Sepúlveda for their collaboration and comments on this manuscript; as well as T. Gelatt and two anonymous referees, whose comments significantly contributed to improve the final manuscript. Likewise, J. Cornejo and A. Giraldo cooperated significantly during this study. M. Baker contributed enormously with revision and correction of the manuscript. LAH was supported by the Graduate School, University of Concepcion (Chile) during postgraduate studies, and by SIDA, through the Linnaeus-Palme International Exchange Programme between the Department of Oceanography, University of Gothenburg (Sweden), and the Departamento de Oceanografía, Universidad de Concepción (Chile), during writing of this manuscript. The Society for Marine Mammalogy, through its Program Grants-in-aid-of-research partially supported this research as well. We also thank sponsors of the 22nd Lowell Wakefield

Fisheries Symposium on Sea Lions of the World: Conservation and Research in the 21st Century, and Alaska Sea Grant for their invitation and support (LAH).

References

Aguayo, A., and R. Maturana. 1973. Presencia del lobo marino común (*Otaria flavescens*) en el litoral chileno. Biol. Pesq. (Chile) 6:45-75.

Aguayo-Lobo, A., H. Díaz, J. Yánez, F. Palma, and M. Sepúlveda. 1998. Informe Final Proyecto FIP 96-51: Censo poblacional del lobo marino común en el litoral de la V a IX Regiones. Fondo de Investigación Pesquera, Valparaíso. 218 pp.

Bax, N.J. 1998. The significance and prediction of predation in marine fisheries. ICES J. Mar. Sci. 55:997-1030.

Beverton, R.J.H. 1985. Analysis of marine mammals-fisheries interaction. In: J.R. Beddington, R.J.H. Beverton, and D.M. Lavigne (eds.), Marine mammals. George Allen and Unwin, London, pp. 3-33.

Costello, M.J. 1990. Predator feeding strategy and prey importance: A new graphical analysis. J. Fish Biol. 36:261-263.

Cubillos, L., S. Nuñez, and D. Arcos. 1998. Producción primaria requerida para sustentar el desembarque de peces pelágicos en Chile. Inv. Mar. (Chile) 26:83-96.

FAO. 1978. Report of the FAO Advisory Committee on Marine Resources Research. Mammals in the seas, Vol. 1. FAO Fish. Ser. 5. 246 pp.

George-Nascimento, M., R. Bustamante, and C. Oyarzún. 1985. Feeding ecology of the South American sea lion *Otaria flavescens*: Food contents and food selectivity. Mar. Ecol. Prog. Ser. 21:135-143.

Habitat Consultores Ltda. 1981. Estudio de aprovechamiento del lobo marino. Habitat Consultores Ltda. Intendencia Regional del Maule, Secretaría Regional de Planificación y Coordinación, Talca, Chile. 132 pp.

Harcourt, R. 1993. Individual variation in predation on fur seals by southern sea lions (*Otaria byronia*) in Peru. Can. J. Zool. 71:1908-1911.

Hückstädt, L.A., and T. Antezana. 2003. Behaviour of the southern sea lion (*Otaria flavescens*) and consumption of the catch during purse-seining for jack mackerel (*Trachurus symmetricus*) off central Chile. ICES J. Mar. Sci. 60:1003-1011.

Hyslop, E.J. 1980. Stomach contents analysis: A review of methods and their application. J. Fish Biol. 17:411-429.

Innes, S., D.M. Lavigne, W.M. Earle, and K.M. Kovacks. 1987. Feeding rates of seals and whales. J. Anim. Ecol. 56:115-130.

Jefferson, T.A., S. Leatherwood, and M.A. Webber. 1993. FAO species identification guide: Marine mammals of the world. FAO, Rome. 320 pp.

Kastelein, R.A., J. Kershaw, E. Berghout, and P.R. Wiepkema. 1995. The food consumption of South American sea lions. Aquat. Mamm. 21:43-53.

Krebs, C.J. 1999. Ecological methodology. 2nd edn. Harper Collins Publishers, Menlo Park. 620 pp.

Labropoulou, M., A. Machias, and N. Tsimenides. 1999. Habitat selection and diet of juvenile red porgy, *Pagrus pagrus* (Linnaeus, 1758). Fish. Bull. U.S. 97:495-507.

Manly, B.F.J. 1997. Randomization, Bootstrap and Monte Carlo methods in biology. 2nd edn. Chapman and Hall, London. 399 pp.

Northridge, S.P. 1985. World review of interactions between marine mammals and fisheries. FAO Fish. Rep. 251. 190 pp.

Oliva, D.P. 1984. Espectro trófico y circaritmos de actividad alimentaria en loberías permanentes y temporarias de *Otaria byronia* (Blainville, 1820) (Carnivora: Otariidae). Tesis para optar el Grado de Licenciado en Biología. Univ. Valparaíso, Valparaíso, Chile. 111 pp.

Oporto, J.A., C.L. Mercado, and L.M. Brieva. 1991. Conflicting interactions between coastal fisheries and pinnipeds in southern Chile. Benguela Ecology Programme Workshop on Seal-Fishery Biological Interactions. University of Cape Town. Working Paper BEP/SW91/R2. 22 pp.

Oporto, J.A., L. Brieva, R. Navarro, and A. Turner. 1999. Informe Final Proyecto FIP 97-44. Cuantificación poblacional de lobos marinos en el litoral de la X y XI Regiones. Fondo de Investigación Pesquera, Valparaíso. 238 pp.

Paredes, R., and M. Arias. 1999. Dieta del lobo fino (*Arctocephalus australis*) y lobo chusco (*Otaria byronia*) en la costa peruana durante mayo y junio de 1999. Informe IMARPE. Callao. 10 pp.

Rosas, F.C.W, M. Haimovici, and M.C. Pinedo. 1993. Age and growth of the South American sea lion, *Otaria flavescens* (Shaw, 1800), in Southern Brazil. J. Mammal. 74:141-147.

Sepúlveda, M. 1998. Circaritmos de actividad del lobo marino común *Otaria flavescens* (Carnivora: Otariidae), y su relación con la salmonicultura en la Décima Región, Chile. Tesis para optar al Grado de Licenciado en Biología Marina y al Título de Biólogo Marino. Univ. Valparaíso, Valparaíso, Chile. 107 pp.

SERNAPESCA. 2000. Anuario estadístico de pesca 1995-1999. El Servicio Nacional de Pesca (SERNAPESCA), Ministerio de Economía, Fomento y Reconstrucción, Valparaíso, Chile.

Sielfeld, W. 1983. Mamíferos marinos de Chile. Ediciones de la Universidad de Chile, Santiago. 199 pp.

Sielfeld, K.W., C.C. Venegas, and G.A. Atalah. 1977. Consideraciones acerca del estado de los mamíferos marinos en Chile. An. Inst. Patagonia (Chile) 8:297-312.

Sielfeld, W., C. Guerra, L.R. Durán, E. Acuña, A. Aguayo, M. Sepúlveda, F. Palma, A. Malinarich, G. Cerda, A. Bolvarán, R. Grau, X. Veloso, Y. Guerra, M. Vargas, N. Amado, R. Peredo, and J. Galáz. 1997. Informe Final Proyecto FIP 95-28: Monitoreo de la pesquería y censo del lobo marino común en el litoral de la I-V Regiones. Fondo de Investigación Pesquera, Valparaíso. 105 pp.

Thompson, D., C.D. Duck, B.J. McConnell, and J. Garrett. 1998. Foraging behaviour and diet of lactating female southern sea lions (*Otaria flavescens*) in the Falkland Islands. J. Zool. (Lond.) 246:135-146.

Torres, D.N. 1979. Mamíferos marinos de Chile: Antecedentes y situación actual. Biol. Pesq. (Chile) 11:49-81.

Trites, A.W. 1997. The role of pinnipeds in the ecosystem. In: G. Stone, J. Goebal, and S. Webster (eds.), Pinniped populations, eastern North Pacific: Status, trends and issues. American Fisheries Society, pp. 31-39.

Trites, A.W., and D. Pauly. 1998. Estimating mean body masses of marine mammals from maximum body lengths. Can. J. Zool. 76:886-896.

Vaz-Ferreira, R. 1979. South American sea lion. In: FAO Advisory Committee on Marine Resources Research (eds.), Mammals in the seas, Vol. 2: Pinniped species summaries and report on sirenians. FAO Fish. Ser. 5.

Werner, R., and C. Campagna. 1995. Diving behaviour of lactating southern sea lions (*Otaria flavescens*) in Patagonia. Can. J. Zool. 73:1975-1982.

Wickens, P.A. 1995. A review of operational interactions between pinnipeds and fisheries. FAO Fish. Tech. Pap. 346. 86 pp.

Appendix 1. Analyses of the diet of *Otaria flavescens* conducted along Chilean coast, included in this study.

Source	Location	Sampling year	Sampling mode	Sample size (stomachs with contents)
Aguayo and Maturana 1973	Valparaiso (33º01'S, 71º38'W)	1972	Sacrifice of animals	16
Habitat Consultores Ltda. 1981	Maguellines (35º20'S, 72º27'W)	1981	Sacrifice of animals and stranded carcasses	9
	Cabo Carranza (35º34'S, 72º38'W)			
Oliva 1984	Cochoa (32º57'S, 71º33'W)	1981	Sacrifice of animals and stranded carcasses	67
	Malhueco (35º20'S, 72º27'W)			
	Cabo Carranza (35º34'S, 72º38'W)			
George-Nascimento et al. 1985	Cobquecura (36º07'S, 72º48'W)	1979-1981	Sacrifice of animals	25
	Talcahuano (36º41'S, 73º06'W)			
	Isla Santa María (37º04'S, 73º32'W)			
	Isla Mocha (38º24'S, 73º56'W)			
Sielfeld et al. 1997	Arica (19º29'S, 70º19'W)	1995, 1996	Sacrifice of animals	16
Aguayo-Lobo et al. 1998	Matanzas (33º57'S, 71º52'W)	1997	Sacrifice of animals	12

Appendix 2. Diet composition of *Otaria flavescens*. The data include the parameters frequency of occurrence (%*O*), dominance percentage (%*D*) and gravimetric percentage (%*G*).

Aguayo and Maturana 1973	%*O*	%*D*	%*G*
Merluccius gayi	75	–	–
Sebastodes oculatus		–	–
Strangomera bentincki		–	–
Dosidicus gigas	25	–	–
Tegula sp.		–	–
Concholepas concholepas		–	–
Heterocarpus reedi		–	–
Habitat Consultores Ltda. 1981			
Callorhynchus callorhynchus	0.502	46.15	–
M. gayi	12.51	38.46	–
S. oculatus	72.55	69.23	–
S. bentincki	0.62	7.69	–
Crustaceans	8.3	7.69	–
Unidentified teleosts	5.51	15.39	–
Oliva 1984 (Cochoa)			
C. callorhynchus	5.56	33.33	–
Engraulis ringens	22.22	33.33	–
M. gayi	22.22	66.67	–
Sardinops sagax	50	66.67	–
Oliva 1984 (Malhueco)			
C. callorhynchus	54.32	100	–
Macruronus magellanicus	12.35	33.33	–
M. gayi	7.41	100	–
S. sagax	1.24	33.33	–
Trachurus symmetricus	24.69	66.67	–
Oliva 1984 (Cabo Carranza)			
C. callorhynchus	1.27	33.33	–
E. ringens	1.27	16.67	–
Genypterus chilensis	3.19	16.67	–
G. maculatus	2.55	16.67	–
Isacia conceptionis	0.64	16.67	–
M. magellanicus	38.85	100	–
M. gayi	39.49	66.67	–
S. sagax	3.19	16.67	–

Appendix 2. (continued)

Oliva 1984 (Cabo Carranza)	*%O*	*%D*	*%G*
Scomber japonicus	0.64	16.67	–
Stromateus stellatus	0.64	16.67	–
T. symmetricus	7.01	66.67	–
Bothidae sp. 1	1.27	16.67	–
Bothidae sp. 2	0.65	16.67	–
Sielfeld et al. 1997			
E. ringens	82.8	34.3	77.29
I. conceptionis	2.2	5.7	11.3
Menticirrhus ophicephalus	0.2	2.9	0.53
Sciaena deliciosa	0.2	5.7	1.5
Sympterygia brevicaudata	0.1	2.9	0.02
Trachinotus paitensis	2.7	14.3	8.84
Loligo gahi	11.5	31.4	11.5
Octopus mimus	0.1	2.9	0.1
George-Nascimento et al. 1985			
M. magellanicus	53.8	48.3	34.1
Genypterus spp.	10.4	17.2	32.2
M. gayi	4.9	44.8	5.8
S. sagax	6.6	20.7	4.8
S. stellatus	0.5	10.3	0.3
Tadarodes spp.	0.1	3.5	0.1
T. symmetricus	7.8	58.6	7.4
D. gigas	0.4	10.3	0.8
O. vulgaris	0.1	3.5	0.1
Unidentified Gadidae	15.2	41.4	13.8
Unidentified Rajidae	0.2	6.9	0.6
Aguayo-Lobo et al. 1998			
G. blacodes	–	88.9	–
M. gayi	–		–
Eggs (Chondrichthyes)	–		–
Unidentified teleost	–		–
Crustaceans	–	33.3	–
Cephalopods	–	44.4	–
Sea weeds	–	55.6	–

Appendix 3. Estimation of the total annual consumption by *Otaria flavescens*, according to adult male, adult female, or juvenile.

	Number of individuals	Total consumption (t)
Region I		
Adult males	1,472	4,040.64
Adult females	6,639	10,124.47
Juveniles	2,027	995.35
	Total	15,160.47
Region II		
Adult males	705	1,935.23
Adult females	3,295	5,024.88
Juveniles	491	241.11
	Total	7,201.21
Region III		
Adult males	680	1,866.6
Adult females	1,440	2,196
Juveniles	450	220.97
	Total	4,283.57
Region IV		
Adult males	367	1,007.42
Adult females	734	1,119.35
Juveniles	434	213.12
	Total	2,339.88
Region V		
Adult males	736	2,020.32
Adult females	1630	2,485.75
Juveniles	315	154.68
	Total	4,660.75
Region VI		
Adult males	355	974.48
Adult females	852	1,299.3
Juveniles	241	118.34
	Total	2,392.12

Appendix 3. (continued)

	Number of individuals	Total consumption (t)
Region VII		
Adult males	243	667.04
Adult females	929	1,416.73
Juveniles	198	97.23
	Total	2,180.99
Region VIII		
Adult males	1,776	4,875.12
Adult females	3,573	5,448.83
Juveniles	1,579	775.37
	Total	11,099.31
Region IX		
Adult males	1,776	4,875.12
Adult females	3,573	5,448.83
Juveniles	1,579	775.37
	Total	5,154.24
Region X		
Adult males	2,255	6,189.98
Adult females	14,863	22,666.08
Juveniles	5,665	2,781.8
	Total	31,637.85
Region XI		
Adult males	1,889	5,185.31
Adult females	8,617	13,140.93
Juveniles	3,247	1,594.44
	Total	19,920.67

Potential Effects of Short-Term Prey Changes on Sea Lion Physiology

David A.S. Rosen, Dominic J. Tollit, and Andrew W. Trites
Marine Mammal Research Unit, University of British Columbia, Canada

Arliss J. Winship
Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, St Andrews, Fife, UK

Abstract

Changes in the proximate composition of prey can result in a nutritional imbalance in individual animals, regardless of total energy intake. This mechanism has been hypothesized to have contributed to the decline of Steller sea lions (*Eumetopias jubatus*). Yet little is known about how otariids react physiologically to short-term changes in prey quality and availability. A series of studies with young captive Steller sea lions tested several potential links between prey quality and sea lion health. Body composition (fat to total mass ratio) of animals fed constant, maintenance-level, isocaloric diets of high- or low-lipid prey changed with season, but overall was not affected by prey composition. The sea lions appeared to prioritize maintaining core growth rates even when energy was limited, electing to deplete lipid reserves to fulfill energy deficits, resulting in changes in relative body condition. In contrast, sea lions subject to short-term, sub-maintenance diets of high- or low-lipid prey utilized a greater portion of their lipid reserves when losing body mass on low lipid prey. Experiments with different ad libitum feeding regimes indicated that sea lions are readily able to alter food intake levels to compensate for differences in prey energy content and, to a lesser degree, prey availability. However, the results also suggest that decreases in prey quality and/or foraging opportunities can readily combine to require food intake levels that are greater than the digestive capacity of the individual. This is particularly true for young animals that may already be living "on the edge" energetically.

Introduction

The population of Steller sea lions (*Eumetopias jubatus*) has declined more than 80% since the 1970s (Loughlin 1998), and continues to decrease within the western portion of their range. A prevalent hypothesis to explain this decline proposes that changes in the quality and/or availability of prey have resulted in an undefined nutritional inadequacy affecting sea lion health and, ultimately, has caused changes in key life history parameters (e.g., reproduction, survival) (Alverson 1992).

A number of studies have examined differences in gross morphology between populations of Steller sea lions from the western and eastern populations to test whether there are indications of nutritional stress among the former (Calkins and Goodwin 1988, Calkins et al. 1998, Pitcher et al. 2000). Interpretation of these data has relied upon comparisons to other mammalian species, as few studies have empirically examined the effect of changes in prey quality and intake on otariid physiology and morphology. This paper presents a series of experiments, using captive Steller sea lions, which attempted to empirically address the following questions:

1. Do differences in prey composition—without differences in energy intake—negatively affect sea lion health?
2. Do differences in prey quality magnify the effects of energetically inadequate food intake?
3. Do inherent digestive constraints contribute to inadequate prey intake?

The "nutritional stress" hypothesis proposes diet-induced changes in undefined aspects of sea lion "health." The first two studies specifically investigated the effects of prey composition on body mass, lipid mass, and relative body composition. Other measures of sea lion physiology concurrently measured—metabolism, hematology and blood biochemistry—are not presented here. The first two experiments differ from others on captive pinnipeds in that they controlled for differences in energy intake between diets in an attempt to differentiate between the effects of food quality and energy intake. Our experiments utilized relatively short-term changes in prey type and intake levels (30-42 days) that mimicked hypothesized similar changes in prey availability of wild Steller sea lions.

The third experiment raises the question whether nutritional stress from lack of sufficient food intake is likely to occur in the wild. Foraging theory predicts that animals should proportionately increase their food intake to compensate for reduced nutritional quality and/or prey availability (Perry and Pianka 1997). However, the theoretical intake levels will—at some point—exceed the digestive capacity of the predator

(Weiner 1992). We tested the ability of young, captive Steller sea lions to compensate for short-term changes in prey energy density and availability, and quantified the maximum amount of food a young sea lion could consume.

Methods

General experimental design

The experiments were conducted with a group of Steller sea lions (7 female, 1 male) that had been captured as pups and raised at the Vancouver Aquarium Marine Science Centre (Vancouver, Canada). The normal diet of the sea lions was herring, supplemented with other fish and vitamins (5M26 Vitazu tablets, Purina Test Diets). Some of the sea lions took part in more than one of the three experiments in this study (Table 1).

Our study consisted of three separate experiments (detailed below). In all three experiments, body mass and food intake was measured daily. At the start and end of each trial of experiments 1 and 2, body composition was determined using deuterium dilution (Reilly and Fedak 1990).

Experiment 1: maintenance pollock vs. herring

The experimental design has been previously described in Rosen and Trites (2005). Briefly, three juvenile sea lions were alternately fed controlled amounts of either pollock (6.3-7.4% lipid, 5.36-5.81 kJ g^{-1} wet weight) or herring (13.8% lipid, 9.57 kJ g^{-1}) for 42 days. Food intake between the diets was balanced for gross energy content (i.e., isocaloric), as determined from sample composition analysis (Norwest Labs, Edmonton, Alberta), and kept constant for each sea lion for the entire experiment. Gross energy intake levels for mass maintenance for each sea lion were determined based on previous feeding levels. Food intake averaged 6.5 kg d^{-1} for animals on the herring diet and 9.4 kg d^{-1} when eating pollock, with overall average gross energy intake = 61.5 MJ d^{-1}. The trials were run consecutively from 26 January to 18 July 2000, when the sea lions were 2.5-3.0 years old. To minimize seasonal biases, diet type for each sea lion was alternated between experimental trials, and different sea lions were on different diets during the same trial (Table 1).

Experiment 2: sub-maintenance Atka mackerel vs. herring

The experimental design has been previously described in Rosen and Trites (2005). Briefly, the experiments were conducted on four female Steller sea lions (ages 4.3-5.5 years over the course of trials). They were alternated between isocaloric diets of Atka mackerel (4.9-6.7% lipid, 4.8-5.4 kJ g^{-1} wet weight) and herring (10.3-13.4% lipid, 7.0-8.2 kJ g^{-1}) between October 2001 and January 2003. The level of food intake (~35.6 MJ d^{-1}) was set a priori at a level estimated to produce a 10-15% loss of initial body mass over the 30 day trials.

Table 1. Schedule summary for the two diet manipulation experiments by month (although not all in the same year). Experiment 1: maintenance level pollock (P) versus herring (H); experiment 2: sub-maintenance level Atka mackerel (A) versus herring. Also listed are the length of each trial in days and the individual sea lions used in each study. For experiment 2, A/H refers to a sea lion fed Atka mackerel the first year and herring the following year.

Experiment	N	D	J	F	M	A	M	J	J	No. days	Animal ID
1. Maintenance pollock versus herring				H	P		H	P		42	M97KO F97SI
				P	H		P	H		42	F97HA
2. Sub-maintenance Atka mackerel versus herring	A/H		H/A							29	F97HA
	H/A		A/H							29	F97SI
			H	A						29	F00NU
			A	H						29	F00YA

To control for seasonal and developmental effects, the trials were paired to ensure that individual sea lions were fed alternate species of prey during each period, and that trials were repeated with opposite diets during the same season in the following year (Table 1).

Experiment 3: satiation and compensation

The experimental design has been previously described in Rosen and Trites (2004). Briefly, five female Steller sea lions participated in the study (aged 1 year old at the start of the experiment). The experiment was designed to minimize the effects of training and research staff on the food intake patterns of the sea lions (Shettleworth 1989). The trials took place in dry animal holding runs containing feeding troughs with a continuous water inflow. A weighed amount of fish was added to their feeding troughs, and each sea lion had a full trough of fish for 7 continuous hours, usually starting at 0900 hr. Fish were refreshed and/or replaced as needed.

A crossover design was used with four treatment conditions consisting of a combination of prey type (either high energy density herring or low energy density capelin; *Mallotus villosus socialis*) and prey availability (food available either daily or on alternating days). The four treatments were alternated after 4 consecutive "feeding" days (i.e., 7 experimental days for alternate day treatments) for four of the animals both within and between each trial, so that no two animals repeated the same combination within a trial or during the course of the experiment. Each trial lasted 20 days, and the experiment consisted of 4 trials over one year, denoted as Summer-01 (July-August 2001), Fall-01 (October-November 2001), Winter-02 (January-February 2002), and Fall-02 (October-November 2002). The herring in the study averaged 90.6 g and 21.9 cm (total length), and the capelin 24.0 g and 16.2 cm. Energy density was 8.05 kJ g^{-1} and 4.41 kJ g^{-1}, respectively.

Food intake was averaged for each sea lion for each treatment combination, excluding the first day as an adjustment day. Food intake data were transformed into measures of gross energy intake to test whether the animals changed their food intake to maintain average gross energy intake across diet treatments. The theoretical intakes were calculated in relation to the "baseline" values of the daily herring (DH) treatment. Assigning this treatment a value of 100% of expected values meant that alternate herring (AH) treatments had an expected value of 200%. This is based on the prediction that the sea lions would compensate for fasting days by eating twice as much on the days food was available to them. Based on differences in gross energy content, the daily capelin (DC) intake should be 183% of the DH intake, and the alternate capelin (AC) intake should be 366% of DH intake.

Results

Experiment 1: maintenance pollock vs. herring

Body mass increased an average of 2.9±2.7 kg (mean±SE) over an entire herring trial and 0.2±2.6 kg over a pollock trial. Animals on both diets gained an average of 3.8±1.8 kg of lean tissue mass over a single trial. At the same time, they lost an average of 0.9±2.7 kg lipid mass while eating herring and 3.6±1.4 kg on the pollock diets. There was a good correlation between changes in total body mass and changes in lean tissue mass ($F_{1,10} = 9.84$, $P = 0.01$, $r^2 = 0.50$), largely driven by the strong relationship within the herring treatments ($P = 0.007$, $r^2 = 0.91$). There was no significant relationship between changes in total body mass and lipid mass ($F_{1,10} = 1.98$, $P = 0.20$), regardless of diet. Changes in body composition, measured as lipid mass as a percent of total body mass, declined marginally for both herring (–1.1%) and pollock (–2.1%) diets. The observed changes in relative body condition were related to changes in lipid mass ($F_{1,10} = 80.27$, $P < 0.0001$, $r^2 = 0.89$) rather than changes in lean tissue mass ($F_{1,10} = 4.30$, $P = 0.06$), regardless of diet type.

There was a significant effect of season on changes in body condition ($F_{1,8} = 5.35$, $P = 0.05$), with the rate of lipid mass loss increasing from January to July. Changes in lean tissue mass also differed during the year, and were highest in May (Fig. 1).

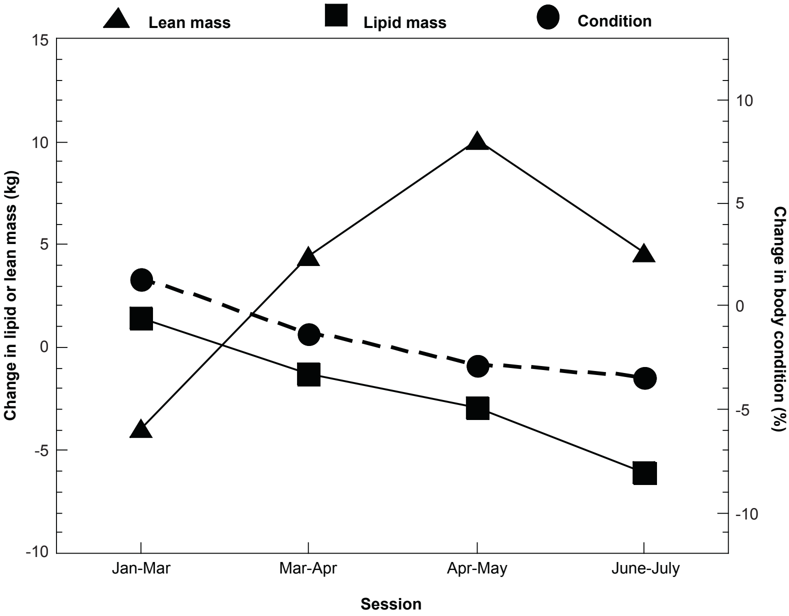


Figure 1. Mean changes in lipid mass (kg), lean tissue mass (kg), and relative body condition (%) during the maintenance level diet manipulations (experiment 1). Data are mean values for all animals eating pollock or herring. Body condition was calculated as: lipid mass/body mass × 100. Figure modified from Rosen and Trites (2005).

Experiment 2: sub-maintenance Atka mackerel vs. herring

Since all of the trials were purposely balanced for season (each animal completed an Atka mackerel and herring trial for each season), we decided to analyze the data using paired *t*-tests with each pair of data corresponding to the two prey types matched for season for each animal.

As predicted for isocaloric diets, there was no difference in absolute or relative body mass loss attributable to diet (Atka mackerel 14.93±1.1 kg, 10.1±0.5%; herring 15.50±1.6 kg, 10.6±1.0%) ($t_5 = 0.453$, $P = 0.67$).

More of the total mass loss was derived from decreases in lipid stores when the animals were consuming Atka mackerel than herring (63.64±15.94% vs. 40.29±9.41%) ($t_5 = -2.82$, $P = 0.037$). On average, sea lions lost more lipid mass (9.16±1.80 kg) while consuming Atka mackerel than herring (6.52±1.65 kg) ($t_5 = -2.98$, $P = 0.031$) (Fig. 2). Although the sea lions lost less lean body mass (5.78±2.77 kg) while consuming Atka mackerel than herring (8.98±1.43 kg), this difference was not significant ($P = 0.18$). A closer examination of the changes in lean body mass indicated

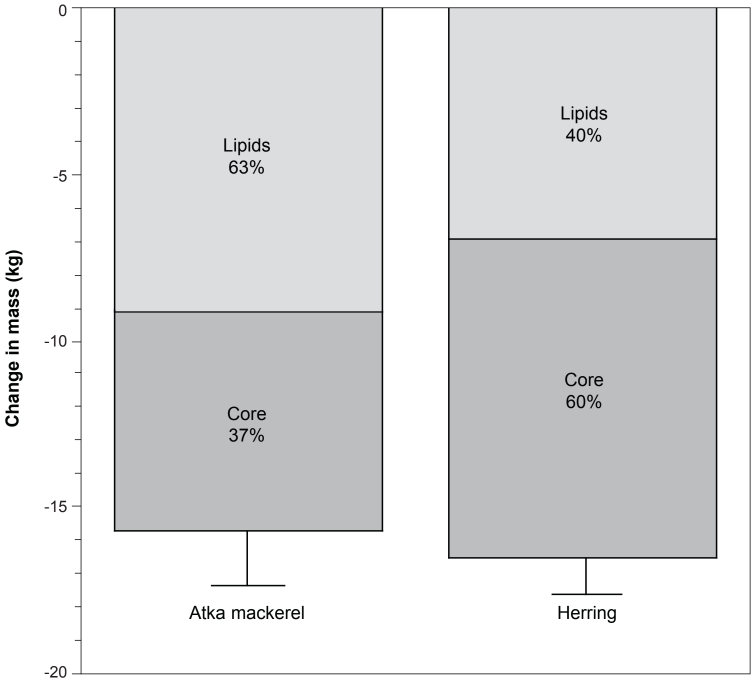


Figure 2. Average change in lipid and lean tissue mass during 30 day sub-maintenance diets of Atka mackerel and herring. There was a significant difference between diets in the amount of lipids lost, but not in the amount of lean tissues lost. Complete data are available in Rosen and Trites (2005).

that, on average, the sea lions lost a total of 1.80±0.38 kg protein while eating Atka mackerel, compared to 2.18±0.32 kg while eating herring. This meant that a large proportion of total mass loss could be attributed to protein catabolism when consuming either herring (14.31±1.5%) or Atka mackerel (11.69±2.3%).

Since relative body condition (lipid mass as % total mass) is a product of changes in both lipid and lean tissues, there were no significant diet-related differences in changes in relative body condition ($P = 0.066$). Relative body condition averaged 16.0±1.5% at the start of the trials, and decreased 5.33±1.67% while sea lions were eating Atka mackerel and 2.04±1.03% while they were consuming herring.

Overall, there was a strong relationship between changes in body condition and changes in lipid mass ($r^2 = 0.92$, $P<0.0001$). There was also a slightly weaker relationship between changes in relative condition and

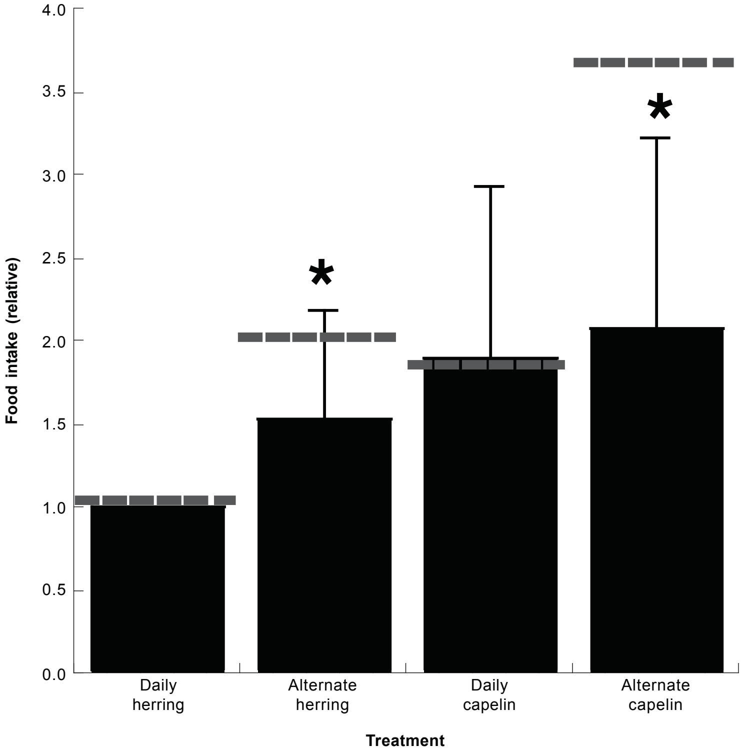


Figure 3. Average daily food intake (±SD) relative to the "baseline" amount of fish consumed during the daily herring phase of the study. Dotted lines represent "expected" values required to maintain an equivalent gross energy intake based on relative energy content of herring and capelin and daily or alternate day prey availability. An asterisk indicates significant differences between observed and expected consumption levels. Modified from Rosen and Trites (2004).

changes in lean body mass ($P = 0.0002$, $r^2 = 0.76$). There was no apparent effect of diet type on either relationship.

Experiment #3: satiation and compensation

There were significant differences in food intake related to type of prey and frequency of feeding ($F_{3,45}=14.23$, $P<0.0001$). Specifically, average food intake during DH treatments (8.31±2.8 kg) was significantly less than during AH treatments (11.54±3.0 kg). Intake during both herring treatments was significantly lower than both the DC (14.04±3.6 kg) and

AC (15.16±5.4 kg) treatments, which did not differ significantly from each other. Although there was no significant difference in the mean intake between the DC and AC treatments, the variation was greater in the latter due to some animals eating extraordinary amounts on individual days. The greatest consumption during a single day was 28.4 kg ingested by a ~100 kg animal during the winter phase.

Food intake during the AH treatment was 1.52±0.67 times that of the DH treatment (Fig. 3), which was significantly lower than the 2.0 times predicted increase required to provide equivalent gross energy intake to the DH treatments. Similarly, the observed 2.07±1.15 times increase in food intake during AC treatments relative to the DH treatments was significantly less than the predicted 3.66 times increase. However, the 1.89±1.04 times increase in food intake during the DC relative to the DH levels was not significantly different from the 1.83 times increase predicted from gross energy contents of herring and capelin.

Discussion

The nutritional stress hypothesis proposes that changes in the diet (or dietary requirements) of Steller sea lions were a contributing factor to their population decline (Alverson 1992, Trites and Donnelly 2003). The implied nutritional imbalance has frequently been interpreted to be the result of decreased energy intake due to changes in prey type, abundance, or distribution.

Several studies have investigated the effects of prey quality on body mass and composition in pinnipeds. Studies with a variety of captive pinnipeds have shown that animals do not appear to alter food intake sufficiently to compensate for differences in prey energy density when switched between *ad libitum* diets of low-energy and high-energy prey. This results in decreased growth rates, body mass, and body condition (Kirsch et al. 2000, Rosen and Trites 2000, Stanberry 2003). However, two other studies (one that used the same animals as Stanberry 2003) failed to find an effect of prey quality on body mass or composition (Castellini 2002, Trumble et al. 2003).

It is difficult to determine from these former studies whether the potential effects of dietary differences were due to prey proximate composition or energy content. This is partly because energy content is closely linked to lipid content in fish (having negligible carbohydrate content), and partly because these studies were conducted using *ad libitum* feeding regimes. The experiments we describe used controlled, isocaloric diets to separate the potential effects of energy and lipid content of prey on sea lion physiology.

Effects on body composition

The combined results of our experiments with captive Steller sea lions indicate that lipid content of prey appears to have no significant effect on body mass or condition when the animals can physically consume sufficient prey to meet all of their energy needs. However, low-lipid prey results in greater losses of lipid reserves when energy intake is insufficient due to increased energy expenditures and/or restricted intake.

The animals on the maintenance-level diet retained the same lean tissue growth regardless of diet type, with greater variation in lipid mass during the year. These results suggest that lean tissue growth is a priority for energy partitioning, and that the "remainder" of the energy budget serves to increase (positive energy state) or decrease (negative energy state) internal lipid reserves. This hypothesis is supported by the evidence that (at maintenance energy intake levels) changes in total mass are driven by changes in lean tissue while changes in relative body condition are driven by changes in lipid stores (Fig. 1). In other words, lipid energy reserves will be proportionately depleted if energy intake is insufficient to support lean body mass growth, a process similarly demonstrated with captive juvenile harp seals (Kirsch et al. 2000). This trend was most evident during the spring season (April-May), when growth rates for total body mass (+7.2 kg) and core tissue (+10.1 kg) were highest, and substantial decreases occurred in lipid stores (–2.9 kg) (Fig. 1).

The differential effect of prey composition on body lipid reserves was most clearly demonstrated in the sub-maintenance, Atka mackerel vs. herring trials (experiment 2). The sea lions lost both lean body mass (and accompanying protein) and lipid stores, although a greater portion (64%) of total mass loss was attributable to changes in lipid stores when the animals consumed the low-lipid Atka mackerel, compared to when consuming herring (40%). As a result, the sea lions had lower relative lipid reserves (as a percent of body mass) when losing mass on the low-lipid diet.

Tissue catabolism

In our second experiment the Steller sea lions used a surprising amount of lean body mass (~48%) to meet their energy requirements during sub-maintenance intake conditions. The reason for the high rate of protein catabolism that we observed is unclear, but such levels of core tissue loss are normally considered a sign of severe nutritional stress (Øritsland 1990). During periods of mass loss, pinnipeds (like many vertebrates) are expected to primarily deplete lipid reserves (Cherel et al. 1992). The relative extent of lipid stores has often been used as a measure of body condition and general health (Pitcher et al. 2000). In these experiments, changes in relative condition were largely driven by changes in lipid mass (despite substantial changes in core tissues during experiment

2). This supports the general concept of using percent body lipids as a health indicator. However, the average decreases in relative condition during a 30 day period of definite nutritional stress was very small (4.2%) with substantial variation, suggesting that such changes would be very difficult to detect in samples of wild Steller sea lions. It is possible that our results were biased due to dehydration in the study animals. Dehydration while using deuterium dilution would result in greater apparent levels of protein catabolism. However, most hematological indicators of this condition were absent (e.g., changes in sodium or potassium levels, although hematocrit did increase). As a diagnostic tool, these physiological changes/differences in hydration state would also be shared by wild sea lions undergoing the same type of nutritional stress. Our results, combined with the large natural seasonal variation in lipid stores and the inherent errors associated with the deuterium dilution technique (Roberts 1989), question the efficacy of using percent lipid mass as a realistic measure of Steller sea lion health status. Other physiological indicators, such as changes in blood biochemistry, may prove to be more effective diagnostic tools (e.g., Rea et al. 1998, 2000).

Compensatory food intake

However, questions arise as to whether the restricted food intake used in these experiments represents a realistic condition. Specifically, would Steller sea lions in the wild not compensate for decreases in prey quality or availability simply by increasing food intake?

The results of our final study (experiment 3) demonstrate that young Steller sea lions appear to have the physiological ability to alter food intake levels to compensate for changes in energy density and, to a lesser degree, availability of prey. The sea lions in our study altered their intake when switched between the daily herring and the daily capelin to retain the same gross energy intake. They also increased their intake when switched between conditions when food was available daily and every other day, although total average intake levels were less in the latter trials.

However, the experiment also clearly demonstrates that this capacity for compensation is limited. It is elementary that there must come a point when the theoretical intake levels needed to compensate for decreasing nutritional value and/or availability of prey will surpass the actual digestive capacity of the predator (Weiner 1992). It is important, therefore, to establish the maximum digestive capacity of Steller sea lions to set realistic limits on foraging and bioenergetic models. As a rough estimate, the sea lions in our experiment seemed unable to consistently ingest food at levels greater than approximately 16-20% of their own body mass.

The results of these experiments support the hypothesis that the intersecting costs to a sea lion faced with decreasing prey availability and net energy value quickly combine to a point where the calculated required food intake surpasses the digestive capacity of the individual sea lion. Such rough estimates of maximum food intake can be integrated with data on available foraging times and ranges of prey energy densities to estimate a variety of variables, including the minimum frequency and energy density of prey needed to sustain an animal (Rosen and Trites 2004). It can also be used to estimate minimum energy deficits that arise from scenarios where an animal is unable to ingest sufficient prey to meet its energy requirements. In general, bioenergetic models would suggest that Steller sea lions that have the highest relative energy demands (young animals and lactating females) may not be able to consume sufficient quantities of low-energy or dispersed prey in the wild to meet their energetic needs (Winship and Trites 2003).

Summary

The combined results of our experiments with captive Steller sea lions suggest that lipid content of prey does not appear to have a significant effect on body mass or condition when energy intake is sufficient to meet all needs. Sea lions appear able to ensure sufficient energy intake by increasing consumption of low-energy prey and, to a lesser degree, altering food intake to compensate for changes in prey availability. This ability is limited, however, by the digestive capacity of the animal. When energy intake is insufficient due to either restricted intake or increased expenditures (such as high growth rates), consumption of low-lipid prey results in greater decreases in lipid reserves. At maintenance levels, sea lions appeared to prioritize lean tissue growth, even at the expense of lipid stores. A surprisingly high rate of lean tissue catabolism was observed during periods of mass loss due to energy restriction. While changes in relative body condition were largely driven by changes in lipid mass, the resulting scope of changes in relative body condition was very small.

Acknowledgments

We are grateful to the training staff of the Marine Mammal Department, Vancouver Aquarium Marine Science Centre for their role in handling and training the sea lions, and to Rebecca Barrick and Chad Nordstrom for data collection and experimental logistics. Ruth Joy assisted with the statistical analyses. Financial support was provided by a grant from the North Pacific Marine Science Foundation to the North Pacific Universities Marine Mammal Research Consortium, with additional support from the U.S. National Oceanic and Atmospheric Administration.

References

Alverson, D.L. 1992. Commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): The conflict arena. Rev. Aquat. Sci. 6:203-256.

Calkins, D., and E. Goodwin. 1988. Investigation of the declining sea lion population in the Gulf of Alaska. Report to Alaska Department of Fish and Game.

Calkins, D.G., E.F. Becker, and K.W. Pitcher. 1998. Reduced body size of female Steller sea lions from a declining population in the Gulf of Alaska. Mar. Mamm. Sci. 14:232-244.

Castellini, M.A. 2002. Captive studies with Steller sea lions at the Alaska SeaLife Center. In: D. DeMaster and S. Atkinson (eds.), Steller sea lion decline: Is it food II? Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 41-44.

Cherel, Y., A. Heitz, C. Calgari, J.-P. Robin, and Y. Le Maho. 1992. Relationships between lipid availability and protein utilization during prolonged fasting. J. Comp. Physiol. B 162:305-313.

Kirsch, P.E., S.J. Iverson, and W.D. Bowen. 2000. Effect of a low-fat diet on body composition and blubber fatty acids of captive juvenile harp seals (*Phoca groenlandica*). Physiol. Biochem. Zool. 73:45-59.

Loughlin, T.R. 1998. The Steller sea lion: A declining species. Biol. Conserv. 1:91-98.

Øritsland, N.A. 1990. Starvation survival and body composition in mammals with particular reference to *Homo sapiens*. B Math. Biol. 52:643-655.

Perry, G., and E.R. Pianka. 1997. Animal foraging: Past, present and future. Trends Ecol. Evol. 12:360-364.

Pitcher, K.W., D.G. Calkins, and G.W. Pendleton. 2000. Steller sea lion condition indices. Mar. Mamm. Sci. 16:427-436.

Rea, L.D., D.A.S. Rosen, and A.W. Trites. 2000. Metabolic response to fasting in 6-week-old Steller sea lion pups (*Eumetopias jubatus*). Can. J. Zool. 78:890-894.

Rea, L.D., M.A. Castellini, B.S. Fadely, and T.R. Loughlin. 1998. Health status of young Alaska Steller sea lion pups (*Eumetopias jubatus*) as indicated by blood chemistry and hematology. Comp. Biochem. Physiol. A 120:617-623.

Reilly, J.J., and M.A. Fedak. 1990. Measurement of the body composition of living gray seals by hydrogen isotope dilution. J. Appl. Physiol. 69:885-891.

Roberts, S.B. 1989. Use of the doubly labeled water method for measurement of energy-expenditure, total-body water, water-intake, and metabolizable energy-intake in humans and small animals. Can. J. Physiol. Pharmacol. 67:1190-1198.

Rosen, D.A.S., and A.W. Trites. 2000. Pollock and the decline of Steller sea lions: Testing the junk food hypothesis. Can. J. Zool. 78:1243-1250.

Rosen, D.A.S., and A.W. Trites. 2004. Satiation and compensation for short-term changes in food quality and availability in young Steller sea lions (*Eumetopias jubatus*). Can. J. Zool. 82:1061-1069.

Rosen, D.A.S., and A.W. Trites. 2005. Examining the potential for nutritional stress in Steller sea lions: Physiological effects of prey composition. J. Comp. Physiol. B 175:265-273.

Shettleworth, S.J. 1989. Animals foraging in the lab: Problems and promises. J. Exp. Psych. 15:81-87.

Stanberry, K. 2003. The effect of changes in dietary fat level on body composition, blood metabolites and hormones, rate of passage, and nutrient assimilation efficiency in harbor seals. M.Sc. thesis, University of Hawaii, Honolulu. 110 pp.

Trites, A.W., and C.P. Donnelly. 2003. The decline of Steller sea lions in Alaska: A review of the nutritional stress hypothesis. Mammal Rev. 33:3-28.

Trumble, S.J., P.S. Barboza, and M.A. Castellini. 2003. Digestive constraints on an aquatic carnivore: Effects of feeding frequency and prey composition on harbor seals. J. Comp. Physiol. B 173:501-509.

Weiner, J. 1992. Physiological limits to sustainable energy budgets in birds and mammals: Ecological implications. Trends Ecol. Evol. 7:384-388.

Winship, A.J., and A.W. Trites. 2003. Prey consumption of Steller sea lions (*Eumetopias jubatus*) off Alaska: How much prey do they require? Fish. Bull. U.S. 101:147-163.

Geographical Variation in Steller Sea Lion Prey Quality in Alaska

Lawrence Schaufler
NOAA, NMFS, Alaska Fisheries Science Center, Juneau, Alaska

Elizabeth Logerwell
NOAA, NMFS, Alaska Fisheries Science Center, Seattle, Washington

Johanna Vollenweider
NOAA, NMFS, Alaska Fisheries Science Center, Juneau, Alaska

Abstract

Nutritional stress is one of the leading hypotheses explaining the decline in Steller sea lion populations of the western stock. Central to this hypothesis is the possibility that western stock sea lions encounter prey of significantly lower quality than those from the eastern stock. We collected and analyzed over 1,200 whole fish representing species identified as sea lion prey items from the Aleutian Islands and southeastern Alaska, including species that reside in both regions. We present proximate composition and calculated mean energy densities based on the lipid and protein contents for the sampled fish. Initial comparisons of the proximate compositions and energy densities between the Aleutian Islands and southeastern Alaska fish on a species basis revealed significant differences in prey energetic content in the two regions for the sampled prey. Overall, the mean energy density for 22 forage species from southeastern Alaska (1.62 ± 0.02 kcal per g on a wet weight basis) was greater than that of 15 species from the Aleutians (1.44 ± 0.03 kcal per g), but these variations could be attributed to size differences among the fish sampled from the two regions as well as species composition and collection season differences. For example, Pacific cod sampled from the Aleutians were significantly larger ($p < 0.001$) than those from southeastern Alaska and had a higher energy density ($p < 0.001$). However, controlling for size revealed no difference in energy density between the two populations of cod ($p > 0.5$). Similarly accounting for size, no difference was found in the energy density of walleye pollock or arrowtooth flounder from the two locations. In contrast, squid and sandfish from southeastern Alaska had higher energy densities ($p < 0.01$) while Aleutian rockfish had higher energy densities than those from southeastern Alaska ($p < 0.001$), though these may represent seasonal and species composition differences. These data reveal the importance of considering size, season, and species when making energy density comparisons of the available prey between geographical regions.

Introduction

The nearly 80% population decline of the western stock of Steller sea lions over the last 30 years has been attributed to a number of factors, including the "junk food hypothesis." This theory postulates that a shift in diet from higher energy forage fish such as Pacific herring, to a diet consisting mainly of lower energy fish such as walleye pollock led to a nutritional deficiency (Alverson 1992, Trites and Donnelly 2003). The lack of a significant decline in the eastern Steller sea lion stock could indicate a difference in the quality of available food between the Aleutian (western) and southeastern Alaska (eastern) regions during the Steller sea lion population decline. Because pinnipeds rely heavily on a piscivorous prey base, prey quality becomes paramount during lactation, molting, and other periods of increased energetic need. Relevant prey quality issues include the amount of fat and protein, vitamin and essential fatty acid contents, and caloric value or energy density. In this study we focused on the fat and protein contents and estimated energy density aspects of prey quality.

The prey items available to and consumed by the western and eastern Steller sea lion stocks vary significantly both in species composition and average prey size (Merrick et al. 1997, Zeppelin et al. 2004). Atka mackerel (*Pleurogrammus monopterygius*) and walleye pollock (*Theragra chalcogramma*) dominate the diets of Aleutian Steller sea lions, while forage fish such as Pacific herring (*Clupea pallasii*), eulachon (*Thaleichthys pacificus*), and capelin (*Mallotus villosus*) as well as walleye pollock form the majority of the southeastern Alaska Steller sea lion diet (Winship and Trites 2003). Other species are common to both regions, such as Pacific cod (*Gadus macrocephalus*), arrowtooth flounder (*Atheresthes stomias*), and certain squid (*Berryteuthis*) and skates (*Bathyraja*), but compose different percentages of the western and eastern stock Steller sea lion diets. Differences in prey sizes have also been reported between the two regions, likely from adaptations to environmental conditions such as water temperature, available food sources, and the particular variety of predators in each region. (Shuter and Post 1990, Tollit et al. 2004, Zeppelin et al. 2004).

This study examines prey quality (i.e., nutritional value of prey) available to Steller sea lion in the Aleutian Islands and southeastern

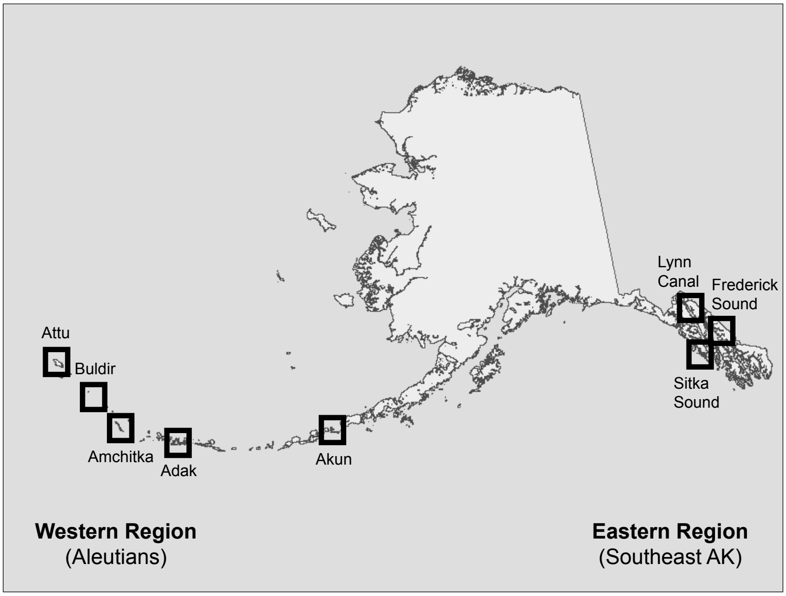


Figure 1. Prey collection sites in the Aleutian Islands and southeastern Alaska.

Alaska. Proximate analysis was used to determine protein, lipid, and moisture content, along with calculated energy densities based on these values for prey collected in the two regions. We present comparisons of proximate composition and energy density values between species common to the regions and energy density values for prey found primarily in only one of the two regions. We report energy density on a wet weight basis since we are considering the nutritional value of a whole fish as it is consumed by a predator such as a marine mammal.

Methods

Sample collection and storage

Opportunistic sample collections were performed on various National Oceanic and Atmospheric Administration (NOAA) cruises and charter vessels in the Aleutian Islands and southeastern Alaska. Specimens were collected in the proximity of (Aleutians) Adak, Akun, Amchitka, Attu, and Buldir Islands; (southeastern Alaska) Berners Bay, Frederick Sound, Lynn Canal, and Sitka Sound (Fig. 1). Aleutian trawls occurred primarily during summer months (April through July), while southeast Alaska trawls were performed year-round, mostly on a quarterly basis

(March, May, September, and December). Typical trawls were mid-water, approximately 20 minutes in duration, performed during daylight hours using a 164 Nordic rope trawl with 1.5 m^2 alloy doors, 7 m × 17 m (height × width) with a 19 mm mesh codend liner. Trawling depths ranged from approximately 75 to 225 meters.

Samples were frozen whole immediately after morphometric measurements and gender were recorded. Gender was determined by direct examination of the gonad, and all gut contents were vacuum-sealed along with the fish in individual bags. When practical due to fish size, specimens were quick-frozen in liquid nitrogen. When this protocol could not be implemented, fish were vacuum-sealed after gender determination and placed in single layers in a commercial-grade –20°C freezer. Upon returning to the laboratory, samples were stored in a –20°C freezer for short-term (0-3 months) or a –80°C freezer for longer-term (4+ months) storage.

Proximate analysis

Entire frozen fish were cut into cross-sections with a Bizerba FK23 industrial meat saw, then homogenized in a Fleetwood M12S meat grinder using a 4.5 mm die. Three to five gram subsamples of the homogenate were randomly chosen for analysis and further liquified using an Oster 4134 blender with food processor attachment. Lipid content was determined gravimetrically after a modified Folch extraction employing 0.1% BHT as an antioxidant (Christie 2003, Vollenweider 2004) using a Dionex 200 accelerated solvent extractor (ASE). Protein content was determined with the Dumas method on a Leco FP-528 nitrogen analyzer and a 6.25 nitrogen-to-protein conversion factor was used (AOAC 1995). Moisture and ash contents were measured gravimetrically using a Leco TGA-601 thermogravimetric analyzer, heating at 135°C for 2-3 hours and then 600°C for 3-4 hours for moisture and ash, respectively. Carbohydrate contents were estimated by subtraction. All proximate contents (lipid, protein, moisture, and ash) are reported as percentages of total wet weight.

All analyses implemented quality control procedures, including a sample replicate, a method blank with no sample material, and a reference standard with each group of 15-20 fish. For lipid analysis, an in-house herring composite reference sample was used to ensure sample group comparability. National Institute of Standards and Technology (NIST) Standard Reference Materials (SRM) 1946 and 2974 were analyzed for protein, moisture, and ash content to verify analytical accuracy. Protein analyses were performed on dried material, in duplicate, with samples reanalyzed if their deviation was more than 1.5 standard deviations from the mean.

Data analysis

For mean comparisons, Levene's test was first performed to confirm homogeneity of variance, then a two-sample, two-tailed Student's t-test was applied to determine significance if the variances were equal. In cases where the variances for the two data sets were not equal, Welch's approximate t was determined, with the calculated degrees of freedom (DF) indicated. A general linear model was employed to identify covariates, and significance levels of $\alpha = 0.05$ were used for all tests.

Results

Over 1,200 whole fish specimens were collected opportunistically from five locations in the Aleutian Islands and three sites in southeastern Alaska (Fig. 1). A total of 316 (26%) fish representing 15 species from the Aleutians and 915 (74%) fish representing 22 species from southeastern Alaska were analyzed. Five species were collected from both regions: arrowtooth flounder, Pacific cod, walleye pollock, Pacific sandfish, and Commander squid (Table 1). Species targeted for collection were based on known prey items for Steller sea lions (Sinclair and Zeppelin 2002, Winship and Trites 2003).

Proximate analysis was performed on all fish samples and the results are presented in Table 1. Lipid and protein contents were used to estimate energy density values using conversion factors: 9.45 kCal per g for lipid (Brody 1945) and 5.65 kCal per g for protein (Van Pelt et al. 1997, Payne et al. 1999). Carbohydrates were typically <1.5% of the total weight, and did not significantly contribute to caloric value. Overall, the prey items examined contained an average of 7.8% lipid, 14.9% protein, 75.4% moisture, and 2.5% ash (mineral). The average energy density for all southeast Alaska prey sampled was 1.62 ± 0.02 kCal per g while the sampled Aleutian prey averaged 1.44 ± 0.03 kCal per g. This significant difference in overall energy densities for prey items from the two regions ($t_{633} = -5.22$, $p < 0.001$) was primarily due to the lower average lipid content of the Aleutian prey. Aleutian items had a higher average protein content, but protein has a significantly lower caloric value than lipid.

Of the species collected only in the Aleutians, Atka mackerel had the highest energy density of 1.93 ± 0.05 kCal per g. Of the species collected exclusively from southeast Alaska, lampfish (2.64 ± 0.02 kCal per g), eulachon (2.22 ± 0.03 kCal per g), and herring (2.04 ± 0.05 kCal per g) had the highest energy densities. Atka mackerel, collected during the summer spawning season, also differed in energy density between males (2.20 ± 0.09 kCal per g) and females (1.77 ± 0.07 kCal per g), as has been previously observed (Logerwell and Schaufler 2005). None of the species collected from southeastern Alaska displayed a significant gender difference in energy density.

Table 1. Average proximate composition and energy densities for sampled prey items.

Species[a]	Region	Collection month[b]	N	Energy density (kCal/g)	% Lipid[c]	% Protein[c]	% Moisture	Length (mm)[d]	Weight (g)
All	Aleutians		316	1.44 ± 0.03	5.94 ± 0.29	15.51 ± 0.07	76.56 ± 0.28		
All	SE AK		915	1.62 ± 0.02	8.40 ± 0.21	14.62 ± 0.07	74.99 ± 0.20		
All	Combined		1,231	1.57 ± 0.02	7.77 ± 0.17	14.85 ± 0.05	75.39 ± 0.17		
Arrowtooth flounder	Aleutians	May-Jun	34	1.38 ± 0.08	5.33 ± 0.80	15.42 ± 0.13	77.23 ± 0.84	411 ± 19	740 ± 130
	SE AK	Sep	5	1.80 ± 0.04	9.62 ± 0.56	15.76 ± 0.35	72.68 ± 0.86	590 ± 49	2365 ± 660
Pacific cod	Aleutians	Apr-Jul	28	1.14 ± 0.02	2.34 ± 0.23	16.32 ± 0.16	79.30 ± 0.29	608 ± 26	2982 ± 408
	SE AK	Jul	11	1.01 ± 0.02	1.31 ± 0.23	15.72 ± 0.11	80.38 ± 0.25	304 ± 27	425 ± 173
Pollock	Aleutians	May-Jun	70	1.14 ± 0.01	2.90 ± 0.13	15.38 ± 0.11	79.46 ± 0.20	373 ± 15	482 ± 39
	SE AK	Quarterly	280	1.15 ± 0.01	3.19 ± 0.10	15.05 ± 0.07	79.16 ± 0.13	320 ± 10	515 ± 31
Rockfish	Aleutians	May	16	1.87 ± 0.06	9.39 ± 0.64	17.46 ± 0.17	70.54 ± 0.64	349 ± 17	714 ± 99
	SE AK	Jul, Dec	23	1.56 ± 0.04	6.21 ± 0.41	17.21 ± 0.16	73.48 ± 0.44	283 ± 12	449 ± 62
Sandfish	Aleutians	May	6	1.10 ± 0.04	3.02 ± 0.32	14.41 ± 0.27	80.09 ± 0.27	157 ± 22	57 ± 24
	SE AK	Dec	3	1.44 ± 0.10	5.41 ± 0.95	16.42 ± 0.33	75.82 ± 0.93	170 ± 39	81 ± 55
Squid	Aleutians	May	15	1.02 ± 0.04	3.06 ± 0.33	12.91 ± 0.14	81.75 ± 0.39	219 ± 8	347 ± 30
	SE AK	Sep	19	1.45 ± 0.04	6.61 ± 0.42	14.60 ± 0.27	77.21 ± 0.45	138 ± 19	238 ± 97
Atka mackerel	Aleutians	May-Jul	100	1.93 ± 0.05	10.92 ± 0.55	15.83 ± 0.07	71.93 ± 0.43	370 ± 5	662 ± 26

Table 1. (continued.)

Species[a]	Region	Collection month[b]	N	Energy density (kCal/g)	% Lipid[c]	% Protein[c]	% Moisture	Length (mm)[d]	Weight (g)
Rock sole	Aleutians	May	18	1.04 ± 0.03	1.74 ± 0.25	15.57 ± 0.25	79.13 ± 0.39	300 ± 10	320 ± 38
Skates	Aleutians	May	14	1.07 ± 0.04	2.49 ± 0.30	14.75 ± 0.31	82.79 ± 0.47	391 ± 27	399 ± 63
Yellow Irish lord	Aleutians	May	15	1.16 ± 0.03	3.73 ± 0.33	14.34 ± 0.11	78.22 ± 0.42	379 ± 20	690 ± 69
Capelin	SE AK	Quarterly	84	1.26 ± 0.03	4.67 ± 0.28	14.40 ± 0.11	78.97 ± 0.36	107 ± 2	8.2 ± 0.4
Eulachon	SE AK	Quarterly	154	2.22 ± 0.03	15.85 ± 0.31	12.70 ± 0.10	70.24 ± 0.36	166 ± 2	33 ± 1
Hake	SE AK	Quarterly	87	1.41 ± 0.02	6.64 ± 0.24	13.87 ± 0.07	77.69 ± 0.23	491 ± 7	878 ± 44
Herring	SE AK	Quarterly	158	2.04 ± 0.05	11.93 ± 0.47	16.19 ± 0.16	69.84 ± 0.48	195 ± 4	90 ± 5
Lampfish	SE AK	Apr, Dec	44	2.64 ± 0.02	18.99 ± 0.16	15.04 ± 0.11	65.15 ± 0.19	101 ± 1	12.0 ± 0.4
Lump-sucker	SE AK	Dec	11	0.69 ± 0.06	3.61 ± 0.47	6.24 ± 0.31	88.97 ± 0.50	270 ± 15	1530 ± 140
Sand lance	SE AK	Jul, Dec	16	1.61 ± 0.06	6.51 ± 0.55	17.53 ± 0.27	73.66 ± 0.68	114 ± 5	8.6 ± 2.2
Smooth-tongue	SE AK	Dec	14	1.54 ± 0.10	10.20 ± 0.94	10.28 ± 0.26	77.63 ± 0.89	120 ± 5	13.5 ± 1.9

[a] Species examined are arrowtooth flounder *Atheresthes stomias*; Atka mackerel *Pleurogrammus monopterygius*; capelin *Mallotus villosus;* eulachon *Thaleichthys pacificus*; hake *Merluccius productus*; herring *Clupea pallasii*; Pacific cod *Gadus macrocephalus*; walleye pollock *Theragra chalcogramma*; rockfish include *Sebastes alutus*, *Sebastes ciliatus*, *Sebastes maliger*, *Sebastes polyspinis*, and *Sebastes variegatus*; rock sole *Lepidopsetta bilineata*; sandfish *Trichodon trichodon*; skates include *Bathyraja interrupta*, *Bathyraja minispinosa*, *Bathyraja parmifera,* and *Bathyraja taranetzi*; squid include *Berryteuthis magister* and *Loligo opalescens*; yellow Irish lord *Hemilepidotus jordani.*

[b] Collection months are indicated, mostly from 2002. "Quarterly" is a minimum of quarterly coverage throughout the year, typically March, May/June, September, and December.

[c] Percentages are given on a wet weight basis.

[d] Lengths for most species were measured as distances from snout tip to the tail fork (fork lengths), or tail center for rounded tails. Mantle lengths (excluding tentacles) were used for squid. Overall body lengths, including tail, were used for skates.

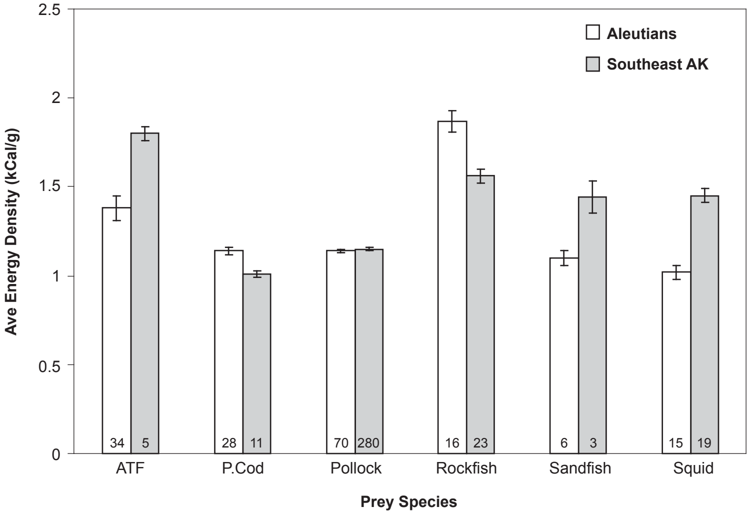


Figure 2. Comparisons of the average energy densities for species collected in the Aleutian Islands and southeastern Alaska. Error bars indicate standard error, and sample sizes are shown at the base of each bar. ATF = arrowtooth flounder; P. cod = Pacific cod.

Comparison of the energy densities for species found in both regions revealed a number of significant differences (Fig. 2). Arrowtooth flounder had a significantly higher average energy density in southeastern Alaska than in the Aleutians ($t_{37} = -4.87$, $p < 0.001$), as did sandfish ($t_7 = -4.09$, $p = 0.005$) and squid ($t_{32} = -5.72$, $p < 0.001$), mainly due to differences in lipid content. Pacific cod had a significantly higher energy density in the Aleutians than in southeastern Alaska ($t_{31} = -4.32$, $p < 0.001$), as did the Aleutian rockfish ($t_{37} = -4.44$, $p < 0.001$), also due to higher lipid content. Interestingly, Pacific cod showed a significant linear correlation ($r^2 = 0.498$) between energy density and fish weight that was not observed for the other species with significant numbers of observations ($N > 20$) (Fig. 3).

Walleye pollock from both regions had similar estimated energy densities (1.14 ± 0.01 kCal per g and 1.15 ± 0.01 kCal per g for the Aleutians and southeastern Alaska, respectively), even though there was a significant difference in fish lengths collected from the two geographical areas ($t_{132} = 2.95$, $p = 0.004$). Overall, age classes sampled included young-of-the-year through adult, with lengths from 7 cm to 67 cm and weights ranging from 2 g to over 2.5 kg. Length was observed to be only weakly correlated with energy density ($r^2 = 0.113$). The lack of substantial dependence of walleye pollock lipid content (and energy density) on fish size

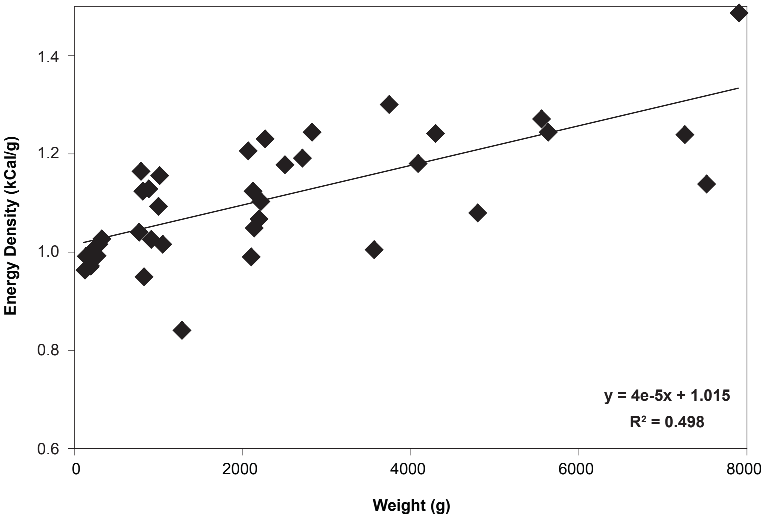


Figure 3. Size correlation of energy density for Pacific cod.

further suggests that this relationship may be species-dependent, as has been previously observed (Anthony et al. 2000, Vollenweider 2004).

Discussion

Knowledge of the species composition of two regional diets as well as the nutritional differences between prey items are critical steps in evaluating the prey quality aspect of the junk food hypothesis. Opportunistic collections of prey species in the western and eastern regions provided a sampling of potential Steller sea lion prey for nutritional analysis from species primarily found in only one region and species common to both areas. Proximate analysis revealed that on an overall basis, the Aleutian prey items collected had a lower average lipid content, and consequently a lower estimated average energy density, than did the potential prey items collected from southeastern Alaska. Therefore, if trawl-based sampling can serve as a proxy for opportunistic foraging by sea lions, and the prey collections used in this study serve as an unbiased representative of the available prey, the difference in overall energy density would suggest that sea lions in the western region encounter, on average, lower energy density prey than those in the eastern region. However, trawl-based sampling tends to be biased toward pelagic species and researcher prey sampling is unavoidably influenced by factors such as daylight, weather and ocean conditions, shore proximity, and other logistical issues (Stoner 2004). Furthermore, while systematic prey collections in southeast Alaska are possible on a year-round basis, they are extremely difficult in the harsh winter conditions of the Aleutian Islands, limiting the available data.

The main objective of this study was to determine the proximate compositions of common Steller sea lion prey items in the Aleutians and southeastern Alaska, and provide comparisons for species found in both regions. However, sampling conditions and whether a given species was located in both areas limited the available comparisons. Some species were not found in one location during a given season, and average sizes of the fish collected sometimes varied by location. Comparing the available data for fish collected from both areas indicated differences overall, but many of these may be attributable to factors such as size and season.

For the species collected from the Aleutians and southeastern Alaska, we wished to address whether they had the same average energy densities in both areas. Energy density estimates were calculated based on the proximate composition, particularly lipid and fat content, of the sampled fish. Comparison of published values obtained using bomb calorimetry with our calculated energy densities showed excellent consistency for species with available data such as walleye pollock (1.15 ± 0.01 kCal per g [this study] vs. 1.11 ± 0.03 kCal per g [Perez 1994]), and Pacific herring (2.04 ± 0.05 kCal per g [this study] vs. 2.05 ± 0.18 kCal per g [Perez 1994]). Proximate values observed for species with published data were also consistent with observed ranges (Payne et al. 1999, Iverson et al. 2002).

Of particular interest was the comparison of average energy densities for walleye pollock from both regions, given that some of the sharpest declines in Steller sea lion populations have occurred in areas where walleye pollock dominates the diet, and the fact that pollock is a major food component to both Steller sea lion stocks (Rosen and Trites 2000, Winship and Trites 2003). The energy densities observed for Aleutian and southeastern Alaska walleye pollock were equivalent ($p > 0.5$), suggesting that the quality of pollock in both regions is similar and is not likely to be a factor in the decline.

Comparisons of average energy densities for other species collected from both regions revealed differences that could be attributed to factors other than geographical region. For instance, arrowtooth flounder collected in southeastern Alaska were significantly larger than those sampled from the Aleutians ($t_{37} = -3.37$, $p = 0.002$), while Aleutian Pacific cod were larger than those from southeastern Alaska ($t_{28} = 8.08$, $p < 0.001$), and in both cases prey size accounted for the observed differences in energy densities (Table 1). For arrowtooth flounder, lipid content, which often dominates the energy density value, varied between locations ($t_{37} = -4.40$, $p < 0.001$) primarily due to size, though protein content did not ($t_{37} = -0.91$, $p = 0.40$). In general, protein content did not appear to vary significantly with size for any of the species we examined.

For sandfish and squid collected from both regions, the observed differences in energy densities were in part attributable to length differences ($p = 0.04$ and $p = 0.01$, respectively), but length did not completely account for the higher energy densities of the samples collected in southeastern Alaska. The season in which these species were encountered in the two regions differed, and is likely to be another source of variation; they were collected in May in the Aleutians, and in the fall in southeastern Alaska. Differences in the spawning state for these species may have caused them to have significantly different lipid content.

Observed differences in the energy densities for rockfish from the Aleutians and southeastern Alaska are likely due to differences in the particular species collected in the two regions. Though all of the rockfish studied were in the same genus, and were therefore grouped together for comparison, the mean lipid content varied significantly per species. For instance, the sampled Aleutian rockfish were Pacific ocean perch and northern rockfish, which had average lipid values of 8.18 ± 1.04% and 10.60 ± 0.51%, respectively. From southeastern Alaska, collections included dusky rockfish, which had an average lipid value of 6.64 ± 0.37%. Furthermore, no single species of rockfish was collected in both regions, and the months in which they were encountered differed, confounding the comparison.

The effect of fish size on energy density makes geographical comparisons of prey quality difficult, particularly when the size of similarly aged fish differs significantly between two regions due to differences in environmental conditions. This effect appears to be specific to certain species. For some pelagic species, such as herring and sandfish, there is a known relationship between size and lipid content (and hence energy density) due to changes in energy allocation with age (Anthony et al. 2000). However, in walleye pollock there is no apparent relationship between energy density and specimen length (Vollenweider 2004).

Differences in the mean size of fish captured in the Aleutians versus southeastern Alaska may be due to sampling-related issues, or may represent real differences in the sizes of prey encountered by Steller sea lions. Little is known regarding the size structures of various prey species in the Aleutians versus southeastern Alaska, but there are several physiological advantages to being a larger size in a harsh environment, and prey size has been observed to vary by location and environmental conditions (Shuter and Post 1990, Zeppelin et al. 2004).

Another aspect of diet quality is the diversity of available quality prey items. Population declines previously have been correlated to diets of low diversity (Merrick et al. 1997), and it has been suggested that aquatic carnivores have increased digestibility when consuming mixed diets (Trumble and Castellini 2005). In addition, prey diversity likely increases foraging efficiency and reduces the dependence of predator consumption on the seasonal energetic cycles of a particular prey species. In comparing Aleutian versus southeastern Alaska prey items, four quality prey species, with energy densities of 1.8 kCal per g or higher, were identified in southeastern Alaska, whereas only two were found in the Aleutian prey subset. Admittedly, we have not yet sampled all of the known prey items from either region, but a significant difference in the number of quality prey items available in the two regions could have a noticeable impact on sea lion foraging success and nutritional state in those areas.

Opportunistic sampling of potential prey items is problematic due to issues such as fish availability, choice of fishing gear, fishing conditions including prior fishing pressure, and particular geographical region sampled. Furthermore, comparison of prey quality between areas is difficult due to regional differences related to environmental conditions such as species assemblages, population structures, and differences in growth rate, as well as the fact that a given species may spawn at different times in the two regions. Comparisons are hindered by these multiple factors and limit interpretation of the data. Even with these limitations, however, proximate composition data and energy density estimates for species from remote regions such as the Aleutian Islands provide a snapshot of prey quality for a given species at a specific time, which is a critical tool to assess the nutritional state of predators in the area such as Steller sea lion. As more data are collected from these regions, more specific comparisons can be made with fewer confounding factors.

Acknowledgments

The authors would like to thank Robert Bradshaw and Darcie Neff for their focused efforts and careful attention to detail in sample analysis and data archiving, as well as Ron Heintz for his helpful comments on the data and manuscript. The authors are especially grateful to the reviewers for their comments and suggestions. Special acknowledgments also go to the vessel crews who assisted in sample collection.

References

Alverson, D.L. 1992. A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): The conflict arena. Rev. Aquat. Sci. 6:203-256.

AOAC. 1995. Official methods of analysis, 16th edn. Association of Official Analytical Chemists, Arlington, Virginia.

Anthony, J.A., D.D. Roby, and K.R. Turco. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. J. Exp. Mar. Biol. 248:53-78.

Brody, S. 1945. Bioenergetics and growth. Hafner Publishing Co., New York. 1023 pp.

Christie, W.W. 2003. Lipid analysis, 3rd edn. Oily Press, England, pp. 101, 208.

Iverson, S.J., K.J. Frost, and S.L.C. Lang. 2002. Fat content and fatty acid composition of forage fish and invertebrates in Prince William Sound, Alaska. Mar. Ecol. Prog. Ser. 241:161-181.

Logerwell, E.A., and L.E. Schaufler. 2005. New data on proximate composition and energy density of Steller sea lion (*Eumetopias jubatus*) prey fills seasonal and geographic gaps in existing information. Aquat. Mamm. 31:62-82.

Merrick, R.L., M.K. Chumbley, and G.V. Byrd. 1997. Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: A potential relationship. Can. J. Fish. Aquat. Sci. 54:1342-1348.

Payne, S.A., A.B. Johnson, and R.S. Otto. 1999. Proximate composition of some northeastern Pacific forage fish species. Fish. Oceanogr. 8:159-177.

Perez, M.A. 1994. Calorimetry measurements of energy value of some Alaskan fishes and squids. NOAA Tech. Memo NMFS-AFSC-32. 32 pp.

Rosen, D.A., and A.W. Trites. 2000. Pollock and the decline of Steller sea lions: Testing the junk-food hypothesis. Can. J. Zool. 78:1243-50.

Shuter, B.J., and J.R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. Trans. Am. Fish. Soc. 119:314-336.

Sinclair, E.H., and T.K. Zeppelin. 2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). J. Mamm. 83:973-990.

Stoner, A.W. 2004. Effects of environmental variables on fish feeding ecology: Implications for the performance of baited fishing gear and stock assessment. J. Fish Biol. 65:1445-1471.

Tollit, D.J., S.G. Heaslip, and A.W. Trites. 2004. Sizes of walleye pollock (*Theragra chalcogramma*) consumed by the eastern stock of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska from 1994 to 1999. Fish. Bull. U.S. 102:522-532.

Trites, A.W., and C.P. Donnelly. 2003. The decline of Steller sea lions *Eumetopias jubatus* in Alaska: A review of the nutritional stress hypothesis. Mamm. Rev. 33:3-28.

Trumble, S.J., and M.A. Castellini. 2005. Diet mixing in an aquatic carnivore, the harbour seal. Can. J. Zool. 83:851-859.

Van Pelt, T.I., J.F. Piatt, B.K. Lance, and D.D. Roby. 1997. Proximate composition and energy density of some north Pacific forage fishes. Comp. Biochem. Phys. 118A:1393-1398.

Vollenweider, J.J. 2004. Variability in Steller sea lion (*Eumetopias jubatus*) prey quality in southeastern Alaska. Master's thesis, University of Alaska Fairbanks, Juneau.

Winship, A.J., and A.W. Trites. 2003. Prey consumption of Steller sea lions (*Eumetopias jubatus*) off Alaska: How much prey do they require? Fish. Bull. U.S. 101:147-167.

Zeppelin, T.K., D.J. Tollit, K.A. Call, T.J. Orchard, and C.J. Gudmundson. 2004. Sizes of walleye pollock and Atka mackerel (*Pleurogrammus monopterygius*) consumed by the western stock of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1998 to 2000. Fish. Bull. U.S. 102:509-521.

Relationship between Steller Sea Lion Diets and Fish Distributions in the Eastern North Pacific

Emma L. Bredesen, Andrea P. Coombs, and Andrew W. Trites
University of British Columbia, Marine Mammal Research Unit, Fisheries Centre, Aquatic Ecosystems Research Laboratory, Vancouver, British Columbia, Canada

Abstract

Distributions of fish species were compared with diet information for Steller sea lions (*Eumetopias jubatus*) to assess the level of correspondence between potential prey availability and sea lion feeding habits. Fish distributions were compiled as part of the Sea Around Us Project at the UBC Fisheries Centre, and were based on published distributions and habitat preferences (e.g., latitude, depth). Sea lion scat samples were collected during the 1990s from seven geographic regions from Oregon to the western and central Aleutian Islands. The frequencies of occurrence of four prevalent species (walleye pollock, *Theragra chalcogramma*; Pacific herring, *Clupea pallasii*; Pacific cod, *Gadus macrocephalus*; and North Pacific hake, *Merluccius productus*) in the Steller sea lion diet were compared to their distributions in the North Pacific Ocean. The data suggest that Steller sea lion diets broadly reflect the distributions of these major prey species. However, some of the fish species that were regionally predicted to be present in high abundance were not proportionally reflected in the Steller sea lion diet, suggesting that other factors in addition to fish abundance influence their diets.

Introduction

The Steller sea lion population declined by more than 80% in western Alaska between the mid-1970s and the early 1990s (Trites and Larkin 1996, Loughlin 1998, NAS 2003) while the smaller eastern population increased. Accordingly, the western and eastern populations of Steller sea lions were listed as "endangered" and "threatened," respectively, under the U.S. Endangered Species Act. In an attempt to better understand their role in the ecosystem and the differences between the decreasing western population and the increasing eastern population, considerable research has focused on determining the diet of Steller sea lions (Merrick et al. 1997, Sinclair and Zeppelin 2002).

Comprehensive changes have occurred to the biomass and composition of the marine community off the Alaska coast since the oceanic regime shift of 1976. Increases were noted following the regime shift in the abundances of flatfish, gadids, and salmonids (Hare and Francis 1995, Hollowed et al. 2001, Benson and Trites 2002, Wilderbuer et al. 2002). A small mesh survey around Kodiak Island (1953-1997) also noted increases in groundfish such as cod and pollock, as well as a decline in the abundance of forage species such as capelin and shrimp (Anderson and Piatt 1999). Such changes in the abundances and distributions of key prey species composition may be related to the decline of Steller sea lions in western Alaska.

One of the leading hypotheses for the decline in western Alaska is nutritional stress caused by a shift in ocean climate that favored the abundance of less nutritious fishes over those that had higher fat content (Alverson 1992, Rosen and Trites 2000, Trites and Donnelly 2003, Trites et al. 2006). Like other pinnipeds, Steller sea lions have often been classified as generalist feeders. However, it is not clear whether Steller sea lions merely eat what is available to them, or whether other factors influence which prey they consume. We therefore sought to assess the level of correspondence between prey distribution and sea lion diets.

Methods

Predicted fish distribution maps were obtained from the Sea Around Us Project (Fisheries Centre, University of British Columbia, www.seaaroundus.org) and were based on published distributions and habitat preferences (e.g., latitude, depth) (Watson et al. 2004). These maps represent the expected percent of world distribution of individual fish species and are an indication of relative abundance of each species across the North Pacific Ocean.

Scat samples were collected during the 1990s (Riemer and Brown 1997, Sinclair and Zeppelin 2002, Trites et al. unpubl. data) from seven geographic regions from Oregon to the Central and Western Aleutian Islands (Oregon [OR], British Columbia [BC], Southeast Alaska [SEA], Gulf of Alaska 1 [GOA1], Gulf of Alaska 2 [GOA2], Eastern Aleutian Islands [EAI], and Western Central Aleutian Islands [WCAI]). Frequently occurring species (walleye pollock, *Theragra chalcogramma*; Pacific herring, *Clupea pallasii*; Pacific cod, *Gadus macrocephalus*; and North Pacific hake, *Merluccius productus*) in the Steller sea lion diet were compared to their predicted distributions. The importance of each prey species was determined by the percent frequency of occurrence (%FO) in scat samples from each region (Croxall 1993).

Proportionally sized circles, representing the %FO, were plotted for comparison with fish distributions in respective regions. Percentages of both diet and distribution data were arcsine transformed to satisfy the assumptions for statistical analysis.

Results and discussion

The data suggest that there is a relationship between fish distributions and Steller sea lion diets (Figs. 1 and 2). For example, in the northern part of the sea lion's range, walleye pollock has a high relative abundance and is an important part of the sea lion diet (Fig. 1A). Although not statistically significant ($r = 0.63$, $P > 0.05$), the correlation is positive and consistent with the relationship found for the other prey species. In the southern part of the sea lion range (e.g., Oregon), the predicted relative abundance of walleye pollock is lower and North Pacific hake is predominant both in relative abundance and in the sea lion diet ($r = 0.74$, $P = 0.05$) (Figs. 1A, 1D, and 2). A similar pattern can be seen with Pacific herring ($r = 0.80$, $P = 0.03$), arrowtooth flounder ($r = 0.83$, $P = 0.02$), and, to a lesser extent, Pacific cod ($r = 0.28$, $P > 0.05$), where the frequency of occurrence of the prey species in the diet of Steller sea lions is higher in regions that also have high predicted relative fish abundance (Figs. 1B, 1C, and 2).

While the relationship between relative fish abundances and Steller sea lion diets seems strong, it is not as straightforward as Figs. 1 and 2 might suggest. For example, in the Gulf of Alaska the biomass of arrowtooth flounder (Turnock et al. 2001) is estimated to be approximately six times the biomass of walleye pollock (Dorn et al. 2001). However, pollock is two to eight times more prominent in the Steller sea lion diet (%FO) than arrowtooth flounder (Sinclair and Zeppelin 2002) (Tables 1 and 2). Atka mackerel is also 35 times more prominent than rockfish in the diet of Steller sea lions in the Aleutian Islands region (Sinclair and Zeppelin 2002) despite the fact that both have a similar biomass estimate (Lowe et al. 2002, Spencer and Ianelli 2002) (Tables 1 and 2). Although not statistically significant, Atka mackerel ($r = -0.18$, $P > 0.05$) and Pacific ocean perch/Rockfish ($r = -0.29$, $P > 0.05$) show a weak negative correlation between the percent of world distribution and percent frequency of occurrence in Steller sea lion diet (Fig. 3).

Many factors likely influence the prey that sea lions choose to eat. These include the presence of spines, and the vertical and horizontal distribution of prey in the water column. Such factors may account for some of the apparent discrepancies between diets and relative prey abundances. For example, arrowtooth flounder may make up a large portion of the relative biomass, but may be harder for sea lions to locate and capture because they tend to be solitary and not school in easily

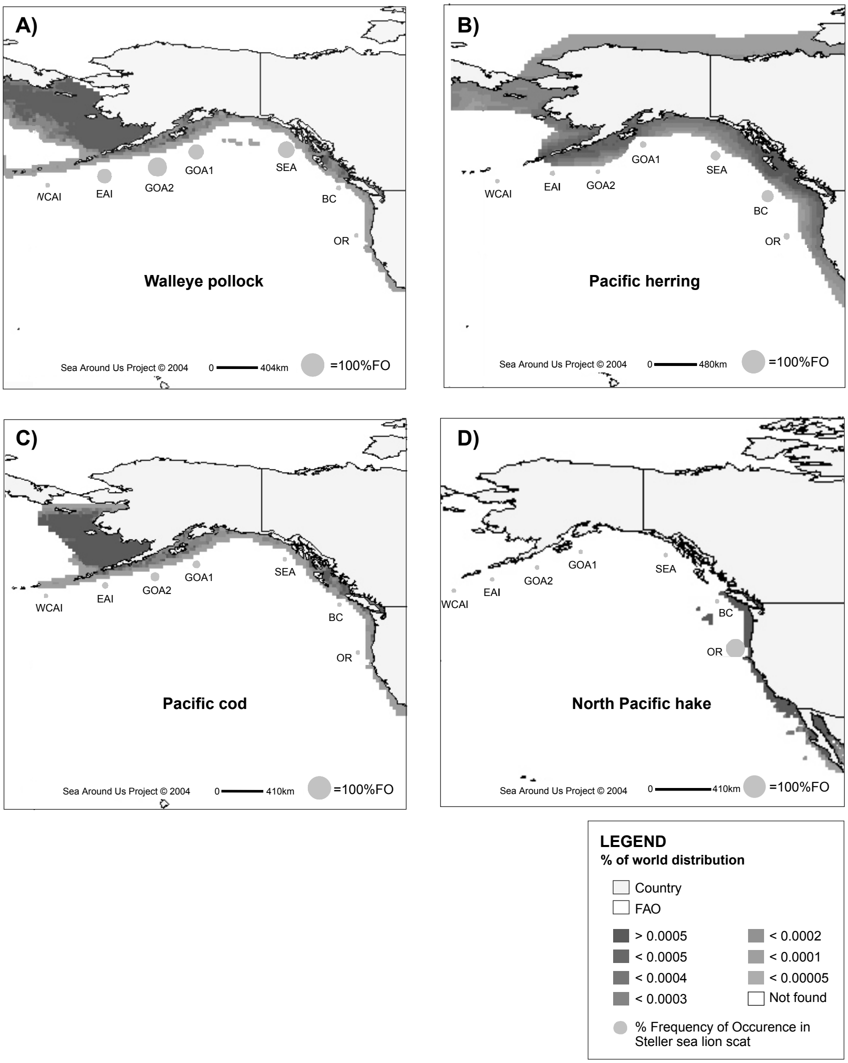


Figure 1. **Predicted distribution and relative abundance of four species of fish in the eastern North Pacific (Watson et al. 2004). Grayscale shading indicates relative abundance of each species. Proportionally sized circles, plotted in respective regions, represent the percent frequencies of occurrence (%FO) of fish species in scat samples from Steller sea lions during the 1990s (from Riemer and Brown 1997, Sinclair and Zeppelin 2002, and Trites et al. unpubl. data). Regions, from left to right, are Western Central Aleutian Islands (WCAI), Eastern Aleutian Islands (EAI), Gulf of Alaska 2 (GOA2), Gulf of Alaska 1 (GOA1), Southeast Alaska (SEA), British Columbia (BC), and Oregon (OR).**

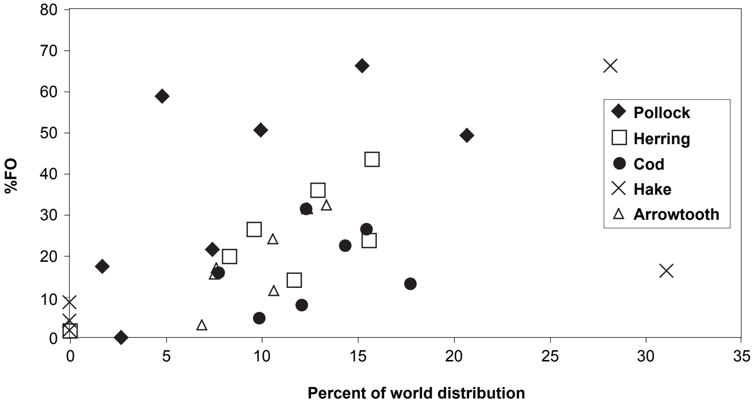


Figure 2. **Relationship between percent frequency of occurrence in the diet of Steller sea lions in the 1990s and percent of world distribution for five prominent prey species in the North Pacific Ocean. Statistically significant positive correlations occur between world distribution and frequency of occurrence for herring, hake, and arrowtooth flounder. Correlations for pollock and cod were positive but not significant.**

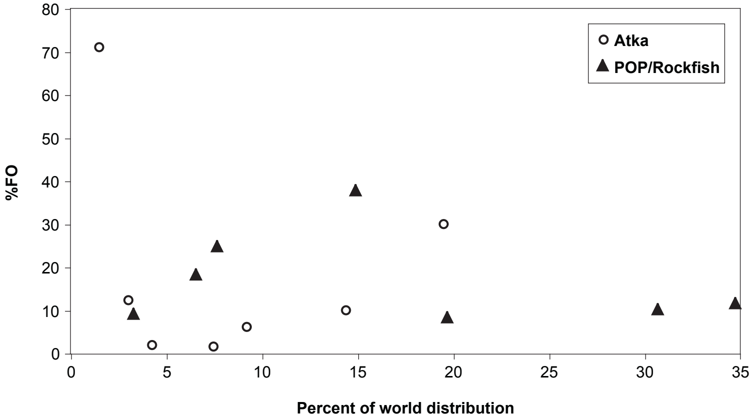


Figure 3. **Percent frequency of occurrence versus percent of world distribution for two Steller sea lion prey species (Atka mackerel and Pacific ocean perch). Neither of the relationships were statistically significant.**

Table 1. Percent frequency of occurrence (%FO) for prominent prey species in Steller sea lion scat.

		%FO[a]						
Region	N[b]	Walleye pollock	Pacific herring	Pacific cod	N. Pacific hake	Arrow-tooth flounder	Atka mackerel	Rockfish
WCAI	1,370	8.85	0.1[c]	7.62	0.1[c]	0.29	89.61	2.51
EAI	889	57.25	11.59	14.75	0.1[c]	3.93	25.32	4.02
GOA2	929	83.56	5.93	27.40	0.1[c]	8.49	3.12	3.13
GOA1	574	59.43	16.21	20.03	0.50	27.18	1.22	2.07
SEA	1,438	73.02	34.56	2.02	2.23	16.48	0.14	17.59
BC	1,077	13.28	47.45	5.29	7.80	28.51	0.09	37.60
OR	256	0	19.92	0.75	83.60	7.03	4.67	9.77

[a] Percentages were arcsine transformed prior to statistical analysis.
[b] Number of scat samples containing identifiable prey used to calculate annual average of percent frequency of occurrence (%FO).
[c] Species present but <1 (Sinclair and Zeppelin 2002).

Table 2. Percent of world distribution for prominent prey species in Steller sea lion scat.

	% of World distribution[a]						
Region	Walleye pollock	Pacific herring	Pacific cod	N. Pacific hake	Arrow-tooth flounder	Atka mackerel	POP/ rockfish
WCAI	0.09	0	1.81	0	1.44	0.06	0.33
EAI	12.50	2.08	6.12	0	3.40	11.09	32.45
GOA2	6.91	4.10	4.52	0	1.77	6.14	26.03
GOA1	2.99	7.22	7.08	0	4.60	2.53	11.34
SEA	0.71	5.00	4.36	0	3.38	0.54	1.78
BC	1.68	7.34	9.25	26.69	5.37	1.66	6.61
OR	0.22	2.77	2.93	22.30	1.73	0.27	1.30

[a] Proportions of world distribution were summed by region for each fish species. Percentages were arcsine transformed prior to statistical analysis.

exploitable densities for much of the year. Similarly, not all fish may be equally available to sea lions if they occur at depths or in areas that are difficult for sea lions to access. Thus, to fully understand the association between Steller sea lion feeding habits and their prey, consideration needs to be given to factors other than the simple distribution of prey species.

The available data suggest that the diets of Steller sea lions broadly reflect the distributions of their major prey species. However, discrepancies suggest that other factors such as nutritional value, relative foraging costs, prey preference, etc., should also be considered to better understand the feeding habits of Steller sea lions. Nonetheless, given the general relationship between fish distributions and Steller sea lion diets, factors that affect fish assemblages (such as climatic change) may also have implications for sea lion populations. Additional analysis is therefore required to achieve a better understanding of Steller sea lion diet and how it is related to the distribution of their prey throughout their range. An analysis at finer spatial and temporal scales, incorporating seasonal or monthly sea lion diet data and fish abundance data would further help to elucidate factors that affect Steller sea lion feeding habits. Consideration should also be given to the different depth ranges that adults and juvenile fish species inhabit, and how it relates to the ability of sea lions to successfully forage.

Acknowledgments

We are grateful to the Sea Around Us Project, particularly Dr. Reg Watson and Mr. Adrian Kitchingman; NOAA; and the North Pacific Marine Science Foundation for providing funding to the North Pacific Universities Marine Mammal Research Consortium.

References

Alverson, D.L. 1992. A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): The conflict arena. Rev. Aquat. Sci. 6:203-256.

Anderson, P.J., and J.F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar. Ecol. Prog. Ser. 189:117-123.

Benson, A.J., and A.W. Trites. 2002. Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. Fish Fish. 3:95-113.

Croxall, J.P. 1993. Diet. In: R.M. Laws (ed.), Antarctic seals: Research methods and techniques. Cambridge University Press, Cambridge, pp. 268-290.

Dorn, M.W., A.B. Hollowed, E. Brown, B.A. Megrey, C. Wilson, and J. Blackburn. 2001. Assessment of the walleye pollock stock in the Gulf of Alaska. In: Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fishery Management Council, www.afsc.noaa.gov/refm/docs/2001/GOA pollock.pdf, pp. 1-88.

Hare, S.R., and R.C. Francis. 1995. Climate change and salmon production in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 121:357-372.

Hollowed, A.B., S.R. Hare, and W.S. Wooster. 2001. Pacific-basin climate variability and patterns of Northeast Pacific marine fish production. Prog. Oceanogr. 49:257-282.

Loughlin, T.R. 1998. The Steller sea lion: A declining species. Biosph. Conserv. 1:91-98.

Lowe, S., J. Ianelli, H. Zenger, and R. Reuter. 2002. Stock assessment of Aleutian Islands Atka mackerel. In: Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. North Pacific Fishery Management Council, www.afsc.noaa.gov/refm/docs/2002/BSatka.pdf, pp. 609-668.

Merrick, R.L., M.K. Chumbley, and G.V. Byrd. 1997. Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: A potential relationship. Can. J. Fish. Aquat. Sci. 54:1342-1348.

NAS (ed.). 2003. Decline of the Steller sea lion in Alaskan waters: Untangling food webs and fishing nets. National Research Council, National Academy of Science, Washington, D.C.: National Academies Press. 204 pp.

Riemer, S.D., and R.F. Brown. 1997. Prey of pinnipeds at selected sites in Oregon identified by scat (fecal) analysis, 1983-1996. Oregon Department of Fish and Wildlife report no. 97-6-02.

Rosen, D.A.S., and A.W. Trites. 2000. Pollock and the decline of Steller sea lions: Testing the junk-food hypothesis. Can. J. Zool. 78:1243-1250.

Sinclair, E.H., and T.K. Zeppelin. 2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). J. Mammal. 83:973-990.

Spencer, P.D., and J.N. Ianelli. 2002. Pacific ocean perch. In: Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. North Pacific Fishery Management Council, www.afsc.noaa.gov/refm/docs/ 2002/BSpop.pdf, pp. 515-558.

Trites, A.W., and C.P. Donnelly. 2003. The decline of Steller sea lions *Eumetopias jubatus* in Alaska: A review of the nutritional stress hypothesis. Mamm. Rev. 33:3-28.

Trites, A.W., and P.A. Larkin. 1996. Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: How many were there? Aquat. Mamm. 22:153-166.

Trites, A.W., A.J. Miller, H.D.G. Maschner, M.A. Alexander, S.J. Bograd, J.A. Calder, A. Capotondi, K.O. Coyle, E. Di Lorenzo, B.P. Finney, E.J. Gregr, C.E. Grosch, S.R. Hare, G.L. Hunt, Jr., J. Jahncke, N.B. Kachel, H.-J. Kim, C. Ladd, N.J. Mantua, C. Marzban, W. Maslowski, R. Mendelssohn, D.J. Neilson, S.R. Okkonen, J.E. Overland, K.L. Reedy-Maschner, T.C. Royer, F.B. Schwing, J.X.L. Wang, and A.J. Winship. 2006. Bottom-up forcing and the decline of Steller sea lions in Alaska: Assessing the ocean climate hypothesis. Fish. Oceanogr.

Turnock, B.J., T.K. Wilderbuer, and E.S. Brown. 2001. Arrowtooth flounder. In: Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fishery Management Council, www.afsc.noaa.gov/refm/docs/ 2001/goaatf.pdf, pp. 4-1 to 4-29.

Watson, R., A. Kitchingman, A. Gelchu, and D. Pauly. 2004. Mapping global fisheries: Sharpening our focus. Fish Fish. 5:168-177. (www.seaaroundus.org/distribution/ search.aspx).

Wilderbuer, T.K., A.B. Hollowed, W.J. Ingraham Jr., P.D. Spencer, M.E. Connors, N.A. Bond, and G.E. Walters. 2002. Flatfish recruitment response to decadal climatic variability and ocean conditions in the eastern Bering Sea. Prog. Oceanogr. 55:235-247.

Temporal Variation in Steller Sea Lion Diet at a Seasonal Haul-Out in Southeast Alaska

Jamie N. Womble
NOAA National Marine Fisheries Service, Alaska Fisheries Science Center, Auke Bay Laboratory, Juneau, Alaska; and University of Alaska Fairbanks, School of Fisheries and Ocean Sciences, Juneau, Alaska

Michael F. Sigler
NOAA National Marine Fisheries Service, Alaska Fisheries Science Center, Auke Bay Laboratory, Juneau, Alaska

Abstract

Pinniped diet may vary spatially and temporally and can be influenced by prey availability. Several prey species of Steller sea lions are densely aggregated during the nonbreeding season of sea lions and may be seasonally important because sea lion energetic requirements increase during winter and spring. To assess temporal variation in Steller sea lion diet at Benjamin Island in Lynn Canal, Southeast Alaska, we collected scat samples ($n = 787$) each February, April, October, and December from 2001 to 2004. Scat samples were not collected during summer because few sea lions were present at Benjamin Island during that season. Pacific herring (frequency of occurrence [FO] = 90.0%) and walleye pollock (FO = 87.5%) were the two most common prey species in sea lion scat samples, followed by skate, Pacific salmon, Pacific cod, capelin, cephalopods, northern lampfish, sculpins, arrowtooth flounder, eulachon, and Pacific hake. The FO of herring, pollock, skates, Pacific cod, and cephalopods did not differ significantly between seasons; however, the FO of capelin, Pacific salmon, northern lampfish, sculpins, arrowtooth flounder, eulachon, and Pacific hake differed between seasons. Sea lion diet diversity increased in spring and corresponded to the spawning season of several forage fish species. Exploiting salmon in fall, herring during winter, and eulachon, capelin, and northern lampfish in spring likely helps sea lions meet the increased energetic demands that occur during winter and spring.

Introduction

Pinniped diet may vary spatially and temporally (Pierce and Boyle 1991, Pierce et al. 1991, Tollit and Thompson 1996, Browne et al. 2002, Lake et al. 2003, Hume et al. 2004) and can be influenced by the distribution and abundance of prey (Thompson et al. 1991, Tollit et al. 1997, Hall et al. 1998, Harcourt et al. 2002). Prey distribution and abundance are seasonally dynamic; thus in order to identify temporal changes in prey exploitation, diet sampling should be conducted frequently enough to reflect changes in prey availability.

Steller sea lions (*Eumetopias jubatus*) are generalist predators that consume a wide variety of prey species and diet composition can vary considerably between areas (Merrick et al. 1997, Sinclair and Zeppelin 2002). Variation in prey consumption patterns suggests that Steller sea lions forage on seasonally abundant and densely aggregated prey species (Sinclair and Zeppelin 2002); however, several of these prey species are only aggregated for brief periods during their spawning seasons. Therefore seasonally aggregated prey species may not be detected in sea lion diet if diet sampling only occurs infrequently.

Detecting seasonally available prey species in sea lion diet is important for several reasons. First, seasonally available prey species can influence the distribution (Sigler et al. 2004, Womble et al. 2005), foraging methods (Gende et al. 2001), and at-sea and dive behavior of sea lions (Raum-Suryan et al. 2004, Pitcher et al. 2005). Second, the energetic content of sea lion prey species can vary seasonally (Anthony et al. 2000, Iverson et al. 2002, Vollenweider 2005), thus making some species more energetically rewarding than others during certain seasons. Third, energetic demands for individual sea lions vary seasonally and are highest during winter and spring (Winship et al. 2002, Winship and Trites 2003), thus determining prey species that are exploited by sea lions during those seasons is critical.

To address the importance of seasonally available prey species in the diet of Steller sea lions, we focused on Benjamin Island, a terrestrial site that is seasonally occupied by Steller sea lions in Southeast Alaska. Our objective was to assess the temporal variability in the diet of Steller sea lions during the nonbreeding season at Benjamin Island. Specifically we investigated the following hypotheses:

1. The frequency of occurrence of prey species in Steller sea lion diet differs among seasons, and

2. The diet diversity of Steller sea lions differs among seasons.

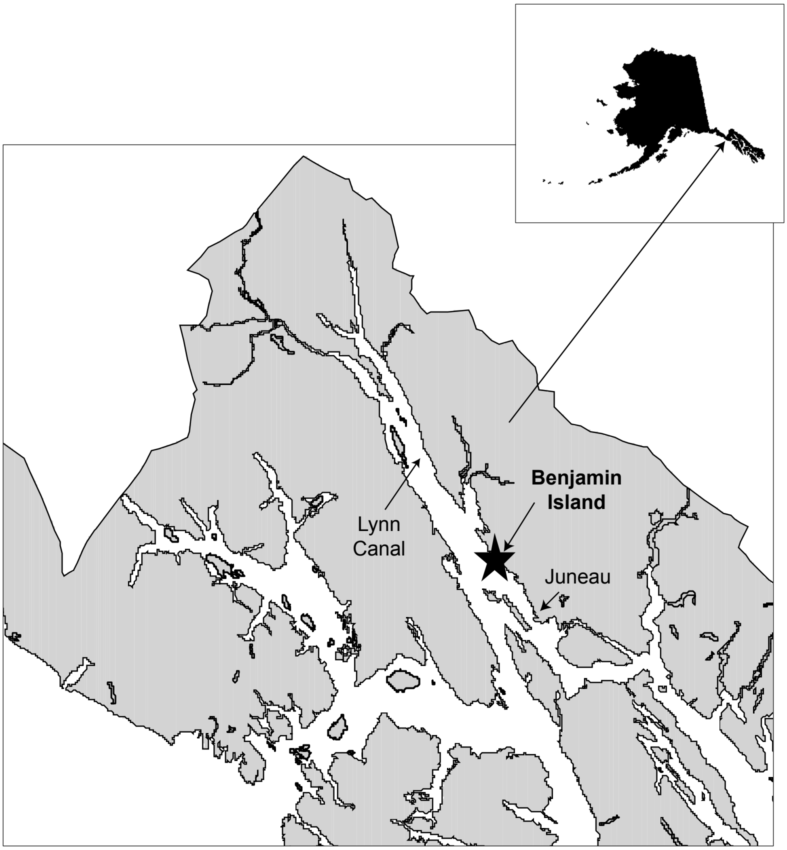


Figure 1. Location of Benjamin Island (58°33.7N, 134°54.8W), a seasonal Steller sea lion haul-out in Lynn Canal, Southeast Alaska.

Materials and methods

Benjamin Island (58°33.7N, 134°54.8W) is located in Lynn Canal, Southeast Alaska (Fig. 1) and is typically occupied from October to June by up to 800 Steller sea lions. Benjamin Island is occupied by adult males, adult females with dependent young, and juvenile sea lions. A total of 787 sea lion scat samples were collected from 2001 to 2004. Scat samples were collected in 2001 ($n = 252$), 2002 ($n = 213$), 2003 ($n = 213$), and 2004 ($n = 109$). To assess the seasonal use of prey by sea lions, scat samples were collected four times per year during February ($n = 210$), April ($n = 207$), October ($n = 205$), and December ($n = 165$). During 2004, scat samples were only collected in February and April. Samples were not collected during the breeding season, as Benjamin Island is not typically used by sea lions at that time.

We collected only fresh fecal samples that had obviously originated from one animal. Samples were collected with a spoon, stored individually in plastic bags, and frozen until processing. Each sample was thawed in water and washed through an elutriator (Bigg and Olesiuk 1990) or a 0.495 mm sieve. All prey remains (fish bones, otoliths, cartilaginous parts, lenses, teeth, cephalopods beaks, lenses, and pens) were recovered, dried, and stored in petri dishes. Using a reference collection prey remains were identified to the lowest possible taxon by Pacific Identifications Inc., Victoria, British Columbia. The all-structures identification technique was to identify all skeletal fragments and other hard parts to account for prey with completely digested otoliths or prey that might not be otherwise represented by otoliths (Olesiuk et al. 1990, Lance et al. 2001, Browne et al. 2002).

Relative importance of each prey species was based on frequency of occurrence (FO). Percentage FO was calculated by dividing the number of scats in which a prey item occurred by the total number of scats that contained identifiable prey remains and multiplying by 100% (Lance et al. 2001). Samples were pooled for FO calculations across seasons (Feb., Apr., Oct., and Dec.) and years (2001, 2002, and 2003). FO is an index of presence or absence of a prey species in a scat sample and is a measure of the proportion of time a certain species is consumed (Lance et al. 2001). FO does not provide insight into the quantity or mass of prey that was consumed; however, with large sample sizes the FO of prey species is equal to the numerical rank of each prey species (Sinclair et al. 1994, Antonelis et al. 1997). Only prey species that occurred in at least 5% of scat samples across years were reported.

Chi-square analysis was used to test for differences in FO of prey species in scat samples between seasons from 2001 to 2003. The analysis was limited to prey items occurring in at least 5% of scats across years. Diet diversity was calculated for each year and each season using Shannon's index of diversity (H) where p_i is the proportion of the ith species in the sample (Zar 1984).

$$H = -\sum_{i=1}^{k} p_i \ln p_i$$

Results

A total of 56 prey items were identified from sea lion scat samples from Benjamin Island (2001-2004); however, only 12 species occurred in at least 5% of scat samples across years. The two most common prey species were Pacific herring (*Clupea pallasii*, FO = 90.0%) and walleye pollock (*Theragra chalcogramma*, FO = 87.5%) in all years. Herring and pollock

Table 1. Frequency of occurrence (FO) of prey species in sea lion scat samples from Benjamin Island by year. Only prey species that occur in at least 5% or greater of scat samples across years are shown here.

Prey item	2001-2004 FO (%)	2001 FO (%)	2002 FO (%)	2003 FO (%)	2004 FO (%)
N	787	252	213	213	109
Pacific herring	90.0	92.1	88.3	85.9	96.3
Walleye pollock	87.5	84.5	86.9	90.1	90.8
Skate (*Raja* sp.)	19.4	19.4	21.6	15.5	22.9
Pacific cod	17.5	13.9	18.8	16.4	25.7
Capelin	17.2	14.3	16.0	15.0	30.3
Pacific salmon	15.6	19.8	16.0	12.2	11.9
Cephalopods	13.9	10.7	16.4	11.3	21.1
Northern lampfish	12.1	6.0	22.1	9.9	11.0
Sculpins	9.9	7.9	12.7	8.5	11.9
Arrowtooth flounder	8.1	4.8	10.8	8.0	11.0
Eulachon	8.0	4.0	16.4	6.1	4.6
Pacific hake	4.8	3.2	6.6	4.7	5.5

were followed in importance by skates (*Raja* sp., FO = 19.4%); Pacific cod (*Gadus macrocephalus*, FO = 17.5%); capelin (*Mallotus villosus*, FO = 17.2%); Pacific salmon (*Oncorhynchus* sp., FO = 15.6%); cephalopods (FO = 13.9%); northern lampfish (*Stenobrachius leucopsarus*, FO = 12.1%); sculpins (family Cottidae, FO = 9.9%); arrowtooth flounder (*Atheresthes stomias*, FO = 8.1%); eulachon (*Thaleichthys pacificus*, FO = 8.0 %); and Pacific hake (*Merluccius productus*, FO = 4.8 %) (Table 1). Other prey species occurred in less than 5% of the scat samples. Overall there was little inter-annual variation in the FO of the most common prey items; however, during 2002, the FO of northern lampfish and eulachon substantially increased compared to other years (Table 1).

Some prey species varied seasonally, whereas others did not (Table 2). The FO of capelin, salmon, northern lampfish, sculpins, arrowtooth flounder, eulachon, and Pacific hake differed significantly among seasons. In contrast, the FO of herring, pollock, skates, Pacific cod, and cephalopods did not differ among seasons (Table 3). The FO of herring ranged from 68.6% to 100% with the lowest FO occurring during April 2002 and 2003. The FO of pollock ranged from 71.9% to 92.7%. The FO of capelin was highest in April 2001 and 2004. The FO of eulachon increased in

Table 2. **Frequency of occurrence of prey species in sea lion scat samples by season, February, April, October, and December, 2001-2004.**

Prey item	Feb. 01	Apr. 01	Oct. 01	Dec. 01	Feb. 02	Apr. 02	Oct. 02	Dec. 02	Feb. 03	Apr. 03	Oct. 03	Dec. 03	Feb. 04	Apr. 04
N	50	47	98	57	53	54	53	53	53	51	54	55	54	55
Pacific herring	92.0	95.7	86.7	98.2	96.2	70.4	86.8	100.0	88.7	68.6	88.9	96.4	98.1	94.5
Walleye pollock	82.0	89.4	90.8	71.9	88.7	88.9	77.4	92.5	83.0	86.3	98.1	92.7	94.4	87.3
Skate (*Raja* sp.)	28.0	29.8	16.3	8.8	24.5	22.2	20.8	18.9	9.4	21.6	18.5	12.7	22.2	23.6
Pacific cod	4.0	34.0	11.2	10.5	13.2	24.1	18.9	18.9	22.6	11.8	13.0	18.2	16.7	34.5
Capelin	24.0	48.9	1.0	0	13.2	22.2	18.9	9.4	26.4	17.6	13.0	3.6	25.9	34.5
Pacific salmon	14.0	12.8	25.5	21.1	7.5	3.7	30.2	22.6	7.5	3.9	11.1	25.5	14.8	9.1
Cephalopods	4.0	19.1	14.3	3.5	11.3	24.1	13.2	17.0	11.3	5.9	13.0	14.5	24.1	18.2
Northern lampfish	10.0	12.8	3.1	1.8	5.7	37.0	18.9	26.4	9.4	11.8	11.1	7.3	5.6	16.4
Sculpins	4.0	4.3	9.2	12.3	5.7	22.2	5.7	17.0	5.7	13.7	7.4	7.3	11.1	12.7
Arrowtooth flounder	8.0	17.0	15.3	3.5	9.4	5.6	18.9	9.4	13.2	9.8	7.4	1.8	9.3	12.7
Eulachon	0	19.1	0	1.8	7.5	24.1	17.0	17.0	0	13.7	7.4	3.6	1.9	7.3
Pacific hake	2.0	0	5.1	3.5	7.5	0	1.9	17.0	13.2	2.0	1.9	1.8	5.6	5.5

Table 3. Difference in frequency of occurrence of prey in diet of Steller sea lions between February, April, October, and December, 2001-2003. Chi-square analysis was limited to prey items occurring in at least 5% of scat samples across years.

Prey item	χ^2	*P*
Pacific herring	4.03	0.26
Walleye pollock	0.29	0.96
Skate	5.00	0.17
Pacific cod	6.00	0.11
Capelin	42.00	<0.001
Pacific salmon	23.00	<0.001
Cephalopods	4.0	0.26
Northern lampfish	13.00	<0.005
Sculpins	7.85	<0.05
Arrowtooth flounder	16.00	<0.005
Eulachon	28.00	<0.001
Pacific hake	11.25	<0.025

$\chi^2_{0.05,3} = 7.815$

April and was highest in 2001 and 2002. The FO of northern lampfish was highest in April and December of 2002. The FO of salmon increased during October and December in all years. Pacific hake was highest in December 2002 and February 2003 (Table 2).

The average number of prey species per scat sample was 3.3 ± 2.1 (SD) and ranged from 1 to 13 species. Diet diversity was higher in 2002 ($H = 2.1$) than in 2001 ($H = 1.8$) and 2003 ($H = 1.8$). Seasonal diet diversity was slightly higher in February ($H = 1.9$) and April ($H = 2.1$) than in October ($H = 1.8$) and December ($H = 1.8$).

Discussion

Potential biases

Analysis of scat samples is the most widely used method to determine prey preferences of pinnipeds (Arim and Naya 2003); however, there are several biases associated with using scat samples to determine diet (da Silva and Neilson 1985, Pierce and Boyle 1991, Bowen 2000). Different types of prey pass through digestives tracts at different rates (Pierce and Boyle 1991, Bowen 2000, Orr and Harvey 2001, Tollit et al. 2003) and recovery rates of otoliths vary depending upon prey species. Prey species with smaller, more fragile otoliths can be underestimated if included in a diet with larger otoliths (da Silva and Neilson 1985, Dellinger and Trillmich 1988, Orr and Harvey 2001) and the degree of erosion during the digestive process can be species and size specific (Bowen 2000). Activity rates and meal sizes can also influence passage rates and degree of erosion (Cottrell et al. 1996, Tollit et al. 1997, Bowen 2000, Tollit et al. 2003). However, scat samples are relatively easy to collect, involve a nondestructive sampling procedure, and can provide information regarding the presence of seasonally exploited prey species by pinnipeds if samples are collected frequently enough and if sufficient samples sizes are collected (Trites and Joy 2005).

Temporal variability in prey species

Some prey species differed seasonally in frequency of occurrence in sea lion scat, whereas others did not. Herring and pollock were the predominant prey species and corresponded to the most commonly detected species around Benjamin Island (M. Sigler and D. Csepp unpubl.). Scat samples were collected during the non-breeding season from October to April and correspond to the period when densely aggregated schools of overwintering herring move into areas around Benjamin Island (M. Sigler and D. Csepp unpubl.). Overwintering herring schools remain along the bottom, but at night they vertically migrate in the water column (Carlson 1980). Herring return to the same overwintering grounds year after year (Carlson 1980, M. Sigler and D. Csepp unpubl.) and thus are a seasonally predictable prey resource for sea lions during winter each year. Although herring was the predominant prey species in all seasons at Benjamin Island, the FO of herring was lowest in April 2002 and 2003.

The FO of pollock (87.5%) was only slightly less than that of herring (90.0%) and did not vary seasonally. Similar to diet studies conducted in other parts of the range of Steller sea lions, pollock was one of the predominant prey species in sea lion diet (Imler and Sarber 1947, Pitcher 1981, Merrick et al. 1997, Sinclair and Zeppelin 2002). Around Benjamin Island, pollock is available to sea lions throughout the year (M. Sigler, pers. obs.); however, when herring are densely aggregated in areas near Benjamin Island, herring may be more energetically rewarding than pollock and may supplement the lower energetic content of pollock diet during winter, which is estimated to be an energetically demanding time for sea lions (Winship et al. 2002). Furthermore, a mixed diet of pollock and herring may confer benefits over a single-species diet. Trumble and Castellini (2005) documented increased digestible energy intake in harbor seals fed a mixed diet of pollock and herring rather than a single-species diet of only pollock or only herring.

Pollock may be overestimated in Steller sea lion diet because recovery rates for pollock in the scat of captive Steller sea lions ranged from 22 to 156%, whereas herring recovery rates ranged from 15 to 60% (Tollit et al. 2003). Cottrell and Trites (2002) found that on average the number of pollock hard parts recovered from the scat of captive sea lions was 31.2 per pollock, in contrast to only 7.9 per herring. In addition, passage rates are higher for pollock than herring, which may tend to overestimate pollock and underestimate herring in sea lion diet (Tollit et al. 2003). Pollock typically have larger, more robust otoliths than herring and are able to withstand the digestive process better than the smaller otoliths of herring.

Capelin was present in 48.9% of the scat samples in April 2001 and in 34.5% in April 2004. Capelin has been reported spawning in several locations in Lynn Canal in spring. In Prince William Sound, capelin was primarily consumed by sea lions in spring and summer (Pitcher 1981). Prior to the 1970s, capelin was an important part of sea lion diet in the Gulf of Alaska and Unimak Pass (Fiscus and Baines 1966, Pitcher 1981); however, capelin was infrequent in scat samples of western stock sea lions collected from 1990 to 1998 (Sinclair and Zeppelin 2002). With some exceptions (Pahlke 1985), there have been few directed studies on capelin in Alaska, although it is an important forage species for many marine birds and mammals and deserves further attention (Brown 2002).

In all years, eulachon FO was greatest in April with the highest FO of eulachon occurring in April 2002, and corresponding with higher biomass estimates of pre-spawning eulachon in nearby Berners Bay compared to 2003 (Sigler et al. 2004). Eulachon are high in lipid content (Payne et al. 1999, Anthony et al. 2000, Iverson et al. 2002, Vollenweider 2005) and spawn from March until May in southeastern Alaska. Sea lions aggregate at several eulachon spawning sites in southeastern Alaska (Womble et al. 2005), and the distribution and abundance of eulachon influences the distribution (Sigler et al. 2004), diet, and feeding strategies (Gende et al. 2001) of sea lions. Yet previous diet studies (Fiscus and Baines 1966, Pitcher 1981, Merrick et al. 1997, Calkins 1998, Sinclair and Zeppelin 2002) indicate that eulachon is not a common prey species for sea lions. Given the ephemeral nature of eulachon it is possible for the presence of eulachon in sea lion diet to go undetected if scat collections do not correspond to eulachon spawn timing in specific areas. In addition, sea lions raft up at eulachon spawning sites and defecate in the water instead of at the haul-out (Womble et al. 2005). Prey species, such as eulachon, that may be of only minor importance throughout the range of Steller sea lions, could be very important in particular regions for Steller sea lions.

Northern lampfish also increased in importance during spring with a particularly dramatic increase in April 2002. Northern lampfish have one of the highest lipid contents (Van Pelt et al. 1997, Anthony et al. 2000) of any sea lion prey species and are one of the most abundant species in the mesopelagic zone of the Gulf of Alaska (Purcell 1996). Typically they inhabit depths of 300-600 m during the day with vertical migrations to 50 m at night (Frost and McCrone 1979). Northern lampfish are common in deepwater north and east of Benjamin Island. In Glacier Bay in southeastern Alaska, northern lampfish have been found as shallow as 10-15 m during the day (Abookire et al. 2002).

Pacific salmon, another seasonally available prey species, increased in frequency of occurrence in October and December, coincident with the run timing of fall salmon (*Oncorhynchus* sp.) (Salo 1991). During fall and early winter (September to December) fall spawning coho salmon (*Oncorhynchus kisutch*) and chum salmon (*Oncorhynchus keta*) are returning to rivers in Lynn Canal and are available to sea lions as high-energy prey (Cline 1982, Bugliosi 1988). In Prince William Sound and in the western stock of sea lions, salmon were consumed primarily in summer, likely reflecting the spawning period of salmon in those areas (Pitcher 1981, Merrick et al. 1997, Sinclair and Zeppelin 2002).

Diet diversity

Increased diet diversity in spring corresponds with high energetic demands for female Steller sea lions (Winship et al. 2002) that are nursing a dependent pup and carrying a developing fetus. Spring is also an energetically demanding time for males as they prepare for extended fasting during the breeding season. Increased diet diversity in April was influenced by the presence of small schooling fish species including eulachon, capelin, and northern lampfish in sea lion diet. Increases in eulachon and capelin in spring were likely due to the availability of densely aggregated pre-spawning schools as both species spawn in nearshore areas in Lynn Canal in April and May. In the western stock, the diet diversity of Steller sea lions was highest in the areas with greatest population stability (Merrick et al. 1997, Sinclair and Zeppelin 2002, Sinclair et al. 2005) suggesting that sea lions need a diverse array of prey species available.

Implications

Our study has demonstrated that there is temporal variation in the diet of sea lions at Benjamin Island. Several of the prey species that are seasonally exploited by sea lions at Benjamin Island are those that are densely aggregated for short time periods each year, during spawning seasons. Given that the energetic demands are highest for sea lions in winter and spring (Winship et al. 2002), these densely aggregated seasonal prey resources around Benjamin Island may be more efficient to exploit than more solitary prey species. Exploiting salmon in fall, herring during winter, and eulachon, capelin, and northern lampfish in spring likely helps sea lions meet the increased energetic demands that occur during winter and spring.

Ultimately, exploitation of densely aggregated, seasonally available prey species may have fitness consequences for Steller sea lions. Future work aimed at combining biomass reconstruction techniques with the seasonal energy content of prey, to estimate the proportion of energy consumed by Steller sea lions by prey species, will further our understanding of sea lion bioenergetics. Furthermore, understanding changes in seasonal exploitation of prey species by Steller sea lions is important as it can reflect changes in prey availability and may signal changing ecosystem conditions.

Acknowledgments

We thank P. Ord (F/V *Williwaw*) for safe passage to Benjamin Island. K. Blejwas, D. Csepp, M. Kunnasranta, J. Scott-Ashe, K. Smikrud, J. Vollenweider, K. White, and numerous volunteers assisted in data collection and logistical support. S. Crockford (Pacific Identifications) and P. Cottrell (Seal Research) provided expertise in prey remains identification and processing. J.N.W. was supported by a Rasmuson Fisheries Research Fellowship during part of the study. This study was carried out under MMPA/ESA Permit No. 782-1532-02.

References

Abookire, A.A., J.F. Piatt, and S.G. Speckman. 2002. A nearsurface, daytime occurrence of two mesopelagic fish species (*Stenobrachius leucopsarus* and *Leuroglossus schmidti*) in a glacial fiord. Fish. Bull. U.S. 100:376-380.

Anthony, J.A., D.D. Roby, and K.R. Turco. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. J. Exp. Mar. Biol. 248:53-78.

Antonelis, G.A., E.H. Sinclair, R.R. Ream, and B.W. Robson. 1997. Inter-island variation in the diet of female northern fur seals (*Callorhinus ursinus*) in the Bering Sea. J. Zool. (Lond.) 242:435-451.

Arim, M., and D.E. Naya. 2003. Pinniped diets inferred from scats: Analysis of biases in prey occurrence. Can. J. Zool. 81:67-73.

Bigg, M.A., and P.F. Olesiuk. 1990. An enclosed elutriator for processing marine mammal scats. Mar. Mamm. Sci. 6:350-355.

Bowen, W.D. 2000. Reconstruction of pinniped diets: Accounting for complete digestion of otoliths and cephalopod beaks. Can. J. Fish. Aquat. Sci. 57:898-905.

Brown, E.D. 2002. Life history, distribution, and size structure of Pacific capelin in Prince William Sound and northern Gulf of Alaska. ICES J. Mar. Sci. 59:983-996.

Browne, P., J. Laake, and R.L. De Long. 2002. Improving pinniped diet analyses through identification of multiple skeletal structures in fecal samples. Fish. Bull. U.S. 100:423-433.

Bugliosi, E.F. 1988. Hydrologic reconnaissance of the Chilkat River basin, Southeast Alaska with special reference to the Alaska Chilkat Bald Eagle Preserve. U.S. Geological Survey Water Resources Investigations Report 88-4023, Anchorage.

Calkins, D.G. 1998. Prey of Steller sea lions in the Bering Sea. Biosphere Conserv. 1:33-44.

Carlson, H.R. 1980. Seasonal distribution and environment of Pacific herring near Auke Bay, Lynn Canal, Southeastern Alaska. Trans. Am. Fish. Soc. 109:71-78.

Cline, D. 1982. Council grounds of the eagles. Alaska Fish Tales and Game Trails. Winter, pp. 23-27.

Cottrell, P.E., and A.W. Trites. 2002. Classifying prey hard part structures recovered from fecal remains of captive Steller sea lions (*Eumetopias jubatus*). Mar. Mamm. Sci. 18:525-539.

Cottrell, P.E., A.W. Trites, and E.H. Miller. 1996. Assessing the use of hard parts in faeces to identify harbour seal prey: Results of captive feeding trials. Can. J. Zool. 74:875-880.

da Silva, J., and J.D. Neilson. 1985. Limitations of using otoliths recovered in scats to estimate prey consumption by seals. Can. J. Fish. Aquat. Sci. 42:1439-1442.

Dellinger, T., and F. Trillmich. 1988. Estimating diet composition from scat analysis in otariid seals (Otariidae): Is it reliable? Can J. Zool. 66:1865-1870.

Fiscus, C.H., and G.A. Baines. 1966. Food and feeding behavior of Steller and California sea lions. J. Mammal. 47:195-200.

Frost, B.W., and L.E. McCrone. 1979. Vertical distribution, diet vertical migration, and abundance of some mesopelagic fishes in the eastern subarctic Pacific Ocean in summer. Fish. Bull. U.S. 76:751-770.

Gende, S.M., J.N. Womble, M.F. Willson, and B.H. Marston. 2001. Cooperative foraging by Steller sea lions. Can. Field-Nat. 115:355-356.

Hall, A.J., J. Watkins, and P.S. Hammond. 1998. Seasonal variation in the diet of harbour seals in the south-western North Sea. Mar. Ecol. Prog. Ser. 170:269-281.

Harcourt, R.G., C.J.A. Bradshaw, K. Dickson, and L.L. Davis. 2002. Foraging ecology of a generalist predator, the female New Zealand fur seal. Mar. Ecol. Prog. Ser. 227:11-24.

Hume, F., M.A. Hindell, D. Pemberton, and R. Gales. 2004. Spatial and temporal variation in the diet of a high trophic level predator, the Australian fur seal (*Artocephalus pusillus doriferus*). Mar. Biol. 144:407-415.

Imler, R.H., and H.R. Sarber. 1947. Harbor seals and sea lions in Alaska. U.S. Fish and Wildlife Service, Spec. Sci. Rep. 28. 23 pp.

Iverson, S.J., K.J. Frost, and S.L.C. Lang. 2002. Fat content and fatty acid composition of forage fish and invertebrates in Prince William Sound, Alaska: Factors contributing to among and within species variability. Mar. Ecol. Prog. Ser. 241:161-181.

Lake, S., H. Burton, and J. Van den Hoff. 2003. Regional, temporal, and fine-scale spatial variation in Weddell seal diet at four coastal locations in east Antarctica. Mar. Ecol. Prog. Ser. 254:293-305.

Lance, M.M., A.J. Orr, S.D. Riemer, M.J. Weise, and J.L. Laake. 2001. Pinniped food habits and prey identification techniques protocol. NMFS Alaska Fisheries Science Center Processed Rep. 2001-04, Seattle. 36 pp.

Merrick, R.L., M.K. Chumbley, and G.V. Byrd. 1997. Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: A potential relationship. Can. J. Fish. Aquat. Sci. 54:1342-1348.

Olesiuk, P.F., M.A. Bigg, G.M. Ellis, S.J. Crockford, and R.J. Wigen. 1990. An assessment of the feeding habitats of harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia, based on scat analysis. Can. Tech. Rep. Fish. Aquat. Sci. 1730:1-135.

Orr, A.J., and Harvey, J.T. 2001. Quantifying errors associated with using fecal samples to determine the diet of the California sea lion (*Zalophus californianus*). Can. J. Zool. 79:1080-1087.

Pahlke, K.A. 1985. Life history and distribution of capelin, *Mallotus villosus*, in Alaskan waters. M.S. thesis, University of Alaska, Juneau.

Payne, S.A., B.A. Johnson, and R.S. Otto. 1999. Proximate composition of some north-eastern Pacific forage fishes. Fish. Oceanogr. 8:159-177.

Pierce, G.J., and P.R. Boyle. 1991. A review of the methods for diet analyses in piscivorous marine mammals. Oceanogr. Mar. Biol. Annu. Rev. 29:409-486.

Pierce, G.J., P.M. Thompson, A. Miller, J.S.W. Diack, D. Miller, and P.R. Boyle. 1991. Seasonal variation in the diet of common seals (*Phoca vitulina*) in the Moray Firth area of Scotland. J. Zool. (Lond.) 223:641-646.

Pitcher, K.W. 1981. Prey of the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska. Fish. Bull. U.S. 79:467-472.

Pitcher, K.W., M.J. Rehberg, G.W. Pendleton, K.L. Raum-Suryan, U.G. Swain, and M.F. Sigler. 2005. Ontogeny of dive performance of pup and juvenile Steller sea lions in Alaska. Can. J. Zool. 83:1214-1231.

Purcell, J. 1996. Mesopelagics. In: D. Paul, V. Christensen, and N. Hagan (eds.), Mass-balance models of northeastern Pacific ecosystems. Fisheries Center Research Report 4(1):23.

Raum-Suryan, K.L, M.J. Rehberg, G.W. Pendleton, K.W. Pitcher, and T.S. Gelatt. 2004. Development of dispersal, movement patterns, and haul-out use by pup and juvenile Steller sea lions (*Eumetopias jubatus*). Mar. Mamm. Sci. 20:823-850.

Salo, E.O. 1991. Life history of chum salmon (*Oncorhynchus keta*). In: C. Groot and L. Margolis (eds.), Pacific salmon life histories. University of British Columbia Press.

Sigler, M.F., J.N. Womble, and J.J. Vollenweider. 2004. Availability to Steller sea lions (*Eumetopias jubatus*) of a seasonal prey resource: A pre-spawning aggregation of eulachon (*Thaleichthys pacificus*). Can. J. Fish. Aquat. Sci. 61:1475-1484.

Sinclair, E.H., and T.K. Zeppelin. 2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). J. Mammal. 83 (4):973-990.

Sinclair, E.H., T. Loughlin, and W. Pearcy. 1994. Prey selection by northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea. Fish. Bull. U.S. 92:132-156.

Sinclair, E.H., S.E. Moore, N.A. Friday, T.K. Zeppelin, and J.M. Waite. 2005. Do patterns of Steller sea lion (*Eumetopias jubatus*) diet, population trend and cetacean occurrence reflect oceanographic domains from the Alaska Peninsula to the central Aleutian Islands? Fish. Oceanogr. 14 (Suppl. 1):223-242.

Thompson, P.M., G.J. Pierce, J.R.G. Hislop, D. Miller, and J.S.W. Diack. 1991. Winter foraging by common seals (*Phoca vitulina*) in relation to food availability in the inner Moray Firth, N.E. Scotland. J. Anim. Ecol. 60:283-294.

Tollit, D.J., and P.M. Thompson. 1996. Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland. Can. J. Zool. 74:1110-1121.

Tollit, D.J., S.P.R. Greenstreet, and P.M. Thompson. 1997. Prey selection by harbour seals, *Phoca vitulina*, in relation to variations in prey abundance. Can. J. Zool. 75:1508-1518.

Tollit, D.J., M. Wong, A.J. Winship, D.A.S. Rosen, and A.W. Trites. 2003. Quantifying errors associated with using prey skeletal structures from fecal samples to determine the diet of Steller sea lion (*Eumetopias jubatus*). Mar. Mamm. Sci. 19:724-744.

Trites, A.W., and R. Joy. 2005. Dietary analysis from fecal samples: How many scats are enough? J. Mammal. 86:704-712.

Trumble, S.J., and M.A. Castellini. 2005. Diet mixing in aquatic carnivore, the harbour seal. Can. J. Zool. 83:851-859.

Van Pelt, T.I., J.F. Piatt, B.K. Lance, and D.D. Roby. 1997. Proximate composition and energy density of some North Pacific forage fishes. Comp. Biochem. Physiol. 118A:1393-1398.

Vollenweider, J.J. 2005. Variability in Steller sea lion (*Eumetopias jubatus*) prey quality in southeastern Alaska. M.S. thesis, University of Alaska Fairbanks.

Winship, A.J., and A.W. Trites. 2003. Prey consumption of Steller sea lions (*Eumetopias jubatus*) off Alaska: How much prey do they require? Fish Bull. U.S. 101:147-167.

Winship, A.J., A.W. Trites, and D.A.S. Rosen. 2002. A bioenergetic model for estimating food requirements for Steller sea lions *Eumetopias jubatus* in Alaska, USA. Mar. Ecol. Prog. Ser. 229:291-312.

Womble, J.N., M.F. Willson, M.F. Sigler, B.P. Kelly, and G.R. Van Blaricom. 2005. Distribution of Steller sea lions *Eumetopias jubatus* in relation to spring-spawning fish species in southeastern Alaska. Mar. Ecol. Prog. Ser. 294:271-282.

Zar, J.H. 1984. Biostatistical analysis. 2nd edn. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Estimation of Seasonal Energy Content of Steller Sea Lion (*Eumetopias jubatus*) Diet

Johanna Vollenweider, Jamie Womble, and Ron Heintz
NOAA Fisheries, Auke Bay Lab, Juneau, Alaska

Abstract

We estimated the energy consumption of Steller sea lions (*Eumetopias jubatus*) in southeastern Alaska by integrating seasonal scat collection data with seasonal energy content of prey species of Steller sea lions. During 2001 and 2002, sea lion scat samples were collected quarterly at Benjamin Island in conjunction with quarterly collections of sea lion prey species from mid-water trawls near Benjamin Island. The biomass of prey species was reconstructed using biomass-variable (BV) and biomass-fixed (BF) techniques, and combined with prey energy content to estimate the amount of energy from each prey species during each season. Energy content of scats was variable across seasons and was lowest in February of both years and highest in December. A total of 41 prey species were identified from scat samples; however, the BV and BF models identified only five prey as constituting the majority of energy in sea lion scats. The five primary prey include salmon (*Oncorhynchus* sp.), skate (Rajidae), Pacific cod (*Gadus macrocephalus*), Pacific herring (*Clupea pallasii*), and walleye pollock (*Theragra chalcogramma*). These prey accounted for 91% of the total energy in the BV model and 84% in the BF model. Both models depicted similar seasonal trends in prey-derived energy, likely related to ephemeral prey aggregations associated with spawning or overwintering. In the BV model the primary prey species contributed relatively equal proportions of energy, with the exception of mature pollock. In contrast, herring was the predominant energy source in the BF model. The relative importance of prey types resulting from BV and BF models were more similar to each other than to raw biomass estimates or frequency of occurrence. Likely the true prey-derived energy is intermediate to the two models due to opposing inherent biases of each model.

Introduction

A thorough understanding of pinniped diet has become particularly important in light of the significant declines of Steller sea lions (*Eumetopias jubatus*) during the past three decades in the North Pacific (Burkanov et al. 2003; Sease et al. 1993, 2001). Several hypotheses have been put forward to explain the decline; however, the nutritional stress hypothesis has received considerable attention (Castellini 1993, Loughlin and York 2000, Rosen and Trites 2000). At the onset of the declines, species composition in the North Pacific Ocean shifted from a previously diverse assemblage of energy-rich forage fish to one in which a few species of energy-poor groundfish predominated (Francis et al. 1998, Anderson and Piatt 1999, Hare and Mantua 2000). Sea lion diet reflected this change (Calkins and Goodwin 1988, Merrick and Calkins 1996, Merrick 1997). Subsequently captive feeding studies demonstrated an inadequacy of groundfish to meet sea lion nutritional requirements (Calkins et al. 2000; Rosen and Trites 2000, 2002). In order to effectively evaluate hypotheses related to nutritional stress of animals in the wild, however, it is necessary to have a more thorough understanding of the seasonal dynamics of sea lion diet and energy sources.

Of the numerous methods used to assess pinniped diet, including analysis of stomach contents, scat samples, fatty acids, and stable isotopes, the analysis of scat samples is the most widely used method to determine prey preferences of pinnipeds (Arim and Naya 2003). Although there are several biases associated with using scat samples to determine diet (da Silva and Neilson 1985, Pierce and Boyle 1991, Bowen 2000, Riemer and Lance 2001), scat samples are relatively easy to collect, involve a non-destructive sampling procedure, provide definitive species identification and quantitative estimates of number and size of prey (Lance et al. 2001, Riemer and Lance 2001), and can provide information regarding the presence of seasonally exploited prey species (Trites and Joy 2005).

Scat analysis data are typically reported as frequency of occurrence (FO) or split-sample frequency of occurrence (SSFO), both of which solely account for the presence or absence of prey taxa. However, understanding the energetic contribution of various prey species to pinniped diet is important given that both the energetic content of prey species (Robards et al. 1999, Kitts et al. 2004, Vollenweider 2005) and energetic requirement of pinnipeds can change seasonally (Winship et al. 2002). Recently, the utility of scat data has been expanded with the estimation of the minimum number of individuals (MNI) of each prey species consumed and subsequent biomass reconstruction by species (Brown et al. 2002, Laake et al. 2002). Our objectives were to extend the biological relevance of scat data to estimate energy acquisition of sea lions compared to their requirements by combining biomass reconstruction techniques with seasonal variability of prey energy (Lea et al. 2002). Specifically, we developed a bioenergetics model to estimate the proportion of species-derived energy in Steller sea lion diet. Results further the understanding of sea lion diet and bioenergetics in southeastern Alaska, providing a comparison for declining populations in the western region.

Materials and methods

Scat analysis

For the data used in this paper, Womble and Sigler (2006) have described the scat collection and analytical methods and provided frequency of occurrence values for these data. As described by Womble and Sigler (2006), sea lion fecal samples were collected four times per year during 2001 (n = 260) and 2002 (n = 220) from Benjamin Island, a Steller sea lion haul-out in Lynn Canal, southeastern Alaska (Fig. 1). Samples were collected during February, April, October, and December to determine the seasonal use of prey by sea lions. Samples were not collected during the breeding season, as Benjamin Island is not typically used by sea lions at that time.

All prey remains were identified to the lowest possible taxon by Pacific Identifications, Victoria, British Columbia. In the case that identification was discernable only to family, the most frequently observed species of the same family during the same scat collection was used as a proxy. Because the majority of cephalopods could not be identified beyond class, all octopus and squid were grouped together. In addition, because of the high proportion of walleye pollock (*Theragra chalcogramma*) in scat and their large size range, they were split into three ontogenetic groups, including young-of-the-year (YOY) (70-180 mm fork length), juvenile (110-380 mm), and mature pollock (290-668 mm) based on length frequencies from concurrent trawl surveys. When identification was not discernable to family, the scat was excluded from analysis.

Minimum number of individuals (MNI)

MNIs were calculated as the highest count of the same structure divided by the mean number of that structure per fish (Ringrose 1993). Asymmetrical paired structures were categorized as left- or right-sided and the side with the greatest number was used as the highest count. Structure size was also considered in the estimation of MNI. For example, if a scat contained one small left otolith and one large right otolith, the MNI was 2. For comparison, MNI was estimated using only otoliths and all structures.

We used recovery correction factors (RCFs) to account for complete digestion of bones (Tollit et al. 2003; Phillips 2005; D.J. Tollit, North Pacific Universities Marine Mammal Research Consortium, Vancouver, B.C., unpubl. data; S. Crockford, Pacific Identification, Victoria, B.C.,

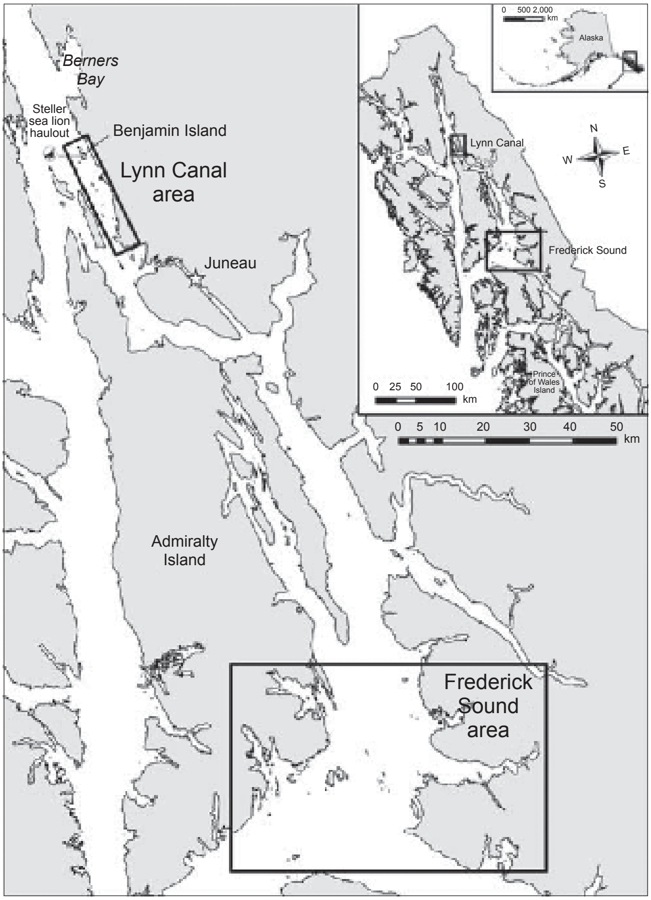


Figure 1. Map of study sites in southeastern Alaska, depicting Benjamin Island from which Steller sea lion scat was collected, and Lynn Canal and Frederick Sound water bodies from which prey were collected.

pers. comm.). If RCFs did not exist for a prey species, then an RCF from the most similar species was used (Table 1). We examined MNI based on otoliths alone, calculated with and without RCFs.

Prey size

Relative size classes of individual fish were estimated by Pacific Identifications based on the sizes of hard structures. We placed numerical values on these size classes by estimating quantitative sizes of prey using cor-

Table 1. Data sources for recovery correction factors (RCFs) and digestion correction factors (DCFs) used in biomass reconstruction estimates of Steller sea lion prey.

	RCF proxy	RCF source	DCF proxy	DCF source
Arrowtooth flounder	Arrowtooth flounder/flatfish sp.	3, 4	Rex sole	6
Capelin	Capelin	2	Capelin	5
Cephalopod sp.	Squid sp.	2	Market squid	5
Eulachon	Capelin	2, 3	Eulachon	5
Lumpsucker sp.	Cephalopod sp.	2	None	None
Northern lampfish	Capelin	3	None	None
Pacific cod	Walleye pollock (Mat)	2, 3	Pacific cod	5
Pacific hake	Walleye Pollock (Mat)	3, 4	None	None
Pacific herring	Pacific herring	2	Pacific herring	2
Rockfish sp.	Rockfish sp.	4	Shortspine thornyhead	6
Sablefish	Walleye pollock (Mat)	1, 2	Pacific cod	5
Salmon sp.	Salmon sp.	1, 2	Coho salmon	5
Sculpin sp.	Salmon sp.	3	Staghorn sculpin	6
Skate sp.	Salmon sp.	3	None	None
Walleye pollock (Juv)	Walleye pollock (Juv)	2	Walleye pollock	7
Walleye pollock (Mat)	Walleye pollock (Mat)	1, 2	Walleye pollock	7
Walleye pollock (YOY)	Walleye pollock (YOY)	1, 2	Walleye pollock	7

Prey listed are those indicated as being among the 15 most important from frequency of occurrence, biomass-variable, and biomass-fixed energy estimations. Proxy indicates an alternate species used when no correction factor could be found for a given species. Sources are (1) Tollit et al. 2003; (2) D.J. Tollit, North Pacific Universities Marine Mammal Research Consortium, Vancouver, B.C., unpubl. data; (3) S. Crockford, Pacific Identification, Victoria, B.C., pers. comm.; (4) Phillips 2005; (5) Orr and Harvey 2001; (6) Harvey 1989; (7) Tollit et al. 2004. Mat = mature, Juv = juvenile, YOY = young-of-the-year.

relations between otolith size and body size for the fish for which otoliths occurred in scats. Quantitative sizes were then extended to similar prey types of the same size class that were not represented by otoliths.

Size composition of prey was estimated using sagittal otoliths and cephalopod beaks based on the allometric relationship between fish size to otolith size and cephalopod size to beak size (Wolff 1982, Harvey et al. 2000). Otoliths were first graded by degree of digestion as being in good, fair, or poor condition (Reid and Arnould 1996, Tollit et al. 1997). Otoliths in good and fair condition were measured lengthwise to the nearest 0.01 mm using a dissecting microscope and digital calipers. Widths of chipped or broken otoliths were measured (Tollit et al. 1997). Otolith sizes were adjusted for partial digestion using condition-specific DCFs if available (Tollit et al. 1997; D.J. Tollit, North Pacific Universities Marine Mammal Research Consortium, Vancouver, B.C., unpubl. data); otherwise mean species-specific DCFs were applied (Harvey 1989, Orr and Harvey 2001). In the case that no DCFs were published for a species, DCFs of a similar species were used (Table 1). Hood lengths of upper cephalopod beaks and rostral lengths of lower beaks were measured (Wolff 1982). Beaks are not eroded significantly during digestion and thus no DCFs were applied to beak measurements (Tollit et al. 1997, Orr and Harvey 2001). Length and mass of prey were calculated from corrected otolith and beak sizes using allometric regressions (Wolff 1982, Harvey 1989, Harvey et al. 2000).

For several species, published allometric regressions did not exist; thus we used allometric regressions for similar species. If no otoliths existed for a prey species that was identified solely by other hard structures, size was estimated from size composition from concurrent trawl catch data (Table 2). The use of trawl data for prey size assumes no size selection by sea lions. In the case that allometric equations were missing in the literature, allometric equations were calculated from trawl catch data using methods of Harvey et al. (2000). If size could not be estimated by otolith measurements or trawl data, published size estimates of the species from the nearest location were used.

Seasonal energy content of prey

Energy content of prey was estimated according to methods outlined in Vollenweider (2005). Prey collections for energy content analyses were conducted in waters within 10 km of Benjamin Island haul-out and 45 km of haul-outs in Frederick Sound, located 160 km south in southeastern Alaska (Fig. 1). Energy content of prey was found to be statistically similar on this spatial scale, and energy content data were pooled among the sampling sites to increase sample size. Prey species included walleye pollock, Pacific herring (*Clupea pallasii*), eulachon (*Thaleichthys pacificus*), capelin (*Mallotus villosus*), and Pacific hake (*Merluccius productus*). Prey were collected on a quarterly schedule similar to the periods of scat collection (March, May, September, December of 2001 and 2002).

Energy content of prey was determined by calculation from the energy-containing proximate fractions of lipid and protein using energy equivalents of 36.43 kJ g^{-1} and 20.10 kJ g^{-1}, respectively. Carbohydrates

Table 2. Methods employed for estimation of Steller sea lion prey sizes used in biomass reconstruction.

	Size method	Proxy	Length source	Mass source
Arrowtooth flounder	Regression	Arrowtooth flounder	Harvey et al. 2000	Harvey et al. 2000
Capelin	Regression	Capelin	Harvey et al. 2000	Harvey et al. 2000
Cephalopod sp.	Regression	Squid sp./*Loligo opalescens*	Orchard 2001	Wolff 1982
Eulachon	Regression	Eulachon	Harvey et al. 2000	Harvey et al. 2000
Lumpsucker sp.	Trawl	n/a	n/a	n/a
Northern lampfish	Trawl	n/a	n/a	n/a
Pacific cod	Regression	Pacific cod	Orchard 2001	J.J. Vollenweider unpubl.
Pacific hake	Trawl	n/a	n/a	n/a
Pacific herring	Regression	Pacific herring	Harvey et al. 2000	Harvey et al. 2000
Rockfish sp.	Regression	*Sebastes* sp./shortspine thornyhead	Orchard 2001	Harvey et al. 2000
Sablefish	Regression	Sablefish	Harvey et al. 2000	Harvey et al. 2000
Salmon sp.	Regression	Coho salmon	Harvey et al. 2000	Harvey et al. 2000
Sculpin sp.	Literature	Great sculpin	n/a	Anthony et al. 2004
Skate sp.	Trawl	n/a	n/a	n/a
Walleye pollock (Juv)	Regression	Walleye pollock (Juv)	Tollit[a]	Harvey et al. 2000
Walleye pollock (Mat)	Regression	Walleye pollock (Mat)	Tollit[a]	Harvey et al. 2000
Walleye pollock (YOY)	Regression	Walleye pollock (YOY)	Tollit[a]	Harvey et al. 2000

[a] D.J. Tollit, North Pacific Universities Marine Mammal Research Consortium, Vancouver, B.C., unpubl. data.

Prey sizes were estimated (1) by calculation from otolith or beak size using allometric regressions, (2) from size availability in waters adjacent to Benjamin Island determined by trawling, and (3) from size estimates in the literature. Proxy indicates an alternate species used when no allometric regression could be found for a given species. Prey listed are those indicated among the 15 most important from frequency of occurrence, biomass-variable, and biomass-fixed energy estimations. Mat = mature, Juv = juvenile, YOY = young-of-the-year.

were considered negligible (Brett 1995, Vollenweider 2005). For those prey types that were not collected during trawl surveys, we used literature values of prey energy content (Stansby 1976, Perez 1994, Van Pelt et al. 1997, Worthy 1997, Payne et al. 1999, Anthony et al. 2000)

Prey species' energy contribution to diet

Biomass reconstruction based on hard part analysis of scat has numerous biases, many of which we corrected for in our models. Data for MNIs were based on identification of all hard parts rather than otoliths alone, a technique that is a significantly better estimator of consumption (Browne et al. 2002, Cottrell and Trites 2002, Tollit et al. 2003). In addition, we applied recovery correction factors (RCFs) to MNIs to account for the complete digestion of some skeletal structures, which significantly reduces the estimated number of prey consumed. RCFs have been estimated primarily for otoliths (Harvey 1989, Bowen 2000, Orr and Harvey 2001); however, there have been recent advances to develop RCFs for other bones (Cottrell and Trites 2002, Tollit et al. 2003) and all hard structures (Tollit et al. 2003; Phillips 2005; D.J. Tollit unpubl. data; S. Crockford, Pacific Identification, Victoria, B.C., pers. comm.). For size estimation of prey, we applied digestion correction factors (DCFs) to account for the partial erosion of hard parts which otherwise causes underestimation of prey sizes (Harvey 1989, Orr and Harvey 2001, Tollit et al. 1997).

We calculated prey-derived biomass using biomass-variable (BV) and biomass-fixed (BF) reconstruction for comparison using the described correction factors. BV calculations are based on the assumption that biomass represented by prey remains in each scat are variable, reflecting variable consumption of pinnipeds in the production of each scat (Laake et al. 2002). In contrast, BF calculations stem from the argument that factors other than variable consumption cause variation in reconstructed biomass (factors that influence digestion and deposition, or scat collection prejudices), and scats should are treated as samples of equal biomass consumed. Assumptions are extreme contrasts of each other, neither of which is likely entirely true. Thus, by comparing BV and BF biomass estimations with prey energy content, we hoped to find a solution intermediate to the two.

To estimate the total energy represented by a scat from each sampling period, we reconstructed prey biomass using the biomass-variable technique. For each scat, total biomass of each prey species was calculated as the minimum number of individuals corrected by RCFs times the mass of those individuals. Species biomass was then combined with seasonal energy content of prey to estimate total energy derived by each prey species in each scat. Species-specific energy was next summed over all scats from each scat collection period, and divided by the number of scats collected to produce an "average scat" representative of each sampling period.

Due to the assumptions of BF reconstruction, this estimator only provides proportional results rather than total energy values. Thus, to compare the two methods, we calculated the proportion of energy derived from each prey type using BV and BF techniques (Laake et al. 2002):

$$\text{BV} \qquad \hat{\pi}_i = \frac{\sum_{k=1}^{s}\left(\frac{b_{ik}}{\sum_{i=1}^{w} b_{ik}}\right)}{s} \qquad\qquad \text{BF} \qquad \hat{\pi}_i = \frac{b_i}{\sum_{i=1}^{w} b_i}$$

Where,

$\hat{\pi}_i$ = proportion of biomass represented by the ith prey type from w possible prey types

b_i = total biomass of species i; b_{ik} = total biomass of species i in the kth scat

s = number of scats from a collection period

Frequency of occurrence (FO) was calculated for comparison (Lance et al. 2001). Energy estimates from BV and BF models, biomass estimates from the two models, and FO results were compared by using least squares linear regression (Zar 1984) and the Spearman rank-order correlation coefficient (Siegel and Castellan 1988). Spearman's test is conducted after first ranking prey types in order of increasing importance (1 being the most important). Ranks of the different models (BV, BF, raw biomass, FO) were then tested for statistical differences.

A post hoc sensitivity analysis was conducted to evaluate the contribution of energy content by skate, which was indicated as one of the primary energy sources from both models, though considerably more so in the BV model. BV calculations tend to overestimate large prey, thus we tested the sensitivity of the model to skate size by reducing the mass of individual skates by 50% and 75% to examine BV model outputs.

Results

A total of 480 scats were collected, 455 of which contained prey remains. Sample sizes during each collection period ranged between 47-97 scats. Of the scats with prey remains, only 30% contained otoliths with a total of 798 otoliths recovered. Identification of prey using otoliths alone detected 16 prey types while the use of all hard parts detected 41 types. Furthermore, the use of all hard parts corrected by RCFs resulted in MNI estimates 2.4 times greater than estimates based on RCF-corrected otoliths alone and 10 times greater than MNI estimates based on otoliths uncorrected by RCFs.

Table 3. Frequency of occurrence of Steller sea lion prey (FO>5%) determined from hard part analysis of sea lion scats from Benjamin Island, southeastern Alaska (Womble and Sigler 2006).

		2001	2001				2002	2002			
	Overall	Mean	Feb	Apr	Oct	Dec	Mean	Feb	Apr	Oct	Dec
Pacific herring	91	93	91	96	88	98	90	96	72	90	100
Walleye pollock (Mat)	71	77	70	89	82	68	62	63	74	37	73
Walleye pollock (Juv)	50	37	21	26	52	48	63	56	64	71	63
Walleye pollock (YOY)	25	26	40	30	14	20	25	35	32	12	21
Skate sp.	21	21	28	30	16	9	22	23	23	22	19
Salmon sp.	18	18	13	13	25	21	16	8	4	31	23
Pacific cod	16	15	4	34	11	11	19	13	25	20	19
Capelin	16	19	26	49	1	0	16	13	23	20	8
Cephalopod sp.	14	11	4	19	16	4	17	15	23	14	17
Northern lampfish	14	7	11	13	3	2	23	6	38	20	27
Arrowtooth flounder	13	12	9	17	15	4	13	12	6	20	10
Eulachon	10	5	0	19	0	2	17	8	25	18	17
Sculpin sp.	6	7	2	2	5	9	12	6	19	4	2
Pacific hake	5	3	2	0	5	4	7	8	0	2	17

Mat = mature, Juv = juvenile, YOY = young-of-the-year.

Frequency of occurrence

A total of 41 prey types were identified in sea lion scat samples from Benjamin Island; however, only 14 species occurred in at least 5% of the scats across years. The two most common prey species were herring (2001 FO = 92.1.0 %; 2002 FO = 88.3) and pollock (2001 FO = 84.5.5 %; 2002 FO = 86.9 %) in all years (Womble and Sigler 2006) (Table 3). Some prey species varied seasonally, whereas other did not. The FO of capelin, salmon, northern lampfish, sculpins, arrowtooth flounder, eulachon, and Pacific hake differed seasonally (Womble and Sigler 2006). FO of juvenile pollock was highest in April and October, while YOY were greatest in February and April. Salmon FO peaked in October and December, and multiple other

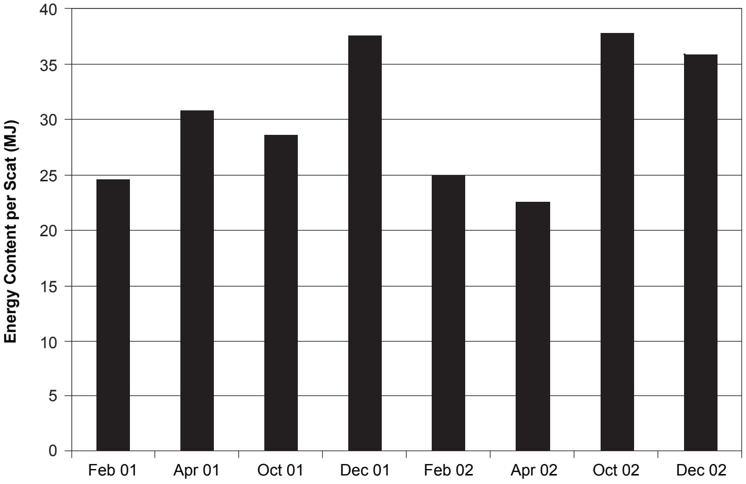


Figure 2. Proportion of prey-derived energy in Steller sea lion scat averaged over all collections in 2001 and 2002 estimated by the biomass-variable model.

taxa peaked in April, including Pacific cod, capelin, cephalopods, northern lampfish, and eulachon. Conversely, hake did not appear in scats in April, though they were present in all other months.

Energy content of scat (BV model)

Mean energy content of scat at Benjamin Island using the BV model (± s.d.) was 30.4±6.2 MJ. BV estimates of energy content were variable across seasons, ranging from 16.6 to 26.6 MJ (Fig. 2). Energy was similarly low in February of both years and high in December, while April and October were more variable between years. Only 4 of the 41 prey types found in scats contributed to the majority of the overall energy. Averaged across all sampling seasons, salmon, skate, herring, and Pacific cod accounted for 87% of the total energy. The addition of mature pollock subsequently accounted for 90% of the total energy, with all other prey types contributing <1.5% each (Table 4).

The model was robust to reductions in skate mass by 50% and 75%, skates remaining in the top five species in both circumstances. When biomass was decreased by 50%, skate-derived energy fell from 23.9% to 13.6%, making skates become the third most important energy source rather than the second. When skate biomass was reduced by an additional 50%, energy content was again cut in half to 7.3%, skates falling in importance to fourth place.

Model comparisons

Both the BV and BF models identified the same five prey types as constituting the majority of energy in sea lion scats, accounting for 91% and 84% of the total energy, respectively. These species included salmon, skate, herring, Pacific cod, and mature pollock (Table 4). Though mature pollock was one of the top five prey, it was relatively less important than the other four species in both models, contributing 3.6% of the total energy in the BV model and 11.3% in the BF model. The greatest discrepancy between the two approaches was that the BV model indicated that the other four of the top five prey types contributed relatively equal proportions of energy (~24% each), whereas the BF model showed a predominance of herring-derived energy (42% of the total energy). Furthermore, BF estimates of the proportion of energy contributed by the remaining prey were consistently greater than or equal to those estimated by the BV model with the exception of sculpin species.

BV and BF estimates of species-derived energy were not statistically different when all 41 prey types were included ($R^2 = 0.55$, $P < 0.001$) (Table 5). However, when comparisons of the models were limited to those species that contributed >1% of the total energy content in either model (n = 11), the two models became more disparate ($R^2 = 0.41$, $P > 0.05$).

Similar seasonal trends in scat energy were detected in both BF and BV models. During all months, herring was the greatest energy source in the BF model (Fig. 3). Herring-derived energy cycled seasonally, peaking in December in both years (56.5±12.0%, mean±s.d.) and decreasing to a minimum in April (24.2±6.1%). The BV model reflected the same seasonal fluctuations in herring derived energy with a peak in December (36.7±22.3%) and a minimum in April (13.5±0.7%), though herring was never the greatest source of energy (Fig. 4). In contrast, salmon and skate alternately provided the most energy in the BV model, salmon becoming the most important in October of both years (43.1±2.8%), and skate the most important in February and April (February = 33.1±4.5%, April = 31.7±0.8%). Similarly, the BF model showed coincident seasonal increases in salmon (21.1±2.6%) and skate (February = 15.6±3.5%, April = 14.8±2.6%). Pacific cod-derived energy also fluctuated seasonally, becoming most important in April in both models (BV = 23.5±0.7%, BF = 16.3±0.7%).

Models vs. FO

Both BF and BV models were correlated with FO when all 41 prey types were compared; however, BF was considerably more similar to FO ($R^2 = 0.71$) than BV was ($R^2 = 0.25$). Furthermore, the relative importance of prey types resulting from both models was not statistically different from FO ($P < 0.001$) (Table 5). However, when comparisons were limited to those species that either contributed ≥1% of the total energy or FO ≥5%,

Table 4. Species-derived energy consumed by Steller sea lions using biomass-variable and biomass-fixed reconstruction techniques.

	BV (%)	BF (%)
Salmon sp.	28.3	11.1
Skate sp.	24.0	11.5
Pacific herring	21.7	41.7
Pacific cod	13.2	8.4
Walleye pollock (Mat)	3.6	11.3
Cephalopod sp.	1.4	2.2
Sculpin sp.	1.4	1.2
Eulachon	1.0	2.4
Walleye pollock (Juv)	0.9	4.2
Lumpsucker sp.	0.8	1.1
Arrowtooth flounder	0.7	0.8
Pacific hake	0.5	1.1
Rockfish sp.	0.4	0.9
Dogfish	0.4	0.6
Sablefish	0.3	0.3
Walleye pollock (YOY)	0.3	0.7
Northern lampfish	0.2	0.6
Capelin	0.2	0.7
Greenling sp.	0.2	0.2
Rock sole	0.1	0.5
Starry flounder	0.1	0.4
Gunnel sp.	0.0	0.6
Cockscomb	0.0	0.4
Pacific sandfish	0.0	0.1
Sand sole	0.0	0.1
Pacific sand lance	0.0	0.1
Flathead sole	0.0	0.1
Irish lord sp.	0.0	0.1

Values are expressed as proportions of total energy consumed averaged over 4 seasons in 2001 and 2002. Mat = mature, Juv = juvenile, YOY = young-of-the-year.

Table 5. Relative importance of prey types in Steller sea lion diets indicated by different techniques, including biomass-variable (BV) energy estimation, biomass-fixed (BF) energy estimation, biomass, and frequency of occurrence (FO).

	BV	BF	Biomass	FO
Salmon sp.	1	4	1	6
Skate sp.	2	2	2	5
Pacific herring	3	1	4	1
Pacific cod	4	5	3	7
Walleye pollock (Mat)	5	3	5	2
Cephalopod sp.	6	8	9	9
Sculpin sp.	7	9	6	13
Eulachon	8	7	12	12
Walleye pollock (Juv)	9	6	11	3
Lumpsucker sp.	10	11	8	17
Arrowtooth flounder	11	13	14	11
Pacific hake	12	10	10	14
Rockfish sp.	13	12	13	15
Dogfish	14	16	18	31
Sablefish	15	22	16	27
Walleye pollock (YOY)	16	14	15	4
Northern lampfish	17	18	19	10
Capelin	18	15	7	8
Greenling sp.	19	23	17	25
Rock sole	20	19	21	26
Starry flounder	21	20	22	28
Pacific sandfish	22	24	20	18
Sand sole	23	25	25	39
Irish lord sp.	24	28	23	32
Gunnel sp.	25	17	24	19
Cockscomb	26	21	27	20
Eelpout sp.	27	34	28	22
Pacific sand lance	28	26	29	21
Flathead sole	29	27	30	24
Poacher sp.	30	29	31	23
Atka mackerel	31	35	32	36

Table 5. (continued.)

	BV	BF	Biomass	FO
Northern smoothtongue	32	31	33	33
3-Spine stickleback	33	36	34	29
Arctic shanny	34	33	35	30
Snailfish sp.	35	32	26	16
Searcher	36	38	38	35
Rex sole	37	41	37	34
Prowfish	38	39	39	38
Slender sole	39	37	40	40
Tubesnout	40	30	41	41
Prickleback sp.	41	40	36	37

Prey types were ranked in order of increasing importance, 1 being the most important. The 10 most important prey are highlighted for each technique. Mat = mature, Juv = juvenile, YOY = young-of-the-year.

similarities between BF and FO declined ($R^2 = 0.65$, $P > 0.05$) while the BV model became disparate from FO ($R^2 = 0.06$, $P > 0.05$).

Discussion

Though we addressed many of the inherent biases associated with scat data in biomass reconstruction, several remained partially or completely unaccounted for due to a lack of quantifiable ways to resolve them. One such prejudice is the tendency for MNI estimates to underestimate the number of individual prey in a scat and consequently under-represent prey consumed in large numbers relative to those consumed in small numbers. This may have the effect of overemphasizing the importance some of the larger species such as salmon and skate, which appeared to contribute significant amounts of energy to sea lions in both models. Additionally, MNI biases may have also diminished the importance of herring, which were also indicated as a principal energy source. BV calculations further enhance the impartiality between small and large prey. By reducing skate size by significant amounts, we evaluated the robustness of the BV model. Despite reductions of 50% and 75%, skate still remained one of the primary energy sources in sea lion diet, though skate declined in terms of relative importance.

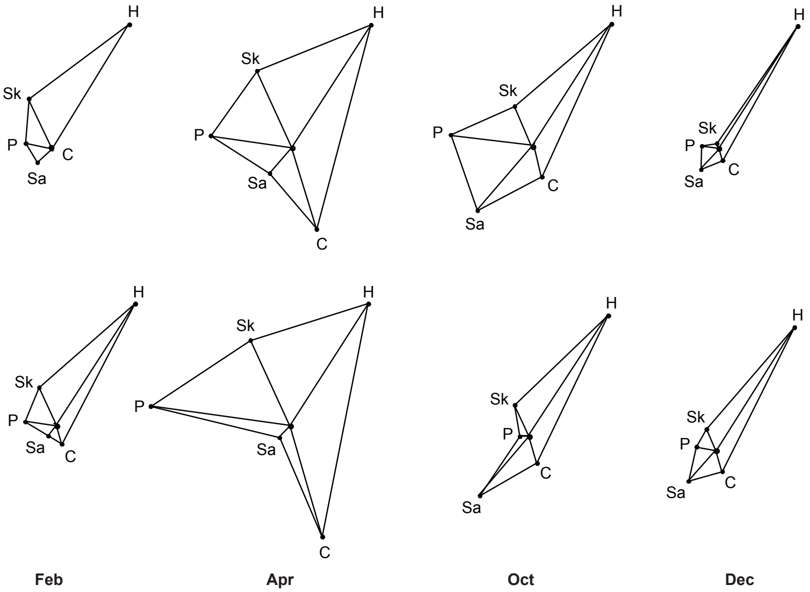


Figure 3. Proportion of prey-derived energy by the five most important prey types in Steller sea lion scat indicated by the biomass-fixed model. Star plots are interpreted by correlating the leg length of each prey type to its relative importance.

Additional biases remaining unaccounted for are the assumptions that the two biomass reconstruction models are based upon. The BV model allows each scat to represent variable biomass consumed, but does not account for variable digestion and deposition rates among sea lions due to factors such as activity level and age (Laake et al. 2001). In contrast, the BF model assumes each scat represents equal quantities of biomass consumed (Laake et al. 2001, Lance et al. 2001). Neither of the models' assumptions are representative of animals in the wild, and thus it is likely that the true energy consumption is intermediate to the two.

BV estimates of energy content of scats ranged from 16.6 to 26.6 MJ, falling within the low end of the range of Steller sea lion energy requirements which vary between 20 MJ d^{-1} for pups and 160 MJ d^{-1} for mature males (Winship et al. 2002). Sea lions in captivity fed ad libitum defecate 0-4 times per day (Tollit et al. 2003), thus inflation of scat energy by multiple daily scats provides estimates of energy consumption that are comparable to sea lion requirements. Seasonal trends in scat energy were apparent between years, with the tendency for scat energy to be high in December and low in February. Sea lion energy requirements are high-

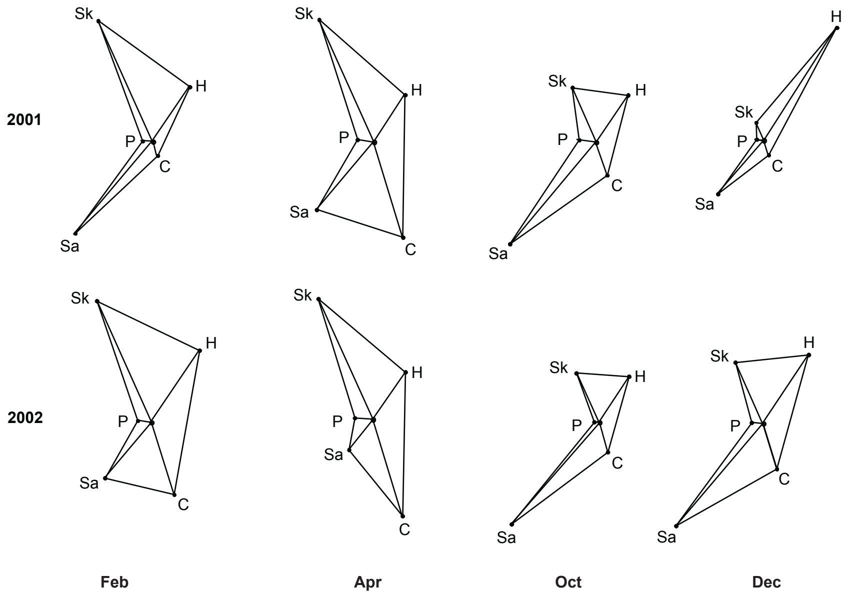


Figure 4. Proportion of prey-derived energy by the five most important prey types in Steller sea lion scat indicated by the biomass-variable model. Star plots are interpreted by correlating the leg length of each prey type to its relative importance.

est between December and May mainly due to seasonal activity budgets associated with reproduction (Winship et al. 2002), suggesting that late winter (February) may be the most energetically tenuous period for sea lions when energy demands are high yet acquisition is low based on these models.

Steller sea lions appear to be somewhat opportunistic in their feeding habits as evidenced by the large number of prey types they consume (n = 41) and the relatively high FO of these prey in the diet. Only five of these prey types contribute to the bulk of energy consumed, however, with the other 36 prey constituting minor amounts of energy. Both BV and BF estimates of prey-derived energy indicate the same five species as being the most important, including salmon, skate, herring, Pacific cod, and mature pollock. The models differ regarding the proportion of energy contributed by each species, however. Pooled over all collection periods, the BV model indicates that with the exception of mature pollock, the remaining four important species contribute nearly equal amounts of energy to sea lion diets while the BF model suggests herring provide nearly four times as much energy as the other top four species.

We tested the sensitivity of the model to skate size to evaluate the potential for overestimation of large prey. Despite reductions in skate size by 50% and 75%, skate remained among the five most important energy sources for sea lions. We believe this may be a factor of so few species contributing to the majority of the energy content in sea lion scats.

Seasonal changes in the derivation of sea lion dietary energy indicate that sea lions may rely on seasonally ephemeral aggregations of prey related to spawning and overwintering habits of the prey. These findings support previous studies that document the availability of seasonal prey aggregations for Steller sea lions in southeastern Alaska (Sigler et al. 2004, Womble et al. 2005). Model results indicate that sea lions forage heavily on spawning salmon in the fall, overwintering aggregations of herring in December, followed by Pacific cod spawning aggregations in the spring. Skate and mature pollock appear to be more of a supplemental energy source due to their consistency year-round.

Of the four methods used to assess relative importance of prey in sea lion diets (BV, BF, raw biomass, and FO), BV and BF models ranked prey in the most similar order of relative importance (Table 5). Relative importance of prey types ranked by raw biomass was less comparable to the models and FO was the most dissimilar to all other methods. These differences were detected primarily when comparisons were limited to the most important prey species, including those that contributed ≥1% of the total energy or ≥5% FO. Inclusion of all prey in model comparisons indicated the models were more similar. Thus, it appears the many species which appear to be of minor importance were leveraging the comparisons and diluting meaningful distinctions between the estimators.

The combination of all four techniques provides an illustrative way to examine sea lion diet and that of other pinnipeds. FO provides a measure of how often prey types are consumed, while biomass reconstruction integrates prey sizes, imparts information regarding size selection of prey, and may also potentially address other ecosystem related issues such as estimating biomass removal from the ecosystem by pinnipeds. The most important estimator in terms of pinniped nutrition and bioenergetics is the magnitude and origin of energy sources, which can potentially be interpolated from BV- and BF-derived energy estimates. With this information, researchers may be able to compare energy consumption of pinnipeds to their energy requirements to assess nutritional condition. Furthermore, periods when energy consumption and energy requirements are most disparate may help to identify potentially tenuous times for pinnipeds, as we did here.

References

Anderson, P.J., and J.F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar. Ecol. Prog. Ser. 189:117-123.

Anthony, J.A., D.D. Roby, and K.R. Turco. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. J. Exper. Mar. Biol. Ecol. 248:53-78.

Arim, M., and D.E. Naya. 2003. Pinniped diets inferred from scats: Analysis of biases in prey occurrence. Can. J. Zool. 81:67-73.

Bowen, W.D. 2000. Reconstruction of pinniped diets: Accounting for complete digestion of otoliths and cephalopod beaks. Can. J. Fish. Aquat. Sci. 57:898-905.

Brett, J.R. 1995. Energetics, Chapter 1. In: C. Groot, L. Margolis, and W.C. Clarke (eds.), Physiological ecology of Pacific salmon. UBC Press, Vancouver, British Columbia.

Browne, P., J.L. Laake, and R.L. Delong. 2002. Improving pinniped diet analyses through identification of multiple skeletal structures in fecal samples. Fish. Bull. U.S. 100:423-433.

Burkanov, V.N., D.G. Calkins, and T.R. Loughlin. 2003. Steller sea lion survey in the western Bering Sea and the Kamchatka Peninsula in 2002. Presented at: Marine science in the northeast Pacific: Science for resource dependent communities. Anchorage, Alaska. (Unpubl.) Abstract: www.afsc.noaa.gov/Stellers/symposium2003.htm.

Calkins, D.G., and E. Goodwin. 1988. Investigation of the declining sea lion population in the Gulf of Alaska. Alaska Department of Fish and Game, Anchorage.

Calkins, D.G., V. Burkanov, and M.A. Castellini. 2000. Steller sea lion feeding regime study. Annual Programmatic Research Report, Alaska SeaLife Center, Seward, Alaska.

Castellini, M. 1993. Report of the marine mammal working group. In: Is it food? Addressing marine mammal and sea bird declines. Alaska Sea Grant College Program, University of Alaska Fairbanks.

Cottrell, P.E., and A.W. Trites. 2002. Classifying prey hard part structures recovered from fecal remains of captive Steller sea lions (*Eumetopias jubatus*). Mar. Mamm. Sci. 18(2):525-539.

Da Silva, J., and J.D. Neilson. 1985. Limitations of using otoliths recovered in scats to estimate prey consumption by seals. Can. J. Fish. Aquat. Sci. 42:1439-1442.

Francis, R.C., S.R. Hare, A.B. Hollowed, and W.S. Wooster. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fish. Oceanogr. 7:1-21.

Hare, S.R., and N.J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog. Oceanogr. 47:103-145.

Harvey, J.T. 1989. Assessment of errors associated with harbour seal (*Phoca vitulina*) faecal sampling. Zool. Soc. London 219:101-111.

Harvey, J.T., T.R. Loughlin, M.A. Perez, and D.S. Oxman. 2000. Relationship between fish size and otolith length for 63 species of fishes from the eastern North Pacific Ocean. NOAA Tech. Rep. NMFS 150.

Kitts, D.D., M.D. Huynhl, C. Hu, and A.W. Trites. 2004. Season variation in nutrient composition of Alaskan walleye pollock. Can. J. Zool. 82:1408-1415.

Laake, J.L., P. Browne, R.L. DeLong, and H.R. Huber. 2002. Pinniped diet composition: A comparison of estimation models. Fish. Bull. U.S. 100:434-447.

Lance, M.M., A.J. Orr, S.D. Riemer, J.J. Weise, and J.L. Laake. 2001. Pinniped food habits and prey identification techniques protocol. NOAA, Alaska Fisheries Science Center Proc. Rep. 2001-04. 36 pp.

Lea, M.A., Y. Cherel, C. Guinet, and P.D. Nichols. 2002. Antarctic fur seals foraging in the polar frontal zone: Inter-annual shifts in diet as shown from fecal and fatty acid analyses. Mar. Ecol. Prog. Ser. 245:281-297.

Loughlin, T.R., and A.E. York. 2000. An accounting of the sources of Steller sea lion, *Eumetopias jubatus*, mortality. Mar. Fish. Rev. 62(4):40-51.

Merrick, R.L. 1997. Current and historical roles of apex predators in the Bering Sea ecosystem. J. Northwest Atl. Fish. Sci. 22:343-355.

Merrick, R.L., and D.G. Calkins. 1996. Importance of juvenile walleye pollock, *Theragra chalcogramma,* in the diet of Gulf of Alaska Steller sea lions, *Eumetopias jubatus.* In: R.D. Brodeur, P.A. Livingston, T.R. Loughlin, and A.B. Hollowed (eds.), Ecology of juvenile walleye pollock, *Theragra chalcogramma*. NOAA Tech. Rep. NMFS 126, pp.153-166.

Orchard, T.J. 2001. The role of selected fish species in Aleut paleodiet. M.A. thesis, University of Victoria, Canada.

Orr, A.J., and J.T. Harvey. 2001. Quantifying errors associated with using fecal samples to determine the diet of the California sea lion (*Zalophus californianus*). Can. J. Zool. 79:1080-1087.

Payne, S.A., A.B. Johnson, and R.S. Otto. 1999. Proximate composition of some north-eastern Pacific forage fish species. Fish. Oceanogr. 8:159-177.

Perez, M.A. 1994. Calorimetry measurements of energy value of some Alaskan fishes and squids. NOAA Tech. Memo. NMFS-AFSC-32.

Phillips, E. 2005. Biases associated with scat analysis of the Pacific harbor seal (*Phoca vitulina richardsii*). M.S. thesis, San Francisco State University.

Pierce, G.J., and P.R. Boyle. 1991. A review of the methods for diet analyses in piscivorous marine mammals. Oceanogr. Mar. Biol. Ann. Rev. 29:409-486.

Reid, K., and J.P.Y. Arnould. 1996. The diet of Antarctic fur seals *Arctocephalus gazelle* during the breeding season at South Georgia. Polar Biol. 16(2):105-114.

Riemer, S.D., and M.M. Lance. 2001. Pinniped prey identification and quantitative analysis workshop. December 4-6, 2000, Seattle, Washington. Oregon Department of Fish and Wildlife, Washington Department of Fish and Wildlife, and National Marine Fisheries Service. 44 pp.

Ringrose, T.J. 1993. Bone counts and statistics: A critique. J. Archaeol. Sci. 20:121-157.

Robards, M.D., J.A. Anthony, G.A. Rose, and J.F. Piatt. 1999. Changes in proximate composition and somatic energy content for Pacific sand lance (*Ammodytes hexapterus*) from Kachemak Bay, Alaska relative to maturity and season. J. Exper. Mar. Biol. Ecol. 241:245-258.

Rosen, D.A.S., and A.W. Trites. 2000. Pollock and the decline of Steller sea lions: Testing the junk food hypothesis. Can. J. Zool. 1978:1243-1250.

Rosen, D.A.S., and A.W. Trites. 2002. Changes in metabolism in response to fasting and food restriction in the Steller sea lion (*Eumetopias jubatus*). Comp. Biochem. Physiol. 132B:389-399.

Sease, J.L., W.P. Taylor, T.R. Loughlin, and K.W. Pitcher. 2001. Aerial and land-based surveys of Steller sea lions (*Eumetopias jubatus*) in Alaska, June and July 1999 and 2000. NOAA Tech. Memo. NMFS-AFSC-122. 52 pp.

Sease, J.L., J.P. Lewis, D.C. McAllister, R.L. Merrick, and S.M. Mello. 1993. Aerial and ship-based surveys of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska, the Gulf of Alaska, and Aleutian Islands during June and July 1992. NOAA Tech. Memo. NMFS F/NWC-17. 57 pp.

Siegel, S., and N.J. Castellan. 1988. Nonparametric statistics for the behavioral sciences. 2nd edn. McGraw-Hill, New York.

Sigler, M.F., J.N. Womble, and J.J. Vollenweider. 2004. Availability to Steller sea lions (*Eumetopias jubatus*) of a seasonal prey resource: a pre-spawning aggregation of eulachon (*Thaleichthys pacificus*). Can. J. Fish. Aquat. Sci. 61:1475-1484.

Stansby, M.E. 1976. Chemical characteristics of fish caught in the northeast Pacific Ocean. Mar. Fish. Rev. 38:1-11.

Tollit, D.J., S.G. Heaslip, and A.W. Trites. 2004. Sizes of walleye pollock (*Theragra chalcogramma*) consumed by the eastern stock of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska from 1994-1999. Fish. Bull. U.S. 102(3):522-532.

Tollit, D.J., M. Wong, A.J. Winship, D.A.S. Rosen, and A.W. Trites. 2003. Quantifying errors associated with using prey skeletal structures from fecal samples to determine the diet of Steller sea lion (*Eumetopias jubatus*). Mar. Mamm. Sci. 19(4):724-744.

Tollit, D.J., M.J. Steward, P.M. Thompson, G.J. Pierce, M.B. Santos, and S. Hughes. 1997. Species and size differences in the digestion of otoliths and beaks: Implications for estimates of pinniped diet composition. Can. J. Fish. Aquat. Sci. 54:105-119.

Trites, A.W., and R. Joy. 2005. Dietary analysis from fecal samples: How many scats are enough? J. Mammal. 86:704-712.

Van Pelt, T.I., J.F. Piatt, B.K. Lance, and D.D. Roby. 1997. Proximate composition and energy density of some north Pacific forage fishes. Comp. Biochem. Physiol. 118A:1393-1398.

Vollenweider, J.J. 2005. Variability in Steller sea lion (*Eumetopias jubatus*) prey quality in southeastern Alaska. M.S. thesis, University of Alaska Fairbanks, Juneau.

Winship, A.J., A.W. Trites, and D.A.S. Rosen. 2002. A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA. Mar. Ecol. Prog. Ser. 229:291-312.

Wolff, G.A. 1982. A beak key for an eastern tropical Pacific cephalopod species with relationships between their beak dimensions and size. NOAA Tech. Rep. NMFS 17. 59 pp.

Womble, J.N., and M.F. Sigler. 2006. Temporal variation in Steller sea lion diet at a seasonal haul-out in Southeast Alaska. In: A.W. Trites, S.K. Atkinson, D.P. DeMaster, L.W. Fritz, T.S. Gelatt, L.D. Rea, and K.M. Wynne (eds.), Sea lions of the world. Alaska Sea Grant College Program, University of Alaska Fairbanks.

Womble, J.N., M.F. Willson, M.F. Sigler, B.P. Kelly, and G.R. Van Blaricom. 2005. Distribution of Steller sea lions *Eumetopias jubatus* in relation to spring-spawning fish species in southeastern Alaska. Mar. Ecol. Prog. Ser. 294:271-282.

Worthy, G.A.J., and T.A. Miculka. 1997. Proximate composition and fatty acid signatures of selected forage fish species in Prince William Sound, Alaska. Exxon Valdez Oil Spill Restoration Project No. 95121 Final Report, NOAA, Seattle.

Zar, J.H. 1984. Biostatistical analysis. 2nd edn. Prentice-Hall, Englewood Cliffs, New Jersey.

Food Consumption by Sea Lions: Existing Data and Techniques

Arliss J. Winship, Andrea M.J. Hunter, David A.S. Rosen, and Andrew W. Trites
University of British Columbia, Marine Mammal Research Unit, Fisheries Center, and Department of Zoology, Vancouver, British Columbia, Canada

Abstract

Knowing the quantity of prey that sea lions consume is a prerequisite for assessing the role of sea lions in aquatic ecosystems and the potential for competition to occur with fisheries. We reviewed the different approaches that have been used to estimate the food requirements for the six species of sea lions. We reviewed data on the quantity of food consumed by sea lions in captivity, and examined how consumption varied by species, body size, and season. We also reviewed and quantified available information on the energetics of sea lions and assessed the potential application of these data to parameterize an existing bioenergetic model that was developed to estimate the food requirements of Steller sea lions. Our study provided ranges of estimates of food consumption for sea lions that can be used in various modeling strategies to assess the impact of sea lions on prey populations, including commercially exploited fish species. The approaches reviewed in our study shared common difficulties arising from the quantity and quality of data, and the integration of data across scales and species. Our modeling exercise, in particular, identified the major uncertainties involved in estimating the food requirements of each sea lion species using an energetics approach. Our results provide direction for future research aimed at improving the accuracy and comparability of estimates of food consumption for sea lions.

Introduction

The foraging ecology of marine mammals is often central to the research and management of their populations. Predator-prey and ecosystem models have been used to explore such topics as the effects of prey availability on the dynamics of marine mammal populations, the accumulation of toxins in food webs, and competition between marine mammals and fisheries. A key parameter in such models is the quantity of prey that individuals and populations consume. It is therefore important to have accurate and comparable estimates of marine mammal food consumption. It is also important to have measures of the uncertainty in these estimates.

The objective of our study was to review existing data on the food consumption of the six extant sea lion species, the Australian sea lion (*Neophoca cinerea*), California sea lion (*Zalophus californianus*), Galapagos sea lion (*Zalophus wollebaeki*), New Zealand sea lion (*Phocarctos hookeri*), South American sea lion (*Otaria flavescens*), and Steller sea lion (*Eumetopias jubatus*). Our study provided a framework for developing accurate and comparable estimates of food consumption by sea lions that can be used in predator-prey and ecosystem models. We also examined the major sources of uncertainty in estimates of food consumption and in doing so sought guidance for future research aimed at reducing this uncertainty.

Methods

We began by surveying the scientific literature for published predator-prey and ecosystem models that included one or more sea lion species. From these, we compiled the estimated amounts (mass) of food consumed by sea lions each day. We then surveyed the scientific literature for studies that documented original estimates of the amount of food consumed by sea lions, including wild and captive animals. Data that were only available from figures were estimated digitally from scanned images of the figures.

Next, we compiled information on the energetics, growth, and life histories of sea lions. These data were used to adapt an existing Steller sea lion bioenergetic model (Winship et al. 2002) to the other five sea lion species. The bioenergetic models were then used to predict the food requirements of individuals of the six sea lion species. Importantly, we noted the availability of data to parameterize the bioenergetic models highlighting the major uncertainties for each species. The predictions of the bioenergetic models were compared with the existing original estimates of sea lion food consumption.

Results

The estimates of sea lion food consumption that have been used in predator-prey and ecosystem models and analyses varied considerably, both across and within species (Fig. 1). These estimates ranged from point estimates of food biomass as a percentage of body mass to allometric equations that related energy or food consumption to body mass. The

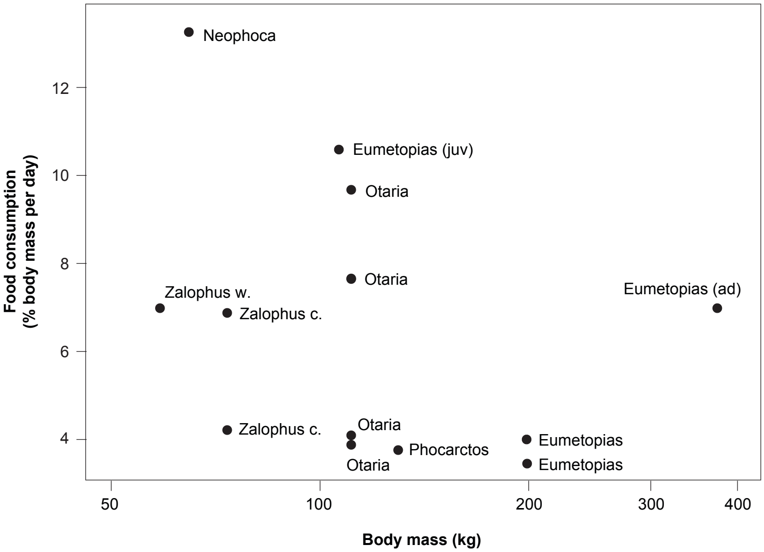


Figure 1. Estimates of food consumption by sea lions used in predator-prey and ecosystem models and analyses. Food consumption is plotted as the mass of food consumed by an individual animal per day as a percentage of body mass. Mean body masses from Trites and Pauly (1998) were used for illustrative purposes when estimates were not associated with a specific body mass. Sources were Muck and Fuentes (1987), Laevastu and Marasco (1991), Jarre-Teichmann (1992), Trites et al. (1997), Goldsworthy et al. (2003), Hückstädt and Antezana (2003), Arreguín-Sánchez et al. (2004), Neira et al. (2004), Okey et al. (2004), and Sylvie Guénette (2005).

minimum values were around 4% of body mass per day (e.g., Trites et al. 1997), while the maximum were 10-15% of body mass per day (e.g., animals <150 kg in Goldsworthy et al. 2003). The variability in these estimates was mainly due to (1) differences in the techniques used to estimate food consumption in the primary sources, and (2) differences in the factors considered to affect food consumption (e.g., age and/or mass).

Primary estimates of food consumption by sea lions were mainly derived from (1) food intake of captive animals, and (2) bioenergetic modeling. However, we also found estimates of food consumption based on body water turnover and mass of gut contents.

The amount of food consumed by sea lions in captivity (as a percent of body mass) was relatively consistent among California, South American, and Steller sea lions (Fig. 2, Table 1). The quantity of food consumed by Steller sea lions >50 kg in mass declined with body mass

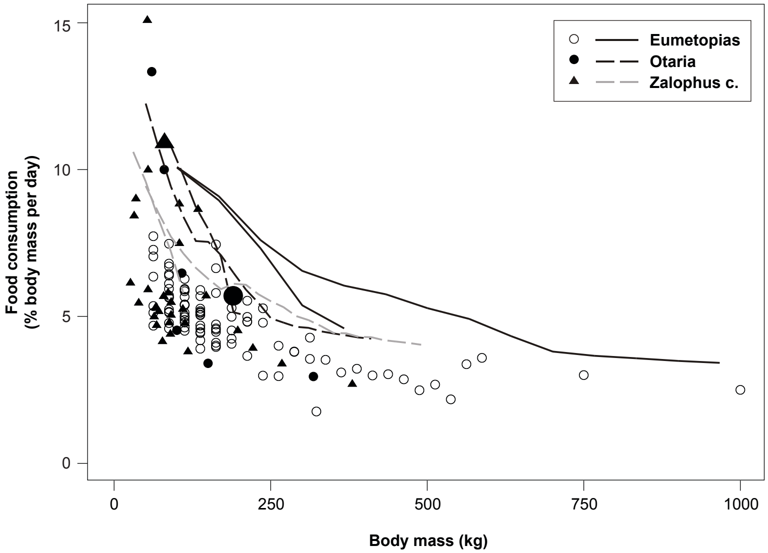


Figure 2. Primary estimates of food consumption by California, South American, and Steller sea lions. Points represent the measured food consumption of captive animals (sources: Innes et al. 1987; Perez et al. 1990; Fadely et al. 1994; Kastelein et al. 1995, 2000; D.A.S. Rosen and A.W. Trites unpubl. data). Captive data are a mix of longitudinal and cross-sectional point estimates and long-term averages for individual and groups of animals. Oversized points represent estimates of food consumption from water turnover (California sea lion—Costa et al. 1991) and gut contents (South American sea lion—George-Nascimento et al. 1985). Lines represent mean food requirements predicted by bioenergetic models assuming the energy content of food is 7 kJ g^{-1}. The upper line for each species represents males, and the lower line represents females.

from approximately 4-8% of body mass per day to 2-4% of body mass for the largest animals. California and South American sea lions consumed amounts of food similar to Steller sea lions, although values ≥10% were observed for smaller animals. The higher values may reflect the fact that the data for Steller sea lions were long term averages, while some of the data for the other species were from shorter periods of time, and thus reflected more variability due to factors such as the energy content of the diet (e.g., Fadely et al. 1994).

Season was an important factor that affected the amount of food consumed by captive sea lions. Captive Steller sea lions, especially adult

Table 1. Daily food consumption of sea lions in captivity (C) and predicted by bioenergetic models (M), as a percentage of body mass (BM in kg).

	Australian				California						Galapagos			
	Male		Female		Male			Female			Male		Female	
Age (years)	BM	M	BM	M	BM	C	M	BM	C	M	BM	M	BM	M
1-3	35-58	11-12	26-41	11-13	34-73	5-9	8-9	27-62	5-15	8-10	34-69	8-9	27-47	9-10
3-5	58-92	8-9	41-52	10	73-139	5-9	6-7	62-79	4-5	7	69-123	6-7	47-59	8
5-7	92-133	7-8	52-61	8-9	139-220	5-6	5-6	79-85	6	6-7	123-185	6	59-65	7
7-10	133-199	5-6	61-69	6-7	220-318	3-4	4-5	85-87	6	6	185-257	4-5	65-68	6
10-15	199-269	4-5	69-74	6	318-370	3	4	87-88	no data	6	257-296	4	68-70	6
15-20	–	–	74-76	6	–	–	–	88	4-5	6	–	–	70	6

	New Zealand				South American						Steller					
	Male		Female		Male			Female			Male			Female		
Age (years)	BM	M	BM	M	BM	C	M	BM	C	M	BM	C	M±SD	BM	C	M±SD
1-3	43-88	10-11	44-74	10-11	58-130	4-10	9-11	34-74	6-13	10-12	96-182	4-8	8-9±2	97-152	4-8	8-9±2
3-5	88-157	7-8	74-94	9	130-219	4	6-7	74-104	5-6	8-9	182-310	3-6	6-7±1	152-194	3-7	7-8±1
5-7	157-237	5-6	94-104	7-8	219-283	3	5-6	104-124	4-5	6-7	310-455	3-4	5-6±1	194-223	5	6-7±1
7-10	237-327	4	104-111	5-6	283-321	3-4	4-5	124-139	4	5-6	455-623	2-4	4±1	223-249	no data	5±1
10-15	327-377	4	111-114	5	321-331	3-4	4	139-147	3-4	5	623-725	3	3-4±1	249-267	no data	5±1
15-20	–	–	114-115	5	–	–	–	147-149	3-4	5	–	–	–	267-272	2	5±1

Values in the BM column represent the ranges of predicted body mass that correspond to the age ranges (Table 2). Food consumption data for captive animals were placed in this table according to body mass, or according to age if body mass was not reported. When body mass of captive animals was not reported we estimated it using the appropriate growth model (Table 2) for the purpose of calculating food consumption. Captive food consumption data for body masses less than the lowest BM category or greater than the highest BM category were included in the lowest and highest BM categories, respectively. Body masses falling exactly between categories were included in the higher category. Bioenergetic model predictions are averages calculated on an annual basis assuming an energy density of food of 7 kJ g^{-1}. See Fig. 2 for data sources.

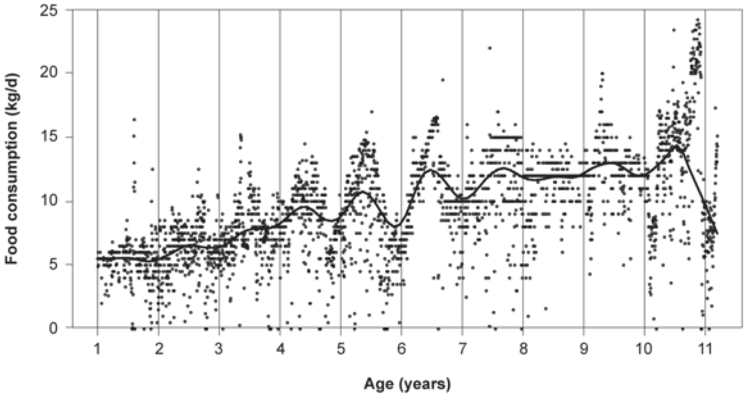


Figure 3. Daily food consumption of a captive, male Steller sea lion by age (D.A.S. Rosen and A.W. Trites unpubl. data). The line represents a nonparametric smooth of the data.

males, exhibited seasonal fluctuations in food intake with the greatest intake occurring during winter and the lowest during summer (Fig. 3 and Kastelein et al. 1990). This likely reflected inherent physiological cycles related to seasonality in sea lion growth and life history in the wild. Seasonal food consumption was also observed in captive male California and South American sea lions (Kastelein et al. 1995, 2000).

The estimated food intake of wild sea lions derived from two other techniques was consistent with the ranges of values observed for captive animals. Costa et al. (1991) estimated that lactating female California sea lions consumed approximately 11% of their body mass in food per day based on measurements of water intake and metabolic water production (Fig. 2). This value was higher than the average observed for captive animals of the same body size (~5%), and was likely due to the fact that these females had additional energy demands associated with nursing a pup, and that the energy content of their diet was lower than the average diet of captive animals. This difference might also be partially due to potentially greater error in the estimation of food consumption from water turnover than from direct measurement of food intake. George-Nascimento et al. (1985) found that the alimentary tracts of wild South American sea lions contained an average of 6% of their body mass in food. They suggested that this was equal to the daily ration of an animal, and the value was similar to that of similarly sized captive California and Steller sea lions (Fig. 2).

The availability of data to parameterize the bioenergetic models varied among the five sea lion species (excluding the Steller sea lion). When data were not available for a parameter for a given species, we used the value from the Steller sea lion model by default (Winship et al. 2002). Energetics data that we found included

Digestive efficiency	(California sea lion: Costa et al. 1991, Fadely et al. 1994)
Pup body composition	(California sea lion: Oftedal et al. 1987)
Adult body composition	(Australian sea lion: Kretzmann et al. 1991)
Resting metabolic rate	(California sea lion: Thompson et al. 1987, Butler et al. 1992, Ono and Boness 1996, Hurley and Costa 2001)
Active metabolic rate	(Australian sea lion: Costa and Gales 2003; California sea lion: Costa et al. 1991, Butler et al. 1992; and New Zealand sea lion: Costa and Gales 2000).

Often these energetics data were only available for certain seasons and age/sex classes. For example, almost all of the data on active metabolic rates of wild sea lions were from lactating females.

Data were also available on the life history of each sea lion species including the proportion of time spent at sea and age at sexual maturity (Odell 1975; Kooyman and Trillmich 1986; Trillmich 1986; Campagna and Le Boeuf 1988a, 1988b; Beentjes 1989; Cappozzo et al. 1991; Kovacs and Lavigne 1992; Higgins and Gass 1993; Ono and Boness 1996; Gales and Mattlin 1997; Thompson et al. 1998; Melin et al. 2000; Perrin et al. 2002; Costa and Gales 2003; Schulz and Bowen 2004). As with active metabolic rate, many of the data on the proportion of time spent at sea were from lactating females during the breeding season.

An important component of our bioenergetic model was a set of equations describing mass-at-age for males and females. We found mass growth curves for Australian and Steller sea lions (Winship et al. 2001, Goldsworthy et al. 2003), and mass-at-age data for captive California sea lions (Schusterman and Gentry 1971, Kastelein et al. 2000) to which we fit simple growth curves by nonlinear least squares. As per the models for Australian sea lions, the logistic equation was used for males:

$$A\left[1+e^{-k(t-t_0)}\right]^{-1},$$

and the von Bertalanffy equation was used for females:

$$A\left[1-e^{-k(t-t_0)}\right]^{3}$$

where A is asymptotic body mass, k is a parameter indicative of growth rate, t is age in years, and t_0 is a time parameter.

Length-at-age growth curves were available for South American sea lions (Rosas et al. 1993). We converted length-at-age as predicted by these models to mass-at-age using mass-length relationships for Steller sea lions (Winship et al. 2001), and then fit logistic and von Bertalanffy models to predicted male and female mass-at-age, respectively. The

Table 2. Parameters of body mass-at-age models for sea lions ≥1 year of age (see text for equations).

	Male			Female		
Species	A	k	t_0	A	k	t_0
Australian	300	0.300	7.74	77.0	0.230	–4.20
California	378	0.441	6.24	87.7	0.554	–1.01
Galapagos	303	0.421	5.91	70.1	0.387	–2.33
New Zealand	385	0.422	5.89	115	0.357	–2.61
South American	331	0.551	3.79	149	0.307	–2.08
Steller	744	0.394	5.86	275	0.247	–3.96

The Australian (Goldsworthy et al. 2003), California (Schusterman and Gentry 1971, Kastelein et al. 2000), and Steller sea lion (Winship et al. 2001) models were fit to mass-at-age data, the South American sea lion models were estimated from length-at-age growth curves (Rosas et al. 1993), and the Galapagos and New Zealand sea lion models were interpolated from the parameter values of the other species' models and data on maximum adult body mass.

asymptotic masses predicted by our growth curves were consistent with measurements of maximum body mass of adult South American sea lions (Vaz-Ferreira 1982, Kovacs and Lavigne 1992, Werner et al. 1996, Perrin et al. 2002, Schulz and Bowen 2004).

We interpolated mass growth curves for Galapagos and New Zealand sea lions by first fitting a series of linear equations (by least squares) to the pair-wise combinations of parameters in the fitted mass-at-age models for the other species. Then we used measurements of maximum adult body mass for Galapagos and New Zealand sea lions (Kovacs and Lavigne 1992, Gales and Mattlin 1997, Costa and Gales 2000, Perrin et al. 2002, Schulz and Bowen 2004) as estimates of their asymptotic body mass (A) to calculate the remaining parameters of their growth curves (Table 2). By equating maximum adult body mass to predicted asymptotic body mass we assumed that asymptotic growth is realized and that there is relatively little growth in body mass with age as an adult.

Data on pup masses were available for all species (Vaz-Ferreira 1982, Cappozzo et al. 1991, Kovacs and Lavigne 1992, Luque and Aurioles-Gamboa 2001, Perrin et al. 2002, Goldsworthy et al. 2003, Schulz and Bowen 2004). We assumed that body mass increased linearly with age during the first year of life from birth mass to the mass of 1-year-old animals as predicted by the growth models (Fig. 4).

Food consumption rates predicted by the bioenergetic models varied among species (Fig. 5, Table 1). It is important to note that the estimates of mean food requirements predicted by the models have substantial uncertainty due to the assumed uncertainty in model parameter values (e.g., see Steller sea lion values in Table 1 and Winship et al. 2002). Rather than

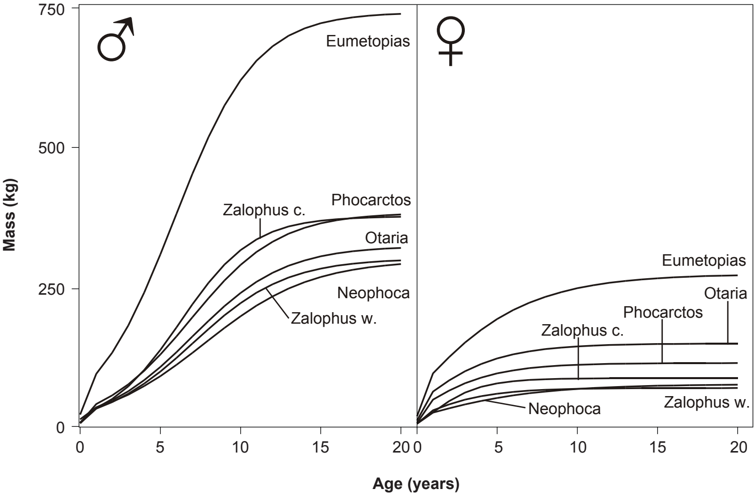


Figure 4. Mass-at-age growth curves used in the bioenergetic models. Birth mass was estimated based on data in the literature, mass after 1 year of age was predicted using fitted growth models (see text and Table 2), and growth was assumed to be linear during the first year of life.

plot food consumption as a function of absolute body mass, we plotted food consumption as a function of relative body mass—body mass as a proportion of the asymptotic body mass predicted by the growth models (*A*, Table 2). We felt this accounted for interspecific differences in body size and allowed for a more meaningful comparison across species. For example, the elevated metabolic rates associated with growth of juvenile animals resulted in the specific food requirement of a 100 kg Steller sea lion (a juvenile) exceeding that of a 100 kg adult female California sea lion—thus the two food requirements are not directly comparable.

The models predicted that food intake (expressed as a proportion of body mass) was lower for the larger species (since adult metabolic rate was assumed to be proportional to body mass$^{0.75}$; Fig. 5). However, young California and Galapagos sea lions had low predicted food requirements relative to other species due to their reported lower resting metabolic rates than young Steller sea lions (Thompson et al. 1987, Ono and Boness 1996, D.A.S. Rosen unpubl. data). The models also predicted that male sea lions had lower food requirements than females at a given proportion of asymptotic mass (Fig. 5) primarily because they were bigger, but also because males were assumed to approach their asymptotic mass more slowly than females (Fig. 4). Thus, a female at 50% of her asymptotic

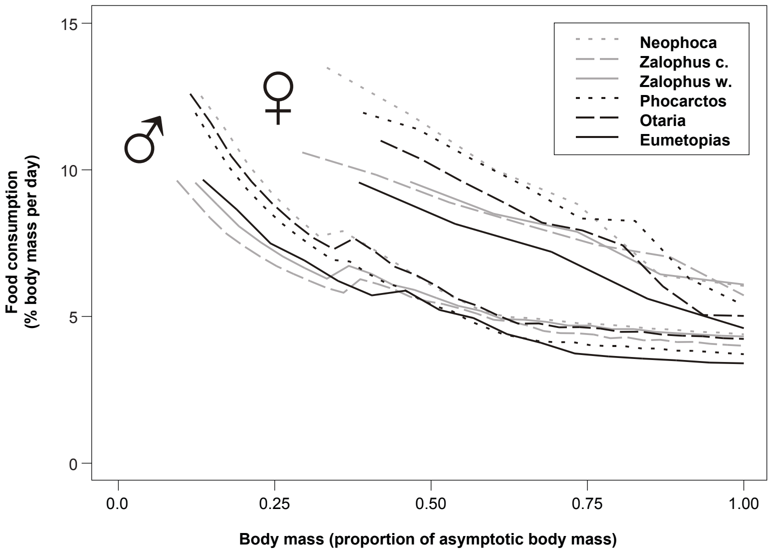


Figure 5. Mean food requirements of the six sea lion species predicted by the bioenergetic models plotted by relative body mass—a proportion of predicted asymptotic body mass. The energy content of food was assumed to be 7 kJ g^{-1}.

mass was younger than a male at 50% of his asymptotic mass, and was assumed to have a more elevated metabolic rate. Upward spikes occurred in predicted food requirements at the assumed sizes at sexual maturity (mature animals were assumed to spend more time at-sea than immature animals; Fig. 5). These spikes were not consistent among species because ages at sexual maturity were assumed to be similar, and thus sizes at sexual maturity were not. If sexual maturity is actually more a function of relative body mass than age, then the ontogenetic patterns of food requirements of the different species would be more similar than the models predicted.

The bioenergetic models for California, South American, and Steller sea lions generally predicted higher food consumption than observed from captive animals of the same body mass when the energy density of food was assumed to be 7 kJ g^{-1} (which is reasonable for the diet of captive sea lions; Fig. 2). Also, these model predictions were lower than the estimate of California sea lion food consumption from water turnover, but similar to the estimate of South American sea lion food consumption from gut contents (Fig. 2). The model predictions were consistent with the water turnover estimate for California sea lions when we assumed the energy density of food was 5 kJ g^{-1}, which was similar to the estimated energy density of prey in that study (Costa et al. 1991).

Discussion

The substantial variability in the estimates of sea lion food consumption that have been used in predator-prey and ecosystem models and analyses complicates comparisons of these studies. Our review highlights the important factors that have been demonstrated to affect food consumption as well as the effect of the techniques used to estimate food consumption. For example, the food intake of captive sea lions varies with age and/or mass, season, and the energy content of the food. These factors, therefore, need to be considered when applying estimates of the food intake of captive animals to wild animals.

Bioenergetic modeling is a more flexible technique for estimating the food consumption of wild sea lions than other methods because it can account for the influence of such factors as age, mass, etc. However, the data that are available to fully parameterize bioenergetic models for the six sea lion species are currently limited. A sensitivity analysis of the Steller sea lion model revealed that data on the activity budgets and active metabolic rates of all sex and age classes would contribute the most to reducing the uncertainty in estimates of food consumption (Winship et al. 2002). To date, these data are generally only available for lactating females of the other sea lion species. Mass-at-age growth curves are also key components of the bioenergetic models. We estimated mass-at-age growth curves for South American sea lions based on length-at-age growth curves and interpolated the mass-at-age growth curves for Galapagos sea lions and New Zealand sea lions based on the growth curves of the remaining four species. It would have been more accurate to have growth models that were fit to mass-at-age data from wild animals for all species.

The amount of food consumed by captive animals was generally lower than what the bioenergetic models predicted for wild animals. This is an important consideration when using estimates from either method in ecosystem models. This difference (if real) might be due to lower activity levels and/or differences in growth rates of captive animals. It might also reflect a higher energy density of fish fed to captive animals than we assumed in the models. However, it is difficult to evaluate these hypotheses given the uncertainty in the predictions of the bioenergetic models.

It is important to consider the factors that affect food consumption and differences in the techniques used to estimate food consumption when using estimates of sea lion food consumption in predator-prey and ecosystem models. Data on the food consumption of captive sea lions have the advantage that they are measured with real animals, but in applying these data to wild animals one must ensure that the effects of age, body size, season, and the energy density of food are considered. There is also the possibility that the energy requirements (and thus food requirements) of captive and wild animals differ. Bioenergetic modeling allows one to predict the food requirements of a sea lion of any age, mass, etc.; however, the data that are available to parameterize bioenergetic models for sea lions are currently limited. We hope that our review will help to guide future research by highlighting some of the data that are needed to provide accurate and comparable estimates of food consumption for all six sea lion species of the world.

Acknowledgments

We are grateful to the researchers whose data were reviewed in this study and wish to point out that we are entirely responsible for any misrepresentations or misinterpretations of these data. We appreciated the comments and suggestions of researchers at the UBC Marine Mammal Research Unit that improved the quality of our manuscript. Funding was provided to the North Pacific Universities Marine Mammal Research Consortium by the National Oceanographic and Atmospheric Administration and the North Pacific Marine Science Foundation.

References

Arreguín-Sánchez, F., A. Hernández-Herrera, M. Ramírez-Rodríguez, and H. Pérez-España. 2004. Optimal management scenarios for the artisanal fisheries in the ecosystem of La Paz Bay, Baja California Sur, Mexico. Ecol. Model. 172:373-382.

Beentjes, M.P. 1989. Haul-out patterns, site fidelity and activity budgets of male Hooker's sea lions (*Phocarctos hookeri*) on the New Zealand mainland. Mar. Mamm. Sci. 5:281-297.

Butler, P.J., A.J. Woakes, I.L. Boyd, and S. Kanatous. 1992. Relationship between heart rate and oxygen consumption during steady-state swimming in California sea lions. J. Exp. Biol. 170:35-42.

Campagna, C., and B.J. Le Boeuf. 1988a. Reproductive behaviour of southern sea lions. Behaviour 104:233-261.

Campagna, C., and B.J. Le Boeuf. 1988b. Thermoregulatory behaviour of southern sea lions and its effect on mating strategies. Behaviour 107:72-90.

Cappozzo, H.L., C. Campagna, and J. Monserrat. 1991. Sexual dimorphism in newborn southern sea lions. Mar. Mamm. Sci. 7:385-394.

Costa, D.P., and N.J. Gales. 2000. Foraging energetics and diving behavior of lactating New Zealand sea lions, *Phocarctos hookeri*. J. Exp. Biol. 203:3655-3665.

Costa, D.P., and N.J. Gales. 2003. Energetics of a benthic diver: Seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. Ecol. Monogr. 73:27-43.

Costa, D.P., G.A. Antonelis, and R.L. DeLong. 1991. Effects of El Niño on the foraging energetics of the California sea lion. In: F. Trillmich and K.A. Ono (eds.), Pinnipeds and El Niño: Responses to environmental stress. Springer-Verlag, Berlin, Germany, pp. 156-165.

Fadely, B.S., J.A. Zeligs, and D.P. Costa. 1994. Assimilation efficiencies and maintenance requirements of California sea lions (*Zalophus californianus*) fed walleye pollock (*Theragra chalcogramma*) and herring (*Clupea harengus*). NOAA, National Marine Mammal Laboratory, Seattle. 28 pp.

Gales, N.J., and R.H. Mattlin. 1997. Summer diving behaviour of lactating New Zealand sea lions, *Phocarctos hookeri*. Can. J. Zool. 75:1695-1706.

George-Nascimento, M., R. Bustamante, and C. Oyarzun. 1985. Feeding ecology of the South American sea lion *Otaria flavescens* food contents and food selectivity. Mar. Ecol. Prog. Ser. 21:135-144.

Goldsworthy, S.D., C. Bulman, X. He, J. Larcombe, and C. Littnan. 2003. Trophic interactions between marine mammals and Australian fisheries: An ecosystem approach. In: N. Gales, M. Hindell, and R. Kirkwood (eds.), Marine mammals: Fisheries, tourism and management issues. CSIRO, Collingwood, Australia, pp. 62-99.

Guénette, S. 2005. Models of Southeast Asia. In: S. Guénette and V. Christensen (eds.), Food web models and data for studying fisheries and environmental impacts on Eastern Pacific ecosystems. Fisheries Centre, University of British Columbia, Vancouver, Canada, pp. 106-178.

Higgins, L.V., and L. Gass. 1993. Birth to weaning: Parturition, duration of lactation, and attendance cycles of Australian sea lions (*Neophoca cinerea*). Can. J. Zool. 71:2047-2055.

Hückstädt, L.A., and T. Antezana. 2003. Behaviour of the southern sea lion (*Otaria flavescens*) and consumption of the catch during purse-seining for jack mackerel (*Trachurus symmetricus*) off central Chile. ICES J. Mar. Sci. 60:1003-1011.

Hurley, J.A., and D.P. Costa. 2001. Standard metabolic rate at the surface and during trained submersions in adult California sea lions (*Zalophus californianus*). J. Exp. Biol. 204:3273-3281.

Innes, S., D.M. Lavigne, W.M. Earle, and K.M. Kovacs. 1987. Feeding rates of seals and whales. J. Anim. Ecol. 56:115-130.

Jarre-Teichmann, A. 1992. Steady-state modelling of the Peruvian upwelling ecosystem. Ph.D. thesis, University of Bremen, Bremen, Germany. 84 pp.

Kastelein, R.A., N. Vaughan, and P.R. Wiepkema. 1990. The food consumption of Steller sea lions (*Eumetopias jubatus*). Aquat. Mamm. 15:137-144.

Kastelein, R.A., J. Kershaw, E. Berghout, and P.R. Wiepkema. 1995. The food consumption of South American sea lions (*Otaria flavescens*). Aquat. Mamm. 21:43-53.

Kastelein, R.A., N.M. Schooneman, N. Vaughan, and P.R. Wiepkema. 2000. Food consumption and growth of California sea lions (*Zalophus californianus californianus*). Zoo Biol. 19:143-159.

Kooyman, G.L., and F. Trillmich. 1986. Diving behavior of Galapagos sea lions. In: R.L. Gentry and G.L. Kooyman (eds.), Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton, pp. 209-219.

Kovacs, K.M., and D.M. Lavigne. 1992. Maternal investment in otariid seals and walruses. Can. J. Zool. 70:1953-1964.

Kretzmann, M.B., D.P. Costa, and L.V. Higgins. 1991. Milk composition of Australian sea lions, *Neophoca cinerea*: Variability in lipid content. Can. J. Zool. 69:2556-2561.

Laevastu, T., and R. Marasco. 1991. Marine mammals and birds: Interactions with fishery resources in the eastern Bering Sea. NOAA National Marine Mammal Laboratory, Seattle. 30 pp.

Luque, S.P., and D. Aurioles-Gamboa. 2001. Sex differences in body size and body condition of California sea lion (*Zalophus californianus*) pups from the Gulf of California. Mar. Mamm. Sci. 17:147-160.

Melin, S.R., R.L. DeLong, J.R. Thomason, and G.R. VanBlaricom. 2000. Attendance patterns of California sea lion (*Zalophus californianus*) females and pups during the non-breeding season at San Miguel Island. Mar. Mamm. Sci. 16:169-185.

Muck, P., and H. Fuentes. 1987. Sea lion and fur seal predation on the Peruvian anchoveta, 1953 to 1982. In: D. Pauly and I. Tsukayama (eds.), The Peruvian anchoveta and its upwelling ecosystem: Three decades of change. Instituto del Mar del Peru, Callao, Peru; Deutsche Gesellschaft für Technische Zusammenarbeit; GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management, Manila, Philippines, pp. 234-247.

Neira, S., H. Arancibia, and L. Cubillos. 2004. Comparative analysis of trophic structure of commercial fishery species off Central Chile in 1992 and 1998. Ecol. Model. 172:233-248.

Odell, D.K. 1975. Breeding biology of the California sea lion *Zalophus californianus*. Rapp. P.-v. Réun. Cons. int. Explor. Mer 169:374-378.

Oftedal, O.T., S.J. Iverson, and D.J. Boness. 1987. Milk and energy intakes of suckling California sea lion *Zalophus californianus* pups in relation to sex growth and predicted maintenance requirements. Physiol. Zool. 60:560-575.

Okey, T.A., S. Banks, A.F. Born, R.H. Bustamante, M. Calvopiña, G.J. Edgar, E. Espinoza, J.M. Fariña, L.E. Garske, G.K. Reck, and others. 2004. A trophic model of a Galápagos subtidal rocky reef for evaluating fisheries and conservation strategies. Ecol. Model. 172:383-401.

Ono, K.A., and D.J. Boness. 1996. Sexual dimorphism in sea lion pups: Differential maternal investment, or sex-specific differences in energy allocation? Behav. Ecol. Sociobiol. 38:31-41.

Perez, M.A., W.B. McAlister, and E.E. Mooney. 1990. Estimated feeding rate relationship for marine mammals based on captive animal data. NOAA Tech. Memo. NMFS F/NWC-184. 30 pp.

Perrin, W.F., B. Würsig, and J.G.M. Thewissen, (eds.). 2002. Encyclopedia of marine mammals. Academic Press, San Diego. 1414 pp.

Rosas, F.C.W., M. Haimovici, and C. Pinedo. 1993. Age and growth of the South American sea lion, *Otaria flavescens* (Shaw, 1800), in southern Brazil. J. Mammal. 74:141-147.

Schulz, T.M., and W.D. Bowen. 2004. Pinniped lactation strategies: Evaluation of data on maternal and offspring life history traits. Mar. Mamm. Sci. 20:86-114.

Schusterman, R.J., and R.L. Gentry. 1971. Development of a fatted male phenomenon in California sea lions. Dev. Psychobiol. 4:333-338.

Thompson, D., C.D. Duck, B.J. McConnell, and J. Garrett. 1998. Foraging behaviour and diet of lactating female southern sea lions (*Otaria flavescens*) in the Falkland Islands. J. Zool. (Lond.) 246:135-146.

Thompson, S.D., K.A. Ono, O.T. Oftedal, and D.J. Boness. 1987. Thermoregulation and resting metabolic rate of California sea lion *Zalophus californianus* pups. Physiol. Zool. 60:730-736.

Trillmich, F. 1986. Attendance behavior of Galapagos sea lions. In: R.L. Gentry and G.L. Kooyman (eds.), Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton, pp. 196-208.

Trites, A.W., and D. Pauly. 1998. Estimating mean body masses of marine mammals from maximum body lengths. Can. J. Zool. 76:886-896.

Trites, A.W., V. Christensen, and D. Pauly. 1997. Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. J. Northwest Atl. Fish. Sci. 22:173-187.

Vaz-Ferreira, R. 1982. *Otaria flavescens* (Shaw), South American sea lion. In: Mammals in the seas. Vol. 4: Small cetaceans, seals, and sirenians. FAO Fisheries Series 5, pp. 477-495.

Werner, R., A.-L. Figueroa-Carranza, and C.L. Ortiz. 1996. Composition and energy content of milk from southern sea lions (*Otaria flavescens*). Mar. Mamm. Sci. 12:313-317.

Winship, A.J., A.W. Trites, and D.G. Calkins. 2001. Growth in body size of the Steller sea lion. J. Mammal. 82:500-519.

Winship, A.J., A.W. Trites, and D.A.S. Rosen. 2002. A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA. Mar. Ecol. Prog. Ser. 229:291-312.

Studying Diving Energetics of Trained Steller Sea Lions in the Open Ocean

Gordon D. Hastie, David A.S. Rosen, and Andrew W. Trites
University of British Columbia, Marine Mammal Research Unit, Vancouver, British Columbia, Canada

Abstract

The costs associated with diving are a central component of a sea lion's energy budget. Accurate estimates of diving costs are needed to assess energetic and physiological constraints on foraging behavior, including the potential effects of changes in prey distribution or density. However, information on sea lion diving physiology is limited to relatively few species of pinnipeds, and there is currently no information for Steller sea lions. Information on diving energetics of pinnipeds has traditionally been gathered using either wild or captive animals. Studies with wild animals are logistically challenging and are limited by the opportunistic nature of data collection, while studies in captivity have been constrained by the physical restrictions of the holding facility. To circumvent some of these limitations, we combined the best aspects of both techniques by conducting diving metabolism studies with trained Steller sea lions in an open ocean environment. Two captive-reared Steller sea lions were housed in a holding pen and transported by boat to a diving trial area. The animals were trained to dive to predetermined depths for controlled periods of time using an underwater light targeting system and a video system to monitor behavior. At the end of each dive the sea lions returned to a respirometry dome on the surface where oxygen consumption was measured to estimate diving metabolism. This paper describes the experimental setup used to evaluate diving metabolism, discusses the logistical challenges of the study and the advantages of using such an approach to carry out physiological experiments with sea lions, and provides preliminary data on the diving energetics of Steller sea lions.

Introduction

Accurate information on the energetic consequences of foraging is required to assess the energetic requirements and physiological constraints of foraging in sea lions (Winship et al. 2002). Such information is integral to constructing predictive bioenergetic models for wild sea lions, and for assessing the impacts of changes in prey distributions or types (Winship et al. 2002). It is also central to understanding the physiological constraints that limit diving behavior (e.g., aerobic dive limits). However, there is only limited information on the energetic costs of locomotion in Steller sea lions (Rosen and Trites 2002), and no data on the energetic costs of diving.

Information on foraging energetics has traditionally been gathered by studying animals in the wild or held in captivity. Early studies of diving metabolism consisted of forced submersions with restrained laboratory harbor seals (e.g., Scholander 1940), which showed that submerged animals dramatically reduced their metabolism and heart rate (by up to 90%) during the submersion period. More recently, a limited number of studies on wild animals (e.g., Kooyman et al. 1973, 1980, 1983; Castellini et al. 1992), and with freely diving animals in captivity (e.g., Gallivan 1981, Reed et al. 1994, Hurley and Costa 2001, Sparling and Fedak 2004) have provided a greater understanding of physiological responses during dives.

Each of these approaches (wild and captive) has inherent limitations. While direct, controlled experiments can be carried out in captivity, studies are restricted by the physical restraints of a confined environment. For example, during measurements of diving metabolic rates, dives are limited to the relatively shallow depths of holding pools (Hurley and Costa 2001), and measures of swimming physiology can be limited by the flow speed of flumes (Rosen and Trites 2002), and rarely account for the biomechanical influence of swimming in an enclosed space. Conversely, although data from wild animals gives a direct measure of foraging energetics in the wild, such studies are generally limited to measurements of average field metabolic rate (e.g., Costa and Gales 2003) and are logistically challenging and often opportunistic in nature.

A unique series of studies in the wild have greatly furthered our understanding of diving and foraging energetics in Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica (e.g., Kooyman et al. 1980, Castellini et al. 1992, Williams et al. 2004). In these previous studies, the diving metabolism of seals was measured using open circuit respirometry on a dive-by-dive basis when the seals returned to breathe at the surface in discrete holes in the ice. However, it is clear that measuring oxygen consumption of wild marine mammals using respirometry techniques can only be used where the surface location is predictable (e.g., in a hole in the ice), making it unsuitable for most other species. One potential solution to overcoming these limitations is to combine the best aspects of both wild and captive techniques, and use trained sea lions to run experimental trials in the open ocean (e.g., Ponganis et al. 1997). Such an approach provides the logistical and experimental advantages of using trained animals without the restrictions of a captive environment. Specifically, by using trained sea lions in the open ocean, we could evaluate the energetic and behavioral mechanisms during dives to realistic foraging depths, and examine potential physiological or biomechanical changes concurrent with factors such as pressure changes at depth.

Trained marine mammals in the open ocean have been successfully employed in the past to study the diving physiology of a limited number of species, including bottlenose dolphins (*Tursiops truncatus*) (Ridgway et al. 1969, Ridgway and Howard 1979), beluga whales (*Delphinapterus leucas*) (Ridgway et al. 1984, Shaffer et al. 1997), and California sea lions (*Zalophus californianus*) (Hurley 1996, Ponganis et al. 1997). These studies have been integral to understanding the diving physiology of marine mammals and their adaptations to foraging at depth. However, this approach has not been used with Steller sea lions (*Eumetopias jubatus*) and no information on their diving physiology is currently available.

The paucity of data on diving physiology of Steller sea lions led to the development of a research program that uses trained Steller sea lions diving in an open ocean environment to investigate the energetics associated with foraging behavior. The following describes the experimental setup used to measure the diving metabolism of trained Steller sea lions, and provides details concerning the logistics associated with taking trained animals into the open ocean. We also discuss the advantages and challenges of using such an approach to carry out physiological experiments on sea lions, and provide preliminary data on the diving energetics of Steller sea lions

Open ocean research station

To provide a mobile base for open ocean research, we developed a research station that consisted of a floating laboratory and a specially designed floating pen to house the sea lions. It was designed to allow us to carry out all aspects of the research, from training of sea lions to data collection and analyses. The floating lab was fully equipped to carry out all aspects of animal husbandry (e.g., health maintenance and food preparation) for the sea lions and provided a base for scientists to work from. The research station was based at a working marina in an inlet close to Vancouver, British Columbia. The design of the research station and holding pen permitted the project to be fully mobile, allowing us to base ourselves in areas appropriate for the needs of particular research projects. However, the use of a vessel as a floating laboratory imposed the logistical challenges of boat work more commonly associated with studies in the wild. These included adverse weather conditions, fouling from marine organisms, power fluctuations, and saltwater corrosion.

Two female sea lions formerly held at the Vancouver Aquarium Marine Science Centre were housed at the research station in a floating animal pen specially designed and built for the project. It allowed the sea lions access to seawater and provided a base for open ocean training. This consisted of a 6.7 m long × 4 m wide × 4 m deep stainless steel mesh pen that allowed seawater to flow through, surrounded by a 2 m wide floating concrete walkway. The sea lions had continuous access to a 2 m × 4 m haul-out area. An 8 m × 4 m shed that adjoins the pen provided equipment storage and an indoor area for training or research. The mesh pen could be fully raised to allow for maintenance and cleaning (and emergency animal access). This was carried out using two large flotation tanks on the base of the pen that could be filled with air from a compressor at the surface. These provided the buoyancy to allow it to be raised (with relative ease) using hand winches at the surface. Due to significant marine growth in the area, cleaning operations were undertaken at least once every two weeks.

Although the design of the holding pen allowed a constant flow of clean seawater through the pen, this occasionally allowed unwanted items such as floating debris and jellyfish to also enter the pen. While the sea lions frequently ingested jellyfish during their initial acclimatization period, this rapidly decreased in frequency. But the occasional ingestion of other man-made and marine debris remained a problem.

Working in the open ocean

Sea lions were transported by truck and boat to the research station at the start of June 2003. After a relatively short period of acclimatization in the holding pen (around a month), initial training in the open water was carried out in the waters immediately surrounding the research station. During this period, the distance that the sea lions could swim from the area was controlled using a tether line attached to a body harness. After approximately one month of tethered work, the restraint was removed and all further work was carried out off tether. Training in the open ocean was generally carried out during three to four sessions during the day, usually during the morning or early afternoon. During training and experimental trials, each sea lion wore a webbing body harness with a VHF tag attached to ensure that it could be located if out of visual contact. A colored, reflective strip on the harness allowed the sea lion to be visible to researchers and trainers while the sea lion was underwater.

The sea lions were transported to dive trial areas, located in Burrard Inlet (49°17'25"N, 122°54'55"W) and Indian Arm (49°19'30"N, 122°55'30"W) near Vancouver, during training and experimental sessions in a specially designed transport boat. This 6.7 m vessel had a front-loading ramp that

Figure 1. A sea lion being trained to undertake diving experiments in the open ocean.

could be lowered to allow the sea lion access to the water (Fig. 1). The sea lions were trained to board the vessel from the holding pen, and enter the water using the loading ramp. Research equipment and staff were housed in a small research vessel that operated independently of the transport vessel. For animal safety, both vessels were generally stationary when sea lions were in the water, and each was fitted with propeller guards to ensure that the sea lions were not injured if boat maneuvers were necessary.

From the outset of the open ocean work, the sea lions were usually comfortable working in the ocean. However, novel visual and acoustic stimuli frequently provided challenges. For example, although routine vessel noise was not problematic, encountering loud impulsive underwater sounds within the hearing range of Steller sea lions such as recreational or commercial boat–based active sonar systems (~30 kHz @ ~210 dB) frequently resulted in adverse behavioral reactions such as refusal to swim in the open ocean. On such occasions, the sea lion's behavioral response was usually to terminate the task being carried out and immediately return to the cage on the transport vessel. Large vessels maneuvering in the immediate vicinity of the transport vessel would often elicit a similar response.

The presence of other marine mammals was not generally a problem during work in the open ocean. The only other species found regularly around the research station were harbor seals (*Phoca vitulina*) and, although interactions were observed, these were short and non-aggressive. The presence of harbor seals did lead to the potential for disease or parasite transmission between species. In response, we developed a strict quarantine protocol for both animals and staff at the research station that minimized the potential for transmission to sea lions housed at the aquarium. In addition, daily health checks were carried out on the sea lions, and regular blood tests were done to monitor health status.

Prior to the start of the project, it was anticipated that the presence of wild fish in the open ocean might be problematic, both from a training (i.e., self-reinforcement) and an experimental (i.e., uncontrolled diet profile) perspective. Although prey captures were occasionally observed, these did not generally lead to significant training problems, and were obvious enough that they could be accounted for during experimental trials.

Diving metabolism experiments

The first set of experiments in this project was designed to evaluate the metabolism of sea lions during dives to depth. Sea lions were conveyed in the transport vessel from their holding pen to dive trial areas where they carried out dives to an underwater target light system at depth and returned to a respiratory chamber at the surface. The sea lions freely chose to cooperate with all data collection and were never restrained or confined during any of the experimental trials. To maintain cooperation during the trials, sea lions were occasionally fed small amounts of fish (maximum of 0.5 kg of herring). Due to the short duration of trials (~20 min) and the small amount of food, this was unlikely to have affected the metabolic rate measurements due to the heat increment of feeding (Rosen and Trites 1997). Although it was not possible to completely discount the possibility of capture of wild fish during the descent and ascent phases of dives, observed prey captures were usually extremely overt and it appeared that the sea lions were swimming directly and quickly between the surface and target at depth during experimental trials.

The respiratory chamber consisted of a 190 liter Plexiglas dome attached to a 1.5 m × 1.5 m floating base. A 0.7 m wide "skirt" made of plastic-coated fabric mesh was draped over the outside edges of the flotation base creating a box effect, thus reducing the likelihood that the sea lion would leave the chamber before the end of the trial. Metabolism at the surface in the respiratory chamber was estimated using open circuit gas respirometry (Kaufmann et al. 1989). Air was drawn through the dome at a constant rate of 200 to 250 liters per minute using a Sable Systems Flow Kit 500H (Sable Systems International, Las Vegas, Nevada). Oxygen

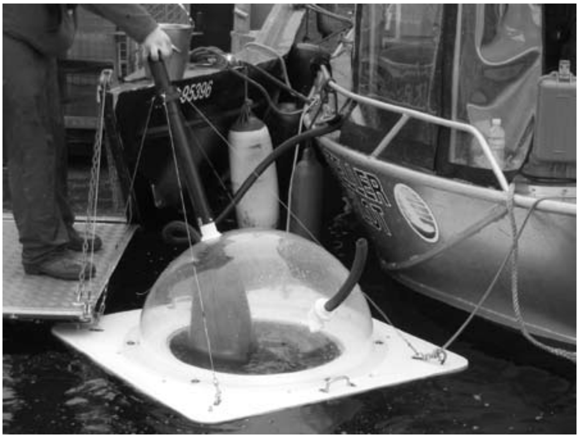


Figure 2. Sea lion in the respiratory dome at the water surface between the transport and research vessels.

concentrations were continuously subsampled using a Sable Systems FC-1B Oxygen Analyzer. A data acquisition system recorded an average gas concentration from the analyzers every second. Flow rate was corrected to standard temperature and pressure (STPD) through automatic concurrent barometric pressure and temperature readings at the flow meter, and gas levels were calibrated daily according to manufacturer instructions. The subsample of air was drawn through two columns of Drierite (W.A. Hammond Drierite Co. Ltd., Xenia, Ohio) and two columns of soda lime to absorb CO_2 from the air sample. Changes in oxygen concentration were converted to oxygen consumption rates using equation 4b from Withers (1977).

All tests were performed in the morning, at least 16 hours postprandial. The respiratory chamber was deployed at the water surface from the research vessel (Fig. 2) and the target light system was positioned beneath the chamber at a predetermined depth (Fig. 3). The target light system consisted of three components: (1) a small white sphere that each sea lion was trained to target on; (2) an underwater light (Multi-Sea Lite P/N 710-040-601, Deep Sea Power and Light Inc., San Diego, California) with a diffuser filter over the front; and (3) an underwater camera (P/N 740-048-601; Deep Sea Power and Light Inc.) that allowed us to monitor the attendance and behavior of the sea lion at the target (Fig. 3).

Each sea lion was trained to remain calm and stationary with its head in the respiratory chamber for a period of 6 minutes to obtain a standard measure of oxygen consumption at the surface. The sea lion then swam to

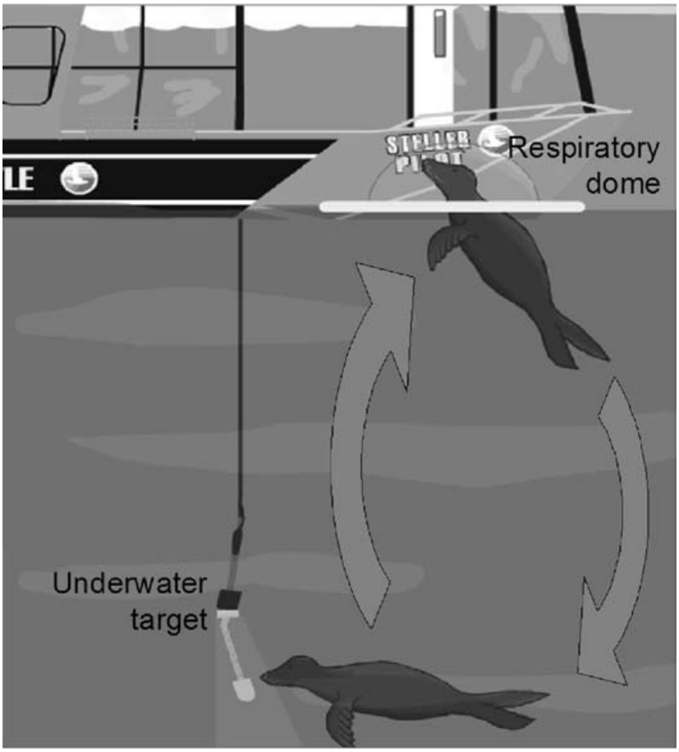


Figure 3. Sea lions are trained to dive from a respiratory dome at the surface to variable depths using an underwater light targeting system and a video system to monitor behavior.

depth on command and remained stationary at the target light for a predetermined duration (between 1 minute and 3 minutes). The sea lion was trained so that when the light was switched off, it returned to the respiratory chamber at the surface where an estimate of post-dive metabolism was made for 10 minutes. Around 3 months of training was required to carry out the dive element of this study, and we attempted to maintain sea lions at each duration for around a week prior to data collection.

To date, we have carried out 31 dive trials with single dives up to 30 meters depth ranging in duration from 65 seconds to 200 seconds. Although these depths and durations are well below the maximums recorded for wild Steller sea lions, they do encompass a significant proportion of their wild dives (Merrick and Loughlin 1997, Loughlin et al. 2003). This confirms that it is possible to use trained Steller sea lions to carry out experimental trials to evaluate diving metabolism, and to collect meaningful

Table 1. Summary of preliminary estimates of oxygen consumption rates at the surface and during 31 dives for two Steller sea lions. Dive durations were between 65 and 200 seconds to depths between 5 m and 30 m. All values of mass, and surface and diving oxygen consumption rates are means (±SD).

Sea lion	n	Mass (kg)	Surface oxygen consumption (ml $kg^{-1}min^{-1}$)	Diving oxygen consumption (ml $kg^{-1}min^{-1}$)
F00BO	13	117.6	11.4 (±1.5)	6.1 (±2.1)
F97SI	18	193.6	10.1 (±1.0)	5.7 (±2.1)

bioenergetic data in the open ocean. Experimental trials with multiple dives have also been carried out ranging from 3 to 5 consecutive dives of 30 seconds. This approach allows realistic simulation of foraging dives without the restraint of a captive environment. Furthermore, it allows the evaluation of diving metabolism on a dive-by-dive basis over a series of dives, and allows researchers to examine the influence of changes in dive parameters and environmental characteristics. Preliminary estimates of oxygen consumption rates at the water surface and during single dives to depth are shown in Table 1.

Overall, despite the logistical and financial investment inherent in a project of this scope, and the challenges of taking captive animals into the wild, the advantages of using trained animals to carry out bioenergetic studies in the wild are significant. A perceived inherent weakness of using trained animals to carry out energetic studies is its applicability to wild animals. For example, it is clear that the trained animals' physiological state and behavioral responses may be governed to an extent by the expectations of the trainer, or be a response to the training itself rather than a "natural" response to diving and foraging. We do not think that the sea lions exhibited an extreme metabolic adjustment based on an assumed maximum dive duration, as they were no longer naïve to the intended dive parameters once data collection began. However, behavioral patterns during dives may be influenced by the training; unlike many diving patterns in the wild (e.g., Le Boeuf et al. 1992, Crocker et al. 2001) ascent rates observed in our studies were generally significantly faster than descent rates, a potential artifact of providing the food resource at the surface rather than at depth. It is clear that an approach that allows the animals to dictate their own dive characteristics and concurrent physiological responses would be preferable in future studies of foraging energetics.

Despite these caveats, using the approach described in this study, many of the apparent shortcomings can be overcome. For example, the inherent physical limitations of a captive environment (e.g., experimental pool dimensions) are no longer an issue, allowing accurate simulation of dives in the wild, and an evaluation of the influence of pressure at depth. Furthermore, with over a year of carrying out trained dives to depth before data collection commenced, the physiological fitness of the animals is likely to be more representative of wild animals than in previous studies with captive animals.

The success of the current project has allowed us to develop a research program focused on detailed aspects of diving physiology and locomotion. These include studies of the consequences of variations in diving and swimming characteristics and the influence in changes in body condition on diving physiology. Overall, the open ocean research program allows the energetic costs of foraging in the wild to be accurately assessed, and provides a means for assessing their energetic requirements and physiological constraints, as well as determining the potential effects of changes in prey distribution or density.

We are currently evaluating whether variations in prey encounter rates at depth result in variations in behavioral patterns (Thompson and Fedak 2001, Cornick and Horning 2003) or metabolic adjustments made by diving sea lions. This will be complemented by a study of the influence that changes in body condition (through simulated changes in buoyancy) have on these processes. Furthermore, we aim to assess the biomechanical and energetic influence of telemetry devices by examining detailed changes in facets of swimming behavior and oxygen consumption while wearing telemetry packages of different shapes and sizes. In addition, our research setup allows investigators to test foraging models and assess their applicability to Steller sea lions, and provides investigators with a means of measuring other important physiological mechanisms, such as hearing sensitivity (e.g., Ridgway et al. 2001, Kastak and Schusterman 2002), and their associations with water depth.

Acknowledgments

Funding for this project was provided to the North Pacific Universities Marine Mammal Research Consortium by the North Pacific Marine Science Foundation and the National Oceanographic and Atmospheric Administration. Thanks to the staff at the Open Water Lab and the Vancouver Aquarium Marine Science Centre.

References

Castellini, M.A., G.L. Kooyman, and P.J. Ponganis. 1992. Metabolic rates of freely diving Weddell seals: Correlations with oxygen stores, swim velocity and diving duration. J. Exp. Biol. 165:181-194.

Cornick, L.A., and M. Horning. 2003. A test of hypotheses based on optimal foraging considerations for a diving mammal using a novel experimental approach. Can. J. Zool. 81:1799-1807.

Costa, D.P., and N.J. Gales. 2003. Energetics of a benthic diver: Seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. Ecol. Monogr. 73(1):27-43.

Crocker, D.E., N.J. Gales, and D.P. Costa. 2001. Swimming speed and foraging strategies of New Zealand sea lions (*Phocarctos hookeri*). J. Zool. (Lond.) 254:267-277.

Gallivan, G.J. 1981. Ventilation and gas exchange in unrestrained harp seals (*Phoca groenlandica*). Comp. J. Biochem. Physiol. 69A:809-813.

Hurley, J.A. 1996. Metabolic rate and heart rate during trained dives in adult California sea lions. Ph.D. thesis, University of California, Santa Cruz. 109 pp.

Hurley, J.A., and D.P. Costa. 2001. Standard metabolic rate at the surface and during trained submersions in adult California sea lions (*Zalophus californianus*). J. Exp. Biol. 204:3273-3281.

Kastak, D., and R.J. Schusterman. 2002. Changes in auditory sensitivity with depth in a free-diving California sea lion (*Zalophus californianus*). J. Acoust. Soc. Am. 112(1):329-333.

Kaufmann, R., H. Forstner, and W. Wieser. 1989. Respirometry: Methods and approaches. In: C.R. Bridges and P.J. Butler (eds.), Techniques in comparative respiratory physiology: An experimental approach. Cambridge University Press, Cambridge, UK, pp. 51-76.

Kooyman, G.L., M.A. Castellini, R.W. Davis, and R.A. Maue. 1983. Aerobic diving limits of immature Weddell seals. J. Comp. Physiol. B 151:171-174.

Kooyman, G.L., D.H. Kerem, W.B. Campbell, and J.J. Wright. 1973. Pulmonary gas exchange in freely diving Weddell seals, *Leptonychotes weddelli*. Resp. Physiol. 17:283-290.

Kooyman, G.L., E.A. Wahrenbrock, M.A. Castellini, R.W. Davis, and E.E. Sinnett. 1980. Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: Evidence of preferred pathways from blood chemistry and behavior. J. Comp. Physiol. B 138:335-346.

Le Boeuf, B.J., Y. Naito, T. Asaga, D. Crocker, and D.P. Costa. 1992. Swim speed in a female northern elephant seal: Metabolic and foraging implications. Can. J. Zool. 70(4):786-794.

Loughlin, T.R., J.T. Sterling, R.L. Merrick, J.L. Sease, and A.E. York. 2003. Diving behavior of immature Steller sea lions (*Eumetopias jubatus*). Fish. Bull. U.S. 101(3):566-582.

Merrick, R.L., and T.R. Loughlin. 1997. Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. Can. J. Zool. 75:776-786.

Ponganis, P.J., G.L. Kooyman, L.M. Winter, and L.N. Starke. 1997. Heart rate and plasma lactate responses during submerged swimming and trained diving in California sea lions, *Zalophus californianus*. J. Comp. Physiol. B 167:9-16.

Reed, J.Z., C. Chambers, M.A. Fedak, and P.J. Butler. 1994. Gas exchange of captive freely diving grey seals (*Halichoerus grypus*). J. Exp. Biol. 191:1-18.

Ridgway, S.H., and R. Howard. 1979. Dolphin lung collapse and intramuscular circulation during free diving: Evidence from nitrogen washout. Science 206:1182-1183.

Ridgway, S.H., B.L. Scronce, and J. Kanwisher. 1969. Respiration and deep diving in the bottlenose porpoise. Science 166:1651-1654.

Ridgway, S.H., C.A. Bowers, D. Miller, M.L. Schultz, C.A. Jacobs, and C.A. Dooley. 1984. Diving and blood oxygen in the white whale. Can. J. Zool. 62:2349-2351.

Ridgway, S.H., D.A. Carder, T. Kamolnick, R.R Smith, C.E. Schlundt, and W.R. Elsberry. 2001. Hearing and whistling in the deep sea: Depth influences whistle spectra but does not attenuate hearing by white whales (*Delphinapterus leucas*) (Odontoceti, Cetacea). J. Exp. Biol. 204:3829-2841.

Rosen, D., and A. Trites. 1997. Heat increment of feeding in Steller sea lions, *Eumetopias jubatus*. Comp. J. Biochem. Physiol. 118A(3):877-881.

Rosen, D.A.S., and A.W. Trites. 2002. Cost of transport in Steller sea lions, *Eumetopias jubatus*. Mar. Mamm. Sci. 18(2):513-524.

Scholander, P.F. 1940. Experimental investigations on the respiratory function in diving mammals and birds. Hvalradets Skrifter 22:1-131.

Shaffer, S.A., D.P. Costa, T.M. Williams, and S.H. Ridgway. 1997. Diving and swimming performance of white whales, *Delphinapterus leucas*: An assessment of plasma lactate and blood gas levels and respiratory rates. J. Exp. Biol. 200(24):3091-3099.

Sparling, C.E., and M.A. Fedak. 2004. Metabolic rates of captive grey seals during voluntary diving. J. Exp. Biol. 207:1615-1624.

Thompson, D., and M.A. Fedak. 2001. How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. Anim. Behav. 61:287-296.

Williams, T.M., L.A. Fuiman, M. Horning, and R.W. Davis. 2004. The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: Pricing by the stroke. J. Exp. Biol. 207:973-982.

Winship, A.J., A.W. Trites, and D.A.S. Rosen. 2002. A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA. Mar. Ecol.-Prog. Ser. 229:291-312.

Withers, P.C. 1977. Measurement of VO2, VCO2, and evaporative water loss with a flow-through mask. J. Appl. Physiol. 42(1):120-123.

Using Simulations to Evaluate Reconstructions of Sea Lion Diet from Scat

Ruth Joy and Dominic J. Tollit
University of British Columbia, Fisheries Centre, Marine Mammal Research Unit, Vancouver, British Columbia, Canada

Jeffrey L. Laake
NOAA National Marine Fisheries Service, National Marine Mammal Laboratory, Alaska Fisheries Science Center, Seattle, Washington

Andrew W. Trites
University of British Columbia, Fisheries Centre, Marine Mammal Research Unit, Vancouver, British Columbia, Canada

Abstract

Models used to describe pinniped diet can provide very different composition estimates. Occurrence indices as well as biomass reconstruction models (which use estimates of the number and sizes of prey consumed) are commonly used and increasingly utilize a variety of fish hard remains (bones) found in scats. However, the importance of any single fish can be overestimated if its bones are deposited in a succession of scats assumed to be from different fish. Similarly, the importance of a species will be underestimated relative to other species if the bones of one species are more fragile and are completely digested or if bones from different fish of the same species are contained in a single scat and assumed to be from a single fish. Species differences in the proportion of fish bones that survive digestion can be assessed from captive feeding studies where the number and species of prey consumed is known. Numerical correction factors can be calculated to take into account the levels of complete digestion. We performed computer simulations using data from captive feeding studies to investigate levels and sources of error in reconstructing simulated mixed species diets. Our simulations used different combinations of hard remains, were conducted both with and without the application of numerical correction factors, and compared four different diet indices (1. Modified frequency of occurrence, 2. Split sample frequency of occurrence, 3. Variable biomass reconstruction, 4. Fixed biomass reconstruction). Simulations indicated that levels of error were related to the MNI method of inferring fish numbers from prey remains, prey size, the number of identifiable prey structures used, and the robustness of the remains to digestive processes (recovery rate). The fewer fish fed, the higher the relative probability of counting the fish, particularly when a multiple element structure or all structure techniques are used. If recovery rates were assumed to be consistent across species, then large fish (particularly when fed in small amounts) were overestimated relative to smaller sized prey in all models, but particularly biomass reconstruction models and when using more than one paired structure. When recovery rates of a paired structure (otoliths) were varied across species (as observed in captive feeding studies) then biomass models with no correction factors applied tended, as expected, to overestimate the species with high recovery rates. In contrast, frequency of occurrence models overestimated the contribution of smaller prey (particularly when fed in small amounts). Simulations also indicated correction factors can reduce levels of error in biomass reconstruction models, but cannot solve problems related to counting fish using MNI. Our work shows simulations can form a valuable component in assessing diet indices and the level (and direction) of associated errors in each.

Introduction

Diet composition is increasingly being estimated from prey hard remains (bones) found in pinniped scat (e.g., Browne et al. 2002). A number of different techniques can be used to describe diet and, therefore, it is important to understand the bias and errors associated with each. In the past, otoliths were the most commonly used structure to enumerate and reconstruct diet. However, otoliths from some species are rarely found in scats (e.g., salmonid species) or are difficult to distinguish to the species level (e.g., salmonid and rockfish species). Recently there has been a trend toward using all recovered structures to circumvent problems of high digestibility and non-differentiation of otoliths (Sinclair and Zeppelin 2002, Tollit et al. 2004). However, the bias and error associated with the multi-structure technique have not been fully investigated (Olesiuk et al. 1990, Cottrell and Trites 2002, Laake et al. 2002, Arim and Naya 2003, Tollit et al. 2003).

In scat analysis, it is important not only to determine species presence, but also the proportional contribution of each species. We selected four commonly used indices that are used to describe contributions of prey from hard remains found in scat. There are two methods that use species occurrence data to estimate prey proportions (modified and split-sample frequency of occurrence), and two variants of a method that use a volumetric technique which combines prey counts and weights to estimate prey biomass proportions (fixed and variable biomass reconstructions; see Laake et al. 2002). However, Laake et al. (2002) found up to a ten-fold difference between consumption estimates using one of each of these models for the smallest and largest prey, highlighting the need for further studies investigating the causes of such differences. Attempts to improve biomass reconstructions include using numerical correction factors, which aim to take into account the different prey species' digestibility (and hence the proportion recovered) or passage probabilities (e.g., Bowen 2000, Browne et al. 2002).

In this paper, we used a computer simulation model that aimed to replicate captive feeding studies. We varied the input parameters of the model to examine the errors associated with methods for enumerating fish, and we investigated the performance of four diet reconstruction indices in assessing a mixed diet (considered a worst case scenario). In particular, we investigated the impact of using different combinations of bones, varying species recovery rates, and applying numerical correction factors to biomass reconstruction indices.

Methods

Prey enumeration methods

Presence or absence

In frequency of occurrence methods, any number of identifiable structures of a species found in a scat indicates species presence regardless of the number of structures found in the scat. The number of individual fish is not enumerated, but instead mere presence is noted (Croxall 1993). For example, one recovered vertebra in a scat contributes the same "weight" in frequency of occurrence reconstructions as 100 recovered otoliths from a different species found in the same scat regardless of fish size.

Minimum number of individuals (MNI)

MNI is a zooarchaeological quantification method that has been widely used in scat analysis as a building block for diet reconstruction (Allen and Guy 1984). MNI is used in volumetric indices and not in occurrence indices to compute the minimum number of individuals that can be recognized using all identified bones of a species or using a frequently occurring paired bone (e.g., otoliths; Nichol and Wild 1984). The number of bones counted is divided by the number of elements of that type per fish and rounded up to the nearest whole number. For example, if five otoliths are found, then the MNI fish count would be three fish (as otoliths are found as pairs in each fish). When multiple structures are used, the maximum count is typically based on the most frequently occurring identifiable paired structure.

If the MNI technique is biased on its ability to count fish from elements found in scat, then the diet reconstruction based on these numbers will also be biased. We assessed the ability of MNI to determine relative importance of different species in the diet with binomial probabilities. The binomial probability distribution is used in experiments such as this when the outcome of a single trial is either presence or absence, and the probability of a structure occurring in a given scat has a probability (p). Therefore, the number of bones passed in a scat is assumed to follow a binomial distribution, where the probability of x bones passing when n bones were eaten each with a probability of passage (p) is

$$P(X=x)=\binom{n}{x}p^{x}(1-p)^{(n-x)}.$$

The expected number of fish $E(F)$ counted is computed as

$$E(F)=\sum_{x=0}^{n} g(x)\times P(X=x),$$

where the value $g(x)$ is

$$\frac{x}{\#\,elements\big/fish},$$

rounded up to the nearest whole number of fish as in MNI. When T bone types are counted then

$$E(F)=\max\left\{E(F_1),\ldots,E(F_T)\right\}.$$

Here F_j = number of fish derived from x_j or the count of elements from structure j where $j = 1,\ldots,T$.

Diet reconstruction indices

Diet reconstruction indices provide information regarding the relative species contributions to the overall diet. We looked at four commonly used indices. Frequency of occurrence indices are simpler to construct given that no information is needed on prey number or size.

Frequency of occurrence (FO) indices

Modified frequency of occurrence (mFO). This is a version of the most commonly used reconstruction index, which is based on the presence of a species within a scat (Croxall 1993) and does not require a count of prey structures. For direct comparison, we used the modified version of the index such that the sum of all prey contributions totaled 100%.

$$mFO_i = \frac{\sum_{k=1}^{s} I_{ik}}{\sum_{i=1}^{\omega}\sum_{k=1}^{s} I_{ik}}$$

$i = 1, \ldots, \omega$ species of fish prey, I is an indicator function equal to 1 if the ith species is present in the kth scat, and 0 otherwise.

Split sample frequency of occurrence (SSFO). This method is also based on the presence of a species within a scat. It assumes that all prey present in a scat were consumed in equal quantities and that all meals were of equal size (fixed meal size). Olesiuk et al. (1990) investigated the potential impact of these assumptions and highlight the value of this index when sample sizes are relatively large. In summary, each species in the scat is given a value of 1 divided by the number of species detected in the scat (Olesiuk et al. 1990, Laake et al. 2002).

$$SSFO_i = \frac{\sum_{k=1}^{s}\left(\frac{I_{ik}}{\sum_{i=1}^{\omega} I_{ik}}\right)}{s}$$

$i = 1, \ldots, \omega$ species of fish prey, $k = 1, \ldots, s$ scats, I is an indicator function equal to 1 if the ith species is present in the kth scat, and 0 otherwise.

Biomass reconstruction indices

Variable biomass reconstruction (VBR). This index uses MNI counts of structure elements and weights estimated from the mean species weight to provide relative biomass estimates. Optimally, an estimate of prey size is derived from each structure by back-calculating from bone measurements and considering the degree of partial digestion (see Tollit et al. 2004). The index divides the biomass estimated for each species by the total biomass estimated for all species in all scats. The rationale for this index is that it allows the contributions in scats to be different (variable) sizes, such that biomass is proportional to the actual number of individuals of each prey species consumed (i.e., scats represent an unweighted cross-section of meals eaten). Thus the variable biomass reconstruction index for the ith species is:

$$FBR_i = \frac{f_i \bar{w}_i}{\sum_{i=1}^{\omega} f_i \bar{w}_i}$$

where f_i is the number of fish of species i, $\bar{w}_i$ is the average weight of a fish of species i, and the summation is taken over the number of prey species $i, \ldots, \omega$ (Laake et al. 2002).

Fixed biomass construction (FBR)

This index also uses MNI enumeration from structures, and prey weights to compute the proportion of biomass by species per scat. The FBR index is the average of species proportions across scats. Similar to SSFO, it assumes that a scat represents a fixed quantity of food consumed, such that the prey proportions within each scat are equally weighted. The fixed biomass reconstruction index for the *i*th species is:

$$VBR_i = \frac{\sum_{k=1}^{s} \left(\frac{f_{ik}\bar{w}_i}{\sum_{i=1}^{\omega} f_{ik}\bar{w}_i} \right)}{s}$$

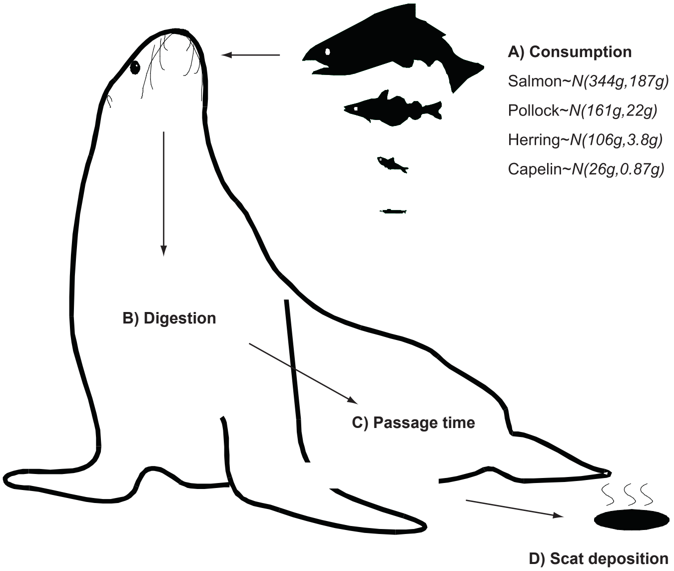
where f_{ik} is the number of fish of species i in scat k, $\bar{w}_i$ is the average weight of species i, s is the number of scats (Laake et al. 2002).

Correction factors

To date, numerical correction factors have typically been calculated only at the species level and for a single paired structure (e.g., otoliths; Bowen 2000). More recently, data on recovery of multiple structures has become available (Cottrell and Trites 2002, Tollit et al. 2003), providing additional information with which to assess diet. In our simulations, we applied numerical correction factors that were unique to each structure and species, and applied them to each structure prior to calculating MNI, and not at the species level after counting the fish. In the first simulation, the recovery rate (passage probability) of all structures was standardized, such that numerical correction factors were identical across species. By setting a constant recovery probability across species, this parameter did not contribute additional error from introducing bias to the results, therefore allowing us to better assess error associated with fish enumeration and biomass reconstruction methods. In the second simulation, experimentally derived numerical correction factors were applied to each species. In both simulations, correction factors were calculated as the inverse of the passage probability and hence can be considered “true” values. This approach, while ignoring the potential error of incorrect values, permitted us to focus on errors in diet reconstruction methodology by omitting error from passage rate variability due to, for example, differences between animals or activity levels.

Simulation experiments

The computer simulation model was designed to replicate captive feeding studies by simulating sea lion consumption, scat deposition, fish enumeration, and biomass reconstruction (Fig. 1.). Simulated meals were composed of four major prey species of the Steller sea lion (walleye pollock, *Theragra chalcogramma*; coho salmon, *Oncorhynchus kisutch*; Pacific herring, *Clupea harengus pallasii*; capelin, *Mallotus villosus*; e.g., Sinclair and Zeppelin 2002); these species also have been used in feeding trials at the Vancouver Aquarium Marine Science Centre and therefore structural passage probabilities were available (Tollit et al. 2003). Meals consumed by individuals were randomized for size (for both total meal size and fish size). The simulated diet was fed for 18 days and scats collected throughout.



- **A) Consumption:** Meals were consumed *(~Exp [24 hr])* for 18 days. The median meal size was 8 kg *(~Unif [0 kg,16 kg])*, or the typical captive meal size for a female Steller sea lion. Prey species weights were normally distributed, proportion biomass was prechosen and reflected a fixed captive diet. Thus the number of individuals eaten in a given meal was a Poisson variable with mean and variance = λ, and λ = *biomass proportion* × *meal size/species weight*. Each fish consumed contained countable structures such as otoliths and vertebrae.
- **B) Digestion:** Probability of structures surviving digestion and being recovered was 0.4 $(\sim Bin\ [x_{ij};n_{ij},p])$ in simulation 1, and differed by species and structure in simulation 2 $(\sim Bin\ [x_{ij};n_{ij},p_{ij}])$, where n_{ij} is the number of structures consumed, and x_{ij} is the number of structures recovered.
- **C) Passage time:** Time it took for a structure to pass through a sea lion $(\sim Gamma[\alpha,\beta])$.
- **D) Scat deposition:** Once a structure has passed through the sea lion, structures accumulated until they were expelled in scat at discrete times points *~Exp (24 hrs)*.

One animal consumes a series of random meals for 18 days, all scats were collected, all structures enumerated, correction factors either were or were not applied, and four diet biomass indices were estimated. This whole procedure was replicated 1,000 times, with the four indices reconstructed each time. 95% confidence intervals were empirically derived.

Figure 1. Diagram with details of simulation study that estimated fish biomass in sea lion diet from prey remains found in scat.

In the first set of simulations, we standardized certain variables in an attempt to isolate sources of error. We used the following parameters for the first simulation: the four prey species were fed to a sea lion for 18 days; passage (or recovery) probabilities and passage times of structures were set as equal across all prey species; passage probability for all structures was 0.40; and passage times were set to the value observed in captive feeding trials (passage time~Gamma [$\hat{\mu} = 33.3$ hours, $s = 21.9$ hours]). Meal size was a random amount with a median meal size of 8,000 g (~Uniform [min = 0 g; max = 16,000 g]), the typical meal size in captive trials. Average mass of the four prey species matched those fed in the captive experiments (salmon = N~($\hat{\mu} = 344$ g, $s = 186.57$), walleye pollock = N~[$\hat{\mu} = 161$ g, $s = 21.9$], herring = N~[$\hat{\mu} = 106$ g, $s = 3.78$], and capelin = N~[$\hat{\mu} = 26$ g, $s = 0.87$]) and were fed as 2.5, 7.5, 22.5, and 67.5% of the biomass, respectively. In short, the number of individual fish fed in a simulated meal, was a random Poisson variable with the mean number (λ) a function of a series of random variables derived elsewhere such that λ = biomass proportion x meal size per species weight.

The biomass proportions were selected specifically to assess the general perception that small prey are underestimated and larger prey are overestimated (Bowen 2000). Thus, in this first selected diet scenario, the larger fish were fed in small amounts and the small fish in large amounts. It should be noted that, the largest fish species contribution was pre-set to a small proportion of biomass (salmon = 2.5%) and therefore might not occur in all meals, but over the length of an 18 day feeding trial would comprise the 2.5% pre-set composition.

To assess the effectiveness of using multiple structures, repeated simulations were conducted (i) using one paired structure (e.g., paired otoliths), (ii) using one structure with 66 elements (e.g., vertebrae), and (iii) using "all structures" in which 10 different paired structures were used to enumerate and estimate biomass.

In the second set of simulations, we used a single paired structure (otoliths) to assess the impact of varying species' passage probabilities (recovery rates) on the performance of the biomass indices. Biomass of salmon, pollock, herring and capelin was pre-set at 3%, 66%, 23%, and 8% respectively. In this scenario, pollock was selected to dominate the diet, a species found in other studies to be overrepresented when estimating numbers using MNI (Tollit et al. 2003). In contrast to simulation 1, capelin only contributed a small proportion. For these species, otolith passage probabilities were 0.10, 0.62, 0.18, and 0.15 respectively and reflected probabilities observed in captive feeding studies (Tollit et al. 2003, D. Tollit unpubl. data).

In both simulations, animals consumed a series of random meals for 18 days and all recovered elements in every scat produced were counted and the four diet indices were calculated both with and without species/structure-specific correction factors. This procedure was replicated 1,000

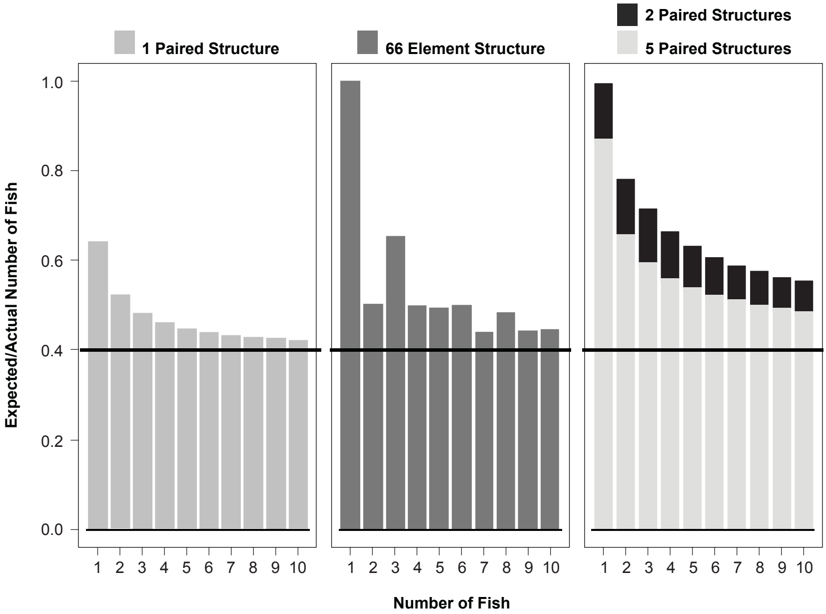


Figure 2. Ratio of fish counted using the minimum number of individuals (MNI) method to actual numbers of fish fed when the passage probability for elements was 0.40. The fewer fish fed, the higher the relative probability of counting the fish, particularly when a multiple element structure (such as vertebrae; middle graph) or all structure techniques (right-most graph) are used. For there to be no enumeration bias, the ratio of expected to actual numbers would be constant for any number of fish eaten (i.e., the bars would all be the same height).

times as if there were 1,000 animals involved in the captive feeding trial. Ninety-five percent confidence intervals were empirically derived as the 25th and 975th ordered observations from 1,000 estimates.

We recognize there are many other sources of error that future simulations need to address, particularly with respect to composition and addressing the significant sampling issues associated with collecting scat from the wild. However, the intention of this simulation study was to look at some of the basic error and bias errors inherent to diet reconstruction in a captive feeding environment. In future simulations, scats could be selected randomly or at one particular time to replicate a scat collection.

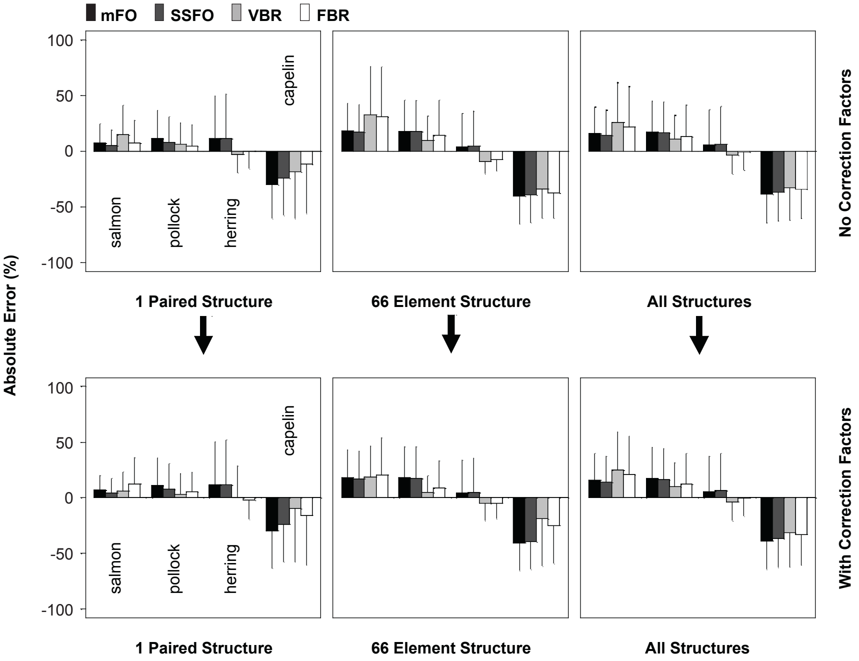


Figure 3a. Results of a simulation experiment in which sea lions were fed a diet of 2.5% salmon, 7.5% pollock, 22.5% herring, and 66.5% capelin. In the left-most graphs, a paired structure such as otoliths was used to infer proportion of fish eaten or relative biomass. In the middle graphs a multiple element structure such as vertebrae was used, and in the right-most graphs all structure techniques (here 10 paired structures) were used. In this simulation the passage probability for all structures was the same (0.40). Fish eaten is represented as four different diet reconstruction indices; for 3a, the y axis denotes the amount of absolute error in these indices, given we know what the animals were fed. The upper graphs are without correction factors applied to the structures found in the scat; the lower graphs are with correction factors applied only to BR indices. The bars represent 95% confidence intervals on the reconstruction indices. In 3b the same data is plotted with the y axis representing the difference between fed and predicted, as a percentage of the amount fed.

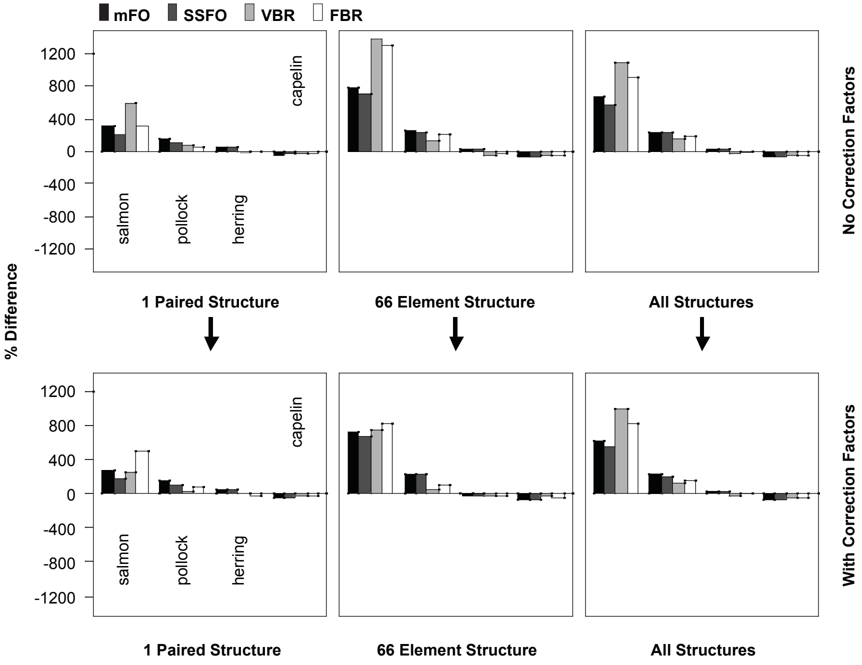


Figure 3b.

Results

Enumeration methods

The first source of error we assessed was the error that arises from estimating fish number using the MNI technique (Fig. 2). For there to be a relative measure of "no error" in fish enumeration, the ratio of expected to observed counts would be constant for any number of fish eaten. Counting fish from structures found in scat using MNI is most problematic when few fish are consumed (Fig. 2). This is true when a paired structure, a 66-element structure, or all structures are used to enumerate fish from structures recovered from scat, but is least for a paired structure. This enumeration problem becomes less important when the number of fish consumed exceeds eight (Fig. 2). The MNI enumeration error observed will contribute to error in biomass reconstruction diet indices (see following sections).

Simulations

It is important to note that simulation results are based on just two mixed diet scenarios, with the aim of taking advantage of computer simulations to understand underlying causes of error due to prey enumeration as well due to the incorporated variability in consumption, digestion rates, passage times, and deposition. Additionally, all scats are collected in these simulations, which is unlikely to be the case in the wild.

We present error using two different measures. Absolute error is defined as the difference in percentage biomass between the estimated and the actual percentages of fish fed. For example if we fed 2.5% salmon and the diet prediction was 5%, then the absolute error would be +2.5%; if the diet prediction was 1.5% then the absolute error would be –1%. An alternative method to describe error is in terms of percent difference. In this case the difference between that fed and that predicted is calculated as a percentage of the amount fed. For example, if salmon is fed at 2.5% and the diet prediction is 5%, then the percent difference would be calculated as +100%.

Frequency of occurrence indices

Frequency of occurrence indices are affected by errors associated with presence/absence data as well as variability in other parameters. In both simulations, absolute error was largest for species fed in the largest amounts (capelin in Fig. 3a and pollock in Fig. 4b). In both simulations, the proportion of a species consumed in large amounts (>65%) was underestimated (by 22-37%) with little difference between the two FO indices. Predictions of the dominant species were poorer (higher absolute error) when using more than one structure or element, as the more structures used to indicate presence increases the chances of detecting minor prey species. Those species eaten in minor amounts are typically overestimated (Figs. 3 and 4), with the exception being where a large prey item has a low recovery rate (i.e., salmon in the second simulation, Fig. 4b).

Biomass reconstruction indices

Because of the MNI enumeration biases observed (Fig. 2), both VBR and FBR indices estimate less biomass contribution from those species eaten in greater numbers than those eaten in smaller numbers. Per unit mass, larger fish will be eaten in fewer numbers, relative to small fish. Therefore, in the simulation in which passage probabilities were set to 0.40 independent of species or structure, the smaller fish (herring and particularly capelin) were underrepresented while larger fish (pollock and particularly salmon) were overrepresented (Fig. 3). Despite the controlled settings of the simulations, absolute error in the BR indices ranged from zero to <40%, but were least when a single paired structure was used. Ninety-five percent confidence limits remained large across different structures used to enumerate, and across species (Fig. 3a). In the second simulation when recovery rates varied by species but no correction factors were applied, the smaller prey (herring and capelin) with relatively low recovery rates were underestimated and pollock (the

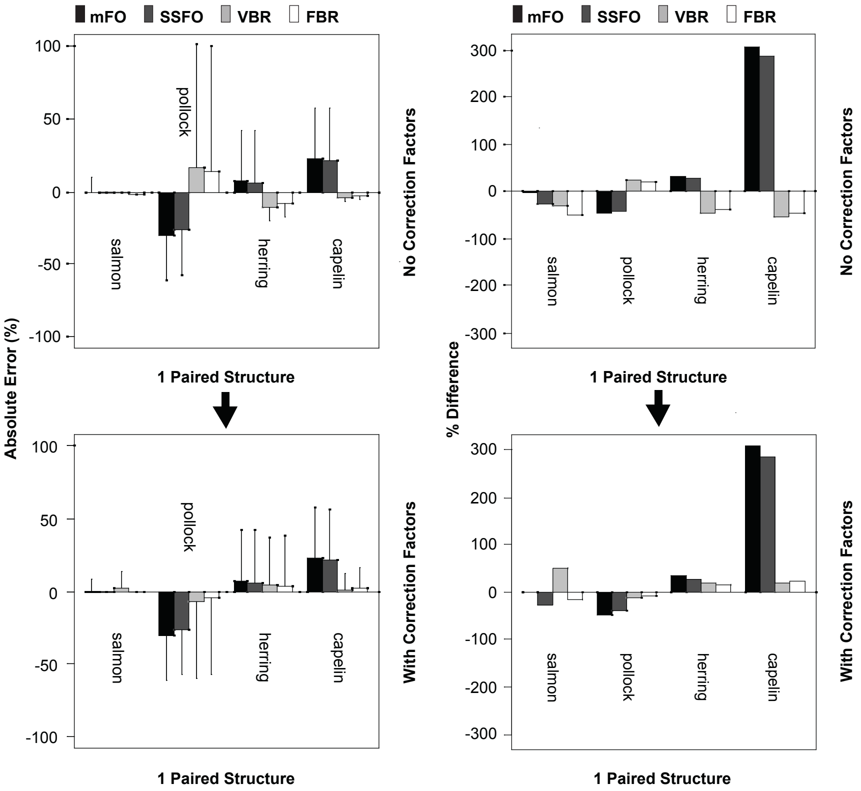


Figure 4. **(Left) Results of a second simulation experiment in which sea lions were fed on a diet of 3% salmon, 66% pollock, 23% herring, and 8% capelin. Passage probabilities for a paired structure such as otoliths were varied by species and reflect those of captive feeding trials. Proportion of prey consumed is shown as four different diet reconstruction indices, where the y axis denotes the amount of absolute error in these indices given we know what the animals were fed. The upper graph is without correction factors applied to the structures found in the scat, and the lower graph is with species and structure specific correction factors applied. The bars represent 95% confidence intervals on the reconstruction indices. (Right) The same data is plotted with the y axis representing the difference between fed and predicted as a percentage of the amount fed.**

species with the highest recovery rate) overestimated. In stark contrast to simulation 1, salmon was slightly underestimated, highlighting the influence of recovery rates to diet predictions (Fig. 4). When correction factors were applied, absolute error decreased, but did not disappear. In the first simulation where recovery rates were held constant (Fig. 3), the correction factor applied did not vary and therefore no change in the direction of error was observed for any species. Conversely, when species-specific correction factors were applied (Fig. 4), the direction of error changed. Prior to application, pollock is overestimated relative to herring and capelin because of its higher passage probability (0.62 vs. 0.18 and 0.15 respectively; i.e., more large robust pollock otoliths are recovered than fragile otoliths of herring and capelin). When correction factors were applied in the second simulation, pollock was slightly underestimated and herring and capelin slightly overestimated. Despite the application of perfect correction factors, error did not disappear completely due to prey enumeration problems, but was low for all species (Fig. 4). In the case of salmon, VBR and FBR indices after the application of correction factors provided contrasting estimates, highlighting the potential effect of using different BR methods to combine compositional data from a collection of scats.

Discussion

A key finding of this study is that the MNI technique can lead to an underestimate in the relative importance of smaller prey and an overestimate in the importance of larger prey in diet biomass reconstructions. We have shown that this bias is closely related to the number of prey consumed (Fig. 2), where smaller prey are consumed in greater numbers than larger prey per unit mass. However, we also demonstrate that this error is strongly influenced by recovery rate (Fig. 4). For example, the low recovery rate of salmon otoliths in the second simulation tends to diminish the impact of the MNI enumeration bias.

Enumeration using a structure with multiple elements brings additional problems. It takes just one structure out of two (with otoliths for example) or just one out of 66 (with vertebrae) for an entire fish to be counted. If a structure with two elements is used for enumeration, it is possible to count two fish if the structures are deposited in different scats. If vertebrae are counted instead, it is possible, although unlikely, to count as many as 66 fish if elements are deposited in different scats over time. When all structures are used to enumerate fish, there are similar problems in that it becomes easier to detect just one fish. Overall, paired structures with reasonable passage probabilities provide the best estimate of diet and using a 66 element structure the worst. In captive feeding experiments, overcounting of large fish from single meals distributed over multiple scats has been reported and can amount to an overestimate in the number of fish of more than 30% when all structure techniques are used (Tollit et al. 2003).

The SSFO method, like FBR, is based on an equal weighting of each scat (Olesiuk et al. 1990, Laake et al. 2002). The SSFO model estimates diet composition by presence only, while FBR determines composition by enumerating bones and estimating prey size. We used diet scenarios with four prey species consumed in very different amounts and collected all scats. Such a scenario is likely to be the greatest challenge to the accuracy of any index that uses frequency of occurrence data. As shown in our simulations (Figs. 3 and 4), the fish species that numerically dominated the diet was always underestimated, with species fed in smaller quantities typically overestimated, unless recovery rates were low. Use of multiple structures increases the chance of counting the first fish (and hence presence), and therefore the likelihood of counting those prey species fed in small numbers. Thus the FO indices perform less well when more elements or structures are used and performance of these indices is likely to be optimal when scats have low species diversity and approximately equal prevalence. Typically FO methods tend to predict prey species proportions close to 1 divided by the number of species consumed; thus perhaps the worst-case scenario is when structures from many large fish are found in a scat with a single structure from one small fish of a different species.

In addition, if the time taken for bones of different species to pass through the gut varies (as seen in Steller sea lions, see Tollit et al. 2003), then this may affect the probability of detecting prey species in scats deposited on shore following a trip to sea. Some alternate kind of transit rate correction factor may be needed to account for the error introduced by some species whose remains pass through in many scats, and others whose remains pass through quickly in few scats.

These simulations have highlighted some of the major differences between frequency of occurrence and biomass reconstruction indices. In the first simulation where large fish were unimportant in the diet (<8% of diet) and passage probabilities were the same for all species/structures, the four indices had similar inclinations in over- and underestimating large and small species. Here, few large fish (pollock and salmon) were eaten but remains were still present in scats; thus both occurrence and MNI methods overestimate the proportion of these species in the diet. In the second simulation, a relatively large species (pollock) made up a large part of the diet and had a relatively high passage probability. When a species' remains dominate in scats but other species' remains are also present, FO methods underestimate the importance of this dominant species. In this second simulation, the overestimation of pollock using BR methods and the high degree of variability is not attributable to MNI, but instead primarily is a result of different passage probabilities by species. VBR and FBR both overestimate pollock's importance in the diet due to the higher passage rate of pollock structures, and the lack of appropriate correction factors.

Correction factors correct for some of these differences in the volumetric indices, and thus both biomass reconstructions showed improvements with their application (lower panels in Figs. 3 and 4). However, correction factors do not completely overcome problems caused by MNI methods. From our small-scale study, it is clear that unless new methods are devised to count the number of individuals represented by multiple structures, then a paired bone with a correction factor applied represents the best method when using biomass reconstruction indices to describe diet. Better counting methods should be explored, for example one that doesn't rely on rounding up to the nearest integer, but uses observed proportions and/or a synthesis of multiple structures. However, this method would undoubtedly lead to additional time to analyze scat samples, as well as increasing the necessary species identification skills. Ideally, if a paired bone is chosen, then it would be the most robust available (i.e., has the highest passage probability), not simply the easiest to identify.

The approach described here (combining computer simulations with data from captive feeding studies) can provide a valuable framework for additional studies. It also appears that differences in estimators occur particularly because of the interaction between prey size and passage probability and their inherent assumptions, as well as from enumeration errors that then translate to errors in biomass reconstruction indices. Increasing the range of diet scenarios tested and selecting the best choice between these indices should be a priority in any future simulation work.

Acknowledgments

Funding for this project was provided to the North Pacific Universities Marine Mammal Research Consortium by the National Oceanographic and Atmospheric Administration and the North Pacific Marine Science Foundation. We would like to thank the marine mammal trainers and staff of the Vancouver Aquarium Marine Science Centre, the contribution of personnel of the Marine Mammal Research Unit and also S. Crockford of Pacific IDentifications Inc., Victoria. We would also like to express gratitude to the organizations and companies that have donated fish to the project. Work was undertaken in accordance with UBC Animal Care Committee guidelines.

References

Allen, J., and J.B.M. Guy. 1984. Optimal estimations of individuals in archaeological faunal assemblages: How minimal is the MNI? Archaeological Oceania 19:41-47.

Arim, M., and D.E. Naya. 2003. Pinniped diets inferred from scats: Analysis of biases in prey occurrence. Can. J. Zool. 81:67-73.

Bowen, W.D. 2000. Reconstruction of pinniped diets: Accounting for complete digestion of otoliths and cephalopod beaks. Can. J. Fish. Aquat. Sci. 57:898-905.

Browne, P., J.L. Laake, and R.L. Delong. 2002. Improving pinniped diet analyses through identification of multiple skeletal structures in fecal samples. Fish. Bull. U.S. 100:423-433.

Cottrell, P.E., and A.W. Trites. 2002. Classifying prey hard part structures recovered from fecal remains of captive Steller sea lions (*Eumetopias jubatus*). Mar. Mamm. Sci. 18:525-539.

Croxall, J.P. 1993. Diet. In: R.M. Laws (ed.), Antarctic seals: Research methods and techniques. Cambridge University Press, Cambridge, pp. 268-290.

Laake, J.L., P. Browne, R.L. DeLong, and H.R. Huber. 2002. Pinniped diet composition: A comparison of estimation models. Fish. Bull. U.S. 100:434-477.

Nichol, R.K., and C.J. Wild. 1984. Numbers of Individuals in faunal analysis: The decay of fish bone in archaeological sites. J. Arch. Sci. 11:35-51.

Olesiuk, P.F., M.A. Bigg, G.M. Ellis, S.J. Crockford, and R.J. Wigen. 1990. An assessment of the feeding habits of harbour seals (*Phoca vitulina*) in the Strait of Georgia British Columbia based on scat analysis. Can. Tech. Rep. Fish. Aquat. Sci. 1730. 135 pp.

Sinclair, E.H., and T.K. Zeppelin. 2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). J. Mamm. 83(4):973-990.

Tollit, D.J., M. Wong, A.J. Winship, D.A.S. Rosen, and A.W. Trites. 2003. Quantifying errors associated with using prey skeletal structures from fecal samples to determine the diet of the Steller sea lion (*Eumetopias jubatus*). Mar. Mamm. Sci. 19:724-744.

Tollit, D.J., S.G. Heaslip, T.K. Zeppelin, R. Joy, K.A. Call, and A.W. Trites. 2004. Improving size estimates of walleye pollock and Atka mackerel consumed by Steller sea lions using digestion correction factors and bones recovered in scats. Fish. Bull. U.S. 102:498-508.

Steller Sea Lion Feeding Habits in the Russian Far East, 2000-2003

Jason N. Waite
Alaska SeaLife Center, Seward, Alaska

Vladimir N. Burkanov
Natural Resources Consultants, Inc., Seattle, Washington, and Kamchatka Branch of the Pacific Institute of Geography, Russian Academy of Sciences, Petropavlovsk-Kamchatsky, Russia

Abstract

During the breeding seasons of 2000-2003 we collected 1,724 scats from seven rookeries and eighteen haul-outs on the Kamchatka Peninsula and in the Kuril Islands, Okhotsk Sea, and Commander Islands to analyze the diet of Steller sea lions (*Eumetopias jubatus*) in the Russian Far-East. The most frequently encountered prey items in all scats combined were Atka mackerel (*Pleurogrammus monopterygius*), walleye pollock (*Theragra chalcogramma*), salmon (*Oncorhynchus* sp.), sculpins (Cottidae), cephalopods, Pacific sand lance (*Ammodytes hexapterus*), Pacific herring (*Clupea pallasii*), Northern smoothtongue (*Leuroglossus stilbius*), snailfish (Liparidae), and Pacific cod (*Gadus macrocephalus*).

Spatial differences were analyzed by comparing frequency of occurrence (FO) values on a site-by-site basis for each year and all years combined. Breeding-season collection sites were grouped into seven geographic regions based on FO similarities using cluster analysis. Diet diversity was calculated for each of these geographic regions. No significant relationship was found between diet diversity and population trend ($P = 0.886$). Significant differences in diet composition were found between geographic regions ($P < 0.001$ for all regions). Significant seasonal differences were also detected at two haul-outs on the Kamchatka Peninsula from which an additional 93 scats were collected during the fall molt ($P < 0.001$ for both locations).

Introduction

The Steller sea lion (*Eumetopias jubatus*) ranges along the continental shelf of the Pacific Ocean from the Kuril Islands and Okhotsk Sea, across the Bering Sea and the Gulf of Alaska, and south along the coast of North America to California. The Steller sea lion population in the United States was listed under the U.S. Endangered Species Act as threatened in 1990. The Steller sea lion was listed in the Russian Red Book as an endangered species in 1994. Based on genetic studies, population dynamics, and morphological studies, the Steller sea lion population was divided into two separate stocks by the National Marine Fisheries Service (NMFS 1995, Bickham et al. 1996). The eastern stock (east of 144°W) appears to be stable or increasing (Calkins et al. 1999), while the Alaska population of the western stock has declined 80-90% over the last 20-30 years (NMFS 1995). In 1997, the western stock in Alaska was classified as "endangered" under the U.S. Endangered Species Act (U.S. Federal Register 62:24345-24355). The Steller sea lion population of the Kuril Islands, Okhotsk Sea, and Bering Sea in Russia is part of the western stock and has also been unstable for the last three decades (Perlov 1977, Burkanov et al. 1991, Loughlin et al. 1992, Burkanov 2000).

Though the cause for the Steller sea lion decline in Alaska has not yet been determined, one of the leading hypotheses is nutritional stress or food limitation as a result of changes in the quantity and/or quality of certain prey items (Calkins and Goodwin 1988; NMFS 1995, 2001). Studies that have been conducted in North American waters to describe the diet of Steller sea lions (Imler and Sarber 1947, Mathisen et al. 1962, Fiscus and Baines 1966, Pitcher 1981, Merrick and Calkins 1996, Merrick et al. 1997, Riemer and Brown 1997, Sinclair and Zeppelin 2002, etc.) allow for spatial and temporal analyses of prey utilization in these areas over time, and a significant relationship between diet diversity and rate of population change has been described (Merrick et al. 1997). Information on the diet of Steller sea lions in Russian waters, however, is intermittent and sparse (Belkin 1966, Panina 1966, Perlov 1975). The primary purpose of this study was to describe the recent diet of Steller sea lions in Russian waters. The data presented here have been used to explore a preliminary relationship between diet diversity and population trends in the Russian Far-East; however, additional scat collections through 2005 and population surveys through 2006 are being performed in order to perform a more comprehensive analysis.

Methods

During the breeding seasons of 2000-2003 (May through August) we collected 1,728 scats from seven rookeries and nineteen haul-outs on the Kamchatka Peninsula and in the Kuril Islands, Okhotsk Sea, and Com-

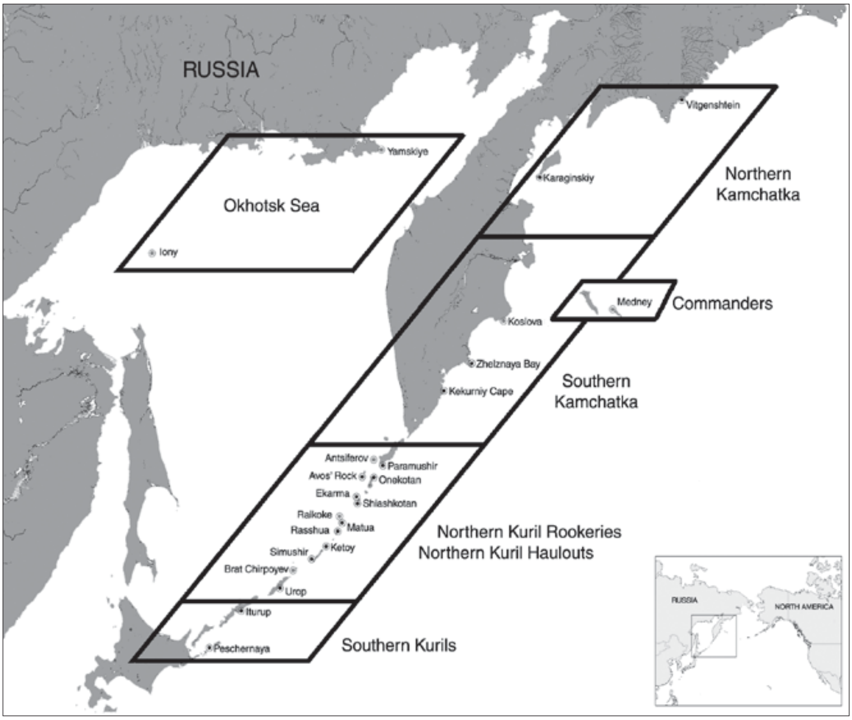


Figure 1. Scat collection sites and geographic regions of diet similarity.

mander Islands (Fig. 1). An additional 93 scats were collected from two of these haul-outs in the fall during molt (Table 1). Scats were collected opportunistically when rookeries and haul-outs were disturbed for other research purposes.

Population counts were performed on rookeries and haul-outs from both land and sea. Land-based counts were performed from an elevated vantage point whenever possible. The few boat-based counts that were performed were only done at haul-outs and only when weather conditions would not allow landing a skiff on the rocks. Field camps were also placed on five of the rookeries and one rookery was monitored via remote video system. At these locations, regular counts were performed throughout the breeding season.

Each scat was placed in a plastic zip-loc bag and processed in the field onboard the support vessel. The plastic bags were filled with water and a mild dishwashing detergent and allowed to soak for 12-24 hours while being agitated by the movement of the vessel. The resulting slurry was rinsed through a series of three nested mesh sieves (VWR Scientific,

Table 1. Total number of scats collected in the Russian Far-East from 2000 to 2003 by year, location, and season.

	2000	2001	2002		2003	
Location	Breed	Breed	Breed	Molt	Breed	Location total
Antsiferov	25	33	70	–	121	249
Avos Rock	–	9	20	–	–	29
Brat Chirpoyev	54	29	32	–	68	183
Ekarma	–	5	–	–	–	5
Iony	–	97	59	–	–	156
Iturup	–	18	–	–	–	18
Karaginsky	–	–	21	21	–	42
Kekurniy	–	12	68	–	16	96
Ketoy	–	28	–	–	–	28
Kozlov	–	9	74	72	–	155
Matua	–	12	–	–	27	39
Medny	–	12	–	–	–	12
Onekotan/KYP	–	39	30	–	–	69
Paramushir	–	40	–	–	–	40
Peshchernaya	–	32	–	–	78	110
Rasshua	–	10	–	–	–	10
Raykoke	–	42	14	–	58	114
Shiashkotan	–	33	40	–	103	176
Simushir	–	38	19	–	45	102
Urop	–	–	–	–	50	50
Vitgenshteyn	–	–	21	–	–	21
Yamskiye	–	16	44	–	–	60
Zheleznaya	–	–	53	–	–	53
Season total	79	518	565	93	566	1,821

#18, #25, and #35 U.S. Standard Size). Solid fecal material was gently wiped with a soft brush and rinsed with water until it passed through the sieves. The remaining undigested elements were frozen and brought back to either the Alaska SeaLife Center (Seward, Alaska) or the National Marine Mammal Lab (Seattle, Washington) where they were then dried, placed into vials, and shipped to Pacific IDentifications (Victoria, British Columbia) for analysis.

The relative importance of each prey item was calculated using simple frequency of occurrences (FO). Scats that were empty and remains that could not be identified with certainty to at least the family level were not included in the analysis.

Spatial differences were analyzed by comparing FO values on a site-by-site basis for each year and all years combined. Identified prey items were grouped into seven categories: (1) gadids; (2) salmon; (3) forage fish; (4) flatfish; (5) hexagrammids; (6) cephalopods; and (7) other prey (Merrick et al. 1997). If a scat contained more than one species from a particular category, it was scored as having a single occurrence of that individual category. The relative importance of each of these categories was calculated using split-sample frequency of occurrence (SSFO) (Merrick et al. 1997). Breeding-season collection sites were grouped into geographic regions based on these SSFO values using an agglomerative hierarchical cluster analysis (Sinclair and Zeppelin 2002). A diet diversity index (DDI) was calculated for each rookery and for each region using the SSFOs and Shannon's index of diversity (Ludwig and Reynolds 1988). The population trends estimated from 2000-2004 for each of these regions were compared to the corresponding DDI.

Seasonal differences were analyzed for the two haul-outs for which scats were collected in both summer and fall.

Results

A total of 83 different prey items were identified (50 to species) in the 1,633 scats that contained identifiable remains. The ten most frequently encountered prey items in all scats combined were Atka mackerel (*Pleurogrammus monopterygius*), walleye pollock (*Theragra chalcogramma*), salmon (*Oncorhynchus* sp.), sculpins (Cottidae), cephalopods, Pacific sand lance (*Ammodytes hexapterus*), Pacific herring (*Clupea pallasii*), northern smoothtongue (*Leuroglossus stilbius*), snailfish (Liparidae), and Pacific cod (*Gadus macrocephalus*).

Plotting the results of the cluster analysis by geographic location resulted in seven distinct geographic areas of prey similarity: Northern Kamchatka Peninsula, Southern Kamchatka Peninsula; Commander Islands; Northern Kuril Island rookeries; Northern Kuril Island haul-outs; Southern Kuril Islands; and the Northern Sea of Okhotsk (Fig. 1). The Commander Islands may have been identified as a separate cluster due to the small sample size from that site ($n = 12$). Chi-square was used to test the hypothesis that there was no difference between the diets of each cluster ($\chi^2 = 2476.914$, $P < 0.001$). Diet composition for each region is given in Table 2.

There was not a significant relationship between diet diversity and rookery population trends ($R^2 = 4.56 \times 10^{-3}$, $P = 0.886$) or population trends by cluster ($R^2 = 0.0616$, $P = 0.591$) (Fig. 2). For example, the South-

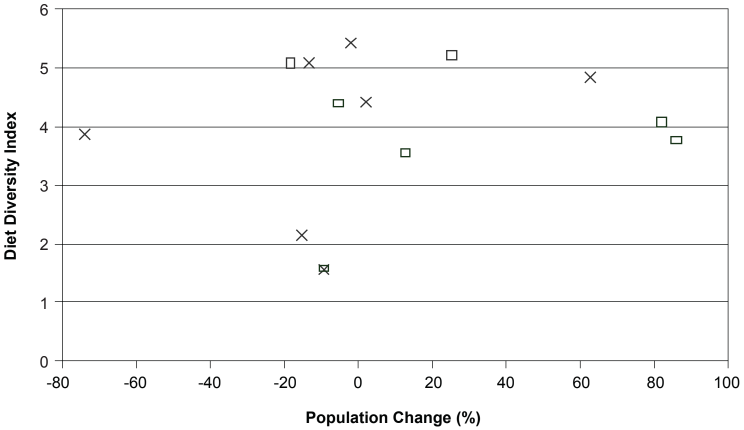


Figure 2. Rate of population change versus diet diversity index. X represents clusters and square represents individual rookeries.

ern Kuril Islands had the highest level of diet diversity (DDI = 5.44), but had a relatively stable population trend, whereas the Southern Kamchatka Peninsula had the second highest level of diet diversity (DDI = 5.07) but also the second highest level of population decline.

The ten most common prey items consumed by Steller sea lions in the Russian Far East were similar to those consumed by the western stock in Alaska waters (Sinclair and Zeppelin 2002); however, the proportions consumed were significantly different ($\chi^2 = 20.727$, $P = 0.014$). The primary contributor to this result is the significantly higher occurrence of sculpins (FO = 26%). Differences in the proportion of other prey items consumed were not significant at the 5% level ($\chi^2 = 10.950$, $P = 0.205$).

The 2002 summer and fall diets of sea lions on Koslova Cape, a rookery on the Kamchatka Peninsula, were significantly different ($\chi^2 = 340.797$, $P < 0.001$). During the breeding season, the three primary prey items were walleye pollock, Atka mackerel, and sculpins. In the fall, Pacific sand fish (*Trichodon trichodon*) and salmon were the dominant prey items. Poachers (Agonidae), pricklebacks (Stichaeidae), and Arctic lampreys (*Lampetra japonica*) occurred in high numbers during the fall but did not occur during the breeding season.

The 2002 summer and fall diets of sea lions on Karaginsky Island, a haul-out on the Kamchatka Peninsula, were also significantly different ($\chi^2 = 529.939$, $P < 0.001$). During the fall, the sea lions switched from a diet of primarily sculpins and sand lance to one consisting almost entirely of salmon and skates (*Raja* sp.).

Table 2. Frequency of occurrence of prey items found in sea lion scat collected in the Russian Far-East during 2000-2003.

	Frequency of occurrence (%)						
Prey item	Russian range $n = 1633$	Northern Kamchatka $n = 42$	Southern Kamchatka $n = 226$	N. Kuril haul-outs $n = 524$	N. Kuril rookeries $n = 503$	Southern Kurils $n = 125$	Sea of Okhotsk $n = 201$
Anchovy sp.	4.2	0.0	0.0	0.2	0.0	50.4	2.0
Atka mackerel	65.7	4.8	69.5	98.1	58.8	27.2	0.5
Capelin	6.6	38.1	35.0	0.0	2.2	0.0	0.5
Cephalopods	14.2	4.8	6.6	8.2	20.9	21.6	14.9
Flatfish sp.	3.4	16.7	11.5	0.4	1.6	5.6	2.5
Greenling sp.	3.1	7.1	7.5	2.9	3.8	8.8	0.0
Gunnel sp.	2.1	4.8	0.4	1.7	0.2	12.8	1.5
Herring	9.2	0.0	0.9	0.2	2.0	0.8	67.7
Lampfish sp.	1.6	0.0	2.2	0.8	2.8	0.0	1.0
Lumpsucker sp.	2.4	2.4	1.3	2.1	3.6	0.8	0.5
N. smoothtongue	7.1	0.0	0.0	1.3	20.9	0.0	2.0
Other gadids	2.1	42.9	1.3	0.4	0.2	6.4	1.0
Pacific cod	6.9	2.4	11.5	1.3	4.4	41.6	1.5
Pollock	32.4	23.8	62.4	6.5	38.4	14.4	65.2
Polychaete worms	10.1	9.5	15.0	7.3	7.2	4.0	16.9
Prickelback sp.	2.8	2.4	0.0	3.2	1.0	12.0	0.5
Salmon sp.	29.9	0.0	14.6	10.7	60.4	5.6	41.8
Sand lance	10.6	95.2	31.4	1.9	2.4	29.6	0.5
Sandfish	2.2	2.4	8.8	1.7	0.6	0.8	0.0
Sculpin sp.	25.7	92.9	53.1	8.6	10.1	76.8	25.4
Skate sp.	3.0	0.0	12.4	0.6	1.4	6.4	1.5
Smelt sp.	0.9	0.0	5.3	0.0	0.0	2.4	0.0
Snailfish sp.	7.1	11.9	7.1	9.5	2.6	8.8	4.0
Stickleback sp.	3.4	14.3	17.7	0.2	1.6	0.0	0.0

Commander Islands are not shown (100% Atka mackerel, 33% polychaete worms, $n = 12$).

Discussion

Plotting the results of the cluster analysis by geographic location resulted in distinct groups of contiguous sites. This pattern is likely to be mainly an artifact of fish distribution due to latitude and season. The effect of normal geographic fish distribution is most evident by the distinctly different diets of sea lions in the northern- and southern-most clusters. Anchovies, most likely Japanese anchovy (*Engraulis japonicus*), occur only in the Southern Kurils cluster where they are the second most frequently occurring prey item (50.4%). The northern range of this species is the southern Sakhalin Islands, the Sea of Japan, and the Pacific coasts of Japan (Whitehead et al. 1988), which explains its occurrence in scat collected in the southern Kuril Islands only. A conglomerate of "other" gadids, such as Arctic cod (*Boreogadus saida*) and saffron cod (*Eleginus gracilis*), but not Pacific cod or walleye pollock, are the third most commonly occurring prey items in the Northern Kamchatka cluster (42.9%). Arctic cod have a more northern distribution and saffron cod are more likely to be found in the shallow coastal waters of the mainland (Cohen et al. 1990) rather than the deep waters surrounding the offshore islands of the Kuril chain.

The timing of local fish runs and scat collection efforts may also have influenced the results of the cluster analysis. The majority of the breeding season scat collections occurred in late June and early July. By this time, offshore salmon schools may have already passed through the southern Kuril chain but not yet reached the near-coastal waters of the Kamchatka Peninsula. During the summer, salmon occurred in only 14.6% of scats in the Southern Kamchatka cluster. However, in the fall the FO of salmon increased to 58.7%.

The diet of sea lions in the Russian Far-East is similar to that of sea lions in the western stock in Alaska (Sinclair and Zeppelin 2002). Like in the Aleutian Islands, Atka mackerel, walleye pollock, and salmon are the most commonly consumed prey items. The most noticeable difference in diet between the two populations is the abundance of sculpins consumed by the sea lions in Russia. Sculpins were found in one quarter of all scats collected and are among the top three most predominant prey items in half of the diet clusters (Table 2). Unfortunately, little is know regarding the nutritional value of this family. Eighteen species of sculpins were identified in the scat, but published nutritional values are available for only a few of these species. However, some species, such as yellow Irish lord (*Hemilepidotus jordani*), have a higher percent lipid value than salmon and energetic densities similar to salmon, adult pollock, and Pacific cod (Logerwell and Schaufler 2005).

Merrick et al. (1997) found that as diet diversity in Alaska decreased, the rate of population decline increased, and suggested that sea lions need a variety of prey as a buffer against major changes in any single prey item; thus a population with a higher diet diversity index would be better prepared in the event of a crash of any given prey species than a population that relied primarily on only one or two prey items. Although Merrick et al. (1997) used diet data from the early 1990s, which may not reflect the oceanographic conditions or prey availability during the years of this study (1999-2003), the diet diversity index is based only on the number of prey groups consumed and does not take into consideration which specific prey items or groups these are or the nutritional quality of those prey items. Therefore, the diet diversity hypothesis as presented by Merrick et al. (1997) should be applicable regardless of the availability of specific prey items, oceanographic conditions, or geographic region. However, this trend was not found in Russian waters, wherein some of the areas with the highest levels of diet diversity also had the highest levels of population decline.

While the availability of alternate food sources may be important, calculating diet diversity based on scat content only provides an index of what a particular population happened to be consuming at the time of scat collection, and does not necessarily represent everything that is available for consumption. Populations that are feeding primarily on one or two species (i.e., "low diet diversity") may be doing so because of a high abundance of those species, not because of a reliance on those species. The absence of other species in the scat does not necessarily indicate the absence of other prey items available for the sea lions to consume in the event that their primary prey item is diminished. The opposite may apply to populations with high diet diversity. While the consumption of many different prey items may indicate the availability of many different prey items, it may also indicate the lack of a primary or abundant food source. The sea lions in these regions may be consuming lower proportions of multiple prey items in an effort to compensate for the lack of an abundant primary prey item.

The current method for calculating Steller sea lion diet diversity indexes may not accurately describe diet diversity in a way that can be used to make inferences to foraging behavior, foraging success, prey availability, and population trends. Using split-sample frequencies of occurrence and presence vs. absence of a limited number of broad prey categories, a collection of scats that contains the remains of only three prey species could have the same diet diversity index as a collection that contains 35 different prey species. Little can be said about the foraging success of these two populations without considering the individual species and nutritional quality of the prey consumed, amounts of each prey item consumed (rather than using presence/absence), and actual prey availability.

Instead of relying on simple frequency of occurrence and diet diversity index, a comprehensive Diet Quality Index should be developed that incorporates size and minimum number of prey individuals consumed, digestive correction factors like those described by Tollit et al. (2004), and the nutritional quality of each prey species. Population structure should be considered before average caloric intake and diet quality can be compared between sites, as different age classes, sexes, and reproductive statuses may have different energy requirements. In addition to describing the prey consumed by sea lions, it is important to determine the prey available for consumption in any given area before an accurate assessment of foraging success can be made.

Acknowledgments

We gratefully acknowledge the National Marine Fisheries Service (NMFS) and the Alaska SeaLife Center for their funding and support of this project, along with the Kamchatka Branch of the Pacific Institute of Geography Russian Academy of Sciences, and Pacific Identifications, Inc. We also thank Y. Artukhin, S. Kornev, S. Purtov, and A. Trukhin for samples collected in 2000 and the personnel from the Alaska SeaLife Center, NMFS, and North Pacific Wildlife Consulting, LLC, who helped collect and process the scats.

References

Belkin, A.N. 1966. Summer distribution, stocks, prospects of harvest, and some features of biology of the sea lions inhabiting the Kuril Islands. Izv. TINRO 58:69-95. (In Russian.)

Bickham, J.W., J.C. Patton, and T.R. Loughlin. 1996. High variability for control region sequences in a marine mammal: Implications for conservation and biogeography of Steller sea lions. J. Mammal. 77:95-108.

Burkanov, V.N. 2000. Steller sea lion population status and dynamics in Russian waters in 1989-1999. Marine mammals of holarctic region: Materials of international scientific conference. Arkhangelsk, 21-23 September, 2000. Pravda Severa, Arkhangelsk, pp. 56-65. (In Russian.)

Burkanov, V.N., A.R. Semenov, and V.V. Vertyankin. 1991. Counts of Steller sea lions at Kamchatka and the Commander Islands, U.S.S.R., during June and July 1989. NMFS AFSC Processed Report 91-31, Seattle.

Calkins, D.G., and E.A. Goodwin. 1988. Investigation of the declining sea lion population in the Gulf of Alaska. Unpubl. Report, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518. 76 pp.

Calkins, D.G., D.C. Mcallister, K.W. Pitcher, and G.W. Pendleton. 1999. Steller sea lion status and trend in Southeast Alaska: 1979-1997. Mar. Mamm. Sci. 15:462-477.

Cohen, D.M., T. Inada, T. Iwamoto, and N. Scialabba. 1990. FAO species catalogue. Vol. 10. Gadiform fishes of the world (order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. FAO Fish. Synop. 10(125). 442 pp.

Fiscus, C.H., and G.A. Baines. 1966. Food and feeding behavior of Steller and California sea lions. J. Mammal. 47:195-200.

Imler, R.H., and H.R. Sarber. 1947. Harbor seals and sea lions in Alaska. U.S. Fish and Wildlife Service, Spec. Sci. Rep. 28. 23 pp.

Logerwell, E.A., and L.E. Schaufler. 2005. New data on proximate composition and energy density of Steller sea lion (*Eumetopias jubatus*) prey fills seasonal and geographic gaps in existing information. Aquat. Mamm. 31(1):62-82.

Loughlin, T.R., A.S. Perlov, and V.A. Vladimirov. 1992. Range-wide survey and estimation of total number of Steller sea lions in 1989. Mar. Mamm. Sci. 8(3):220-239.

Ludwig, J.A., and J.F. Reynolds. 1988. Statistical ecology. John Wiley and Sons, New York.

Mathisen, O.A., R.T. Baade, and R.J. Lopp. 1962. Breeding habits, growth and stomach contents of the Steller sea lion in Alaska. J. Mammal. 43:469-477.

Merrick, R.L., and D.G. Calkins. 1996. Importance of juvenile walleye pollock, *Theragra chalcogramma*, in the diet of Gulf of Alaska Steller sea lions, *Eumetopias jubatus*. NOAA Tech. Rep. NMFS 126, pp. 153-166.

Merrick, R.L., M.K. Chumbley, and G.V. Byrd. 1997. Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: A potential relationship. Can. J. Fish. Aquat. Sci. 54:1342-1348.

NMFS. 1995. Status review of the United States Steller sea lion (*Eumetopias jubatus*) population. NMFS, National Marine Mammal Laboratory, Seattle. 92 pp.

NMFS. 2001. Endangered Species Act. Section 7 Consultation: Biological opinion on authorization of Gulf of Alaska and Bering Sea/Aleutian Islands groundfish fisheries based on the Fishery Management Plan for the Gulf of Alaska and Bering Sea/Aleutian Islands groundfish as modified by amendments 61 and 70. NMFS Alaska Region, Protected Resources Division, Silver Spring, Maryland.

Panina, G.K. 1966. Diet of Steller sea lion and seals on Kuril Islands. Izv. TINRO 58:235-236. (In Russian.)

Perlov, A.S. 1975. The food of sea lions in the vicinity of the Kuril Islands. Ekologia 4:106-108. (Translated from Russian.)

Perlov, A.S. 1977. Number of sea lions in the Okhotsk Sea. Byull. Mosk. Ob-va Ispyt. Prir., Otd. Biol. 82(4):19-22. (Translated by A.Y. Roppel, NMML, Seattle, 1979.)

Pitcher, K.W. 1981. Prey of the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska. Fish. Bull. U.S. 79(3):467-472.

Riemer, S.D., and R.F. Brown. 1997. Prey of pinnipeds at selected sites in Oregon identified by scat (fecal) analysis, 1983-1996. Technical report 97-6-02. Oregon Department of Fish and Wildlife, Wildlife Diversity Program, Marine Region, Newport. 34 pp.

Sinclair, E.H., and T.K. Zeppelin. 2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). J. Mammal. 83(4):973-990.

Tollit, D.J., S.G. Heaslip, T.K. Zeppelin, R. Joy, K.A. Call, and A.W. Trites. 2004. A method to improve size estimates of walleye pollock and Atka mackerel consumed by pinnipeds using digestion correction factors applied to bones and otoliths recovered in scats. Fish. Bull. U.S. 102:498-508.

Whitehead, P.J.P., G.J. Nelson, and T. Wongratana. 1988. FAO species catalogue. Vol. 7. Clupeoid fishes of the world (suborder Clupeoidei). An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. Part 2, Engraulidae. FAO Fish. Synop. 125(7/2):305-579.

Techniques for Real-Time, Active Tracking of Sea Lions

Mary-Anne Lea[1]
University of British Columbia, The Behaviour@Sea Project, Marine Mammal Research Unit, Fisheries Centre, Vancouver, B.C., Canada

Ben Wilson
University of British Columbia, The Behaviour@Sea Project, Marine Mammal Research Unit, Fisheries Centre, Vancouver, B.C. Canada; and Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, Oban, Argyll, Scotland, UK

Abstract

The movements of otariids at sea are generally studied by satellite telemetry. At fine scales (1-20 km), however, the level of precision provided by this technique (± mean 1.5-19 km) may be insufficient to accurately reconstruct the track of an individual and/or integrate such movement data with habitat and environmental features. An alternative technique is the boat-based active tracking of individuals by very high frequency (VHF) or acoustic telemetry. By following an individual equipped with transmitters, detailed observations of habitat use, predator occurrence, social context, behavioral state, and prey availability may be integrated to provide a real-time context in which to place the animals' movements. For species such as the Steller sea lion *(Eumetopias jubatus)*, which are difficult to recapture, such techniques enable the collection of much needed contextual information. Here we describe the methods we applied to actively track Steller sea lions. Twenty-one juveniles were captured in Southeast Alaska during October 2003 and February 2004. They were fitted with a variety of VHF, satellite, and/or acoustic tags and were tracked through the winter and spring of 2003-2004. The use of ship-based VHF telemetry in conjunction with real time navigation plotting software was highly successful and provided 37 fine-scale tracks of coastal and pelagic

---

[1] Current affiliation: University of Tasmania, Antarctic Wildlife Research Unit, School of Zoology, Hobart, Tasmania, Australia.

sea lion movements covering a total distance of 482 km. Acoustic telemetry techniques were less successful because of the suspected overlap in tag transmission frequency and sea lion hearing. The study represents the first active tracking of a sea lion species, highlighting the high-resolution tracks and contextual behavioral and habitat information that can be obtained using VHF telemetry at sea.

Introduction

Understanding the behavior of marine mammals at sea is critical for identifying key relationships between habitat use, foraging preferences, predation risk, and the availability of prey sources. In recent decades, a many kinds of telemetry devices have been developed as tools to provide much needed information on marine mammal distribution and behavior at sea.

Over the last 15 years, the technology of satellite tracking marine mammals has proliferated (Stewart et al. 1989; McConnell et al. 1992a,b; Harcourt and Davis 1997; Stewart et al. 2000; Boyd et al. 2002). More recently, satellite telemetry data have been combined with remotely sensed data on the animal's environment (Hindell et al. 1999, Loughlin et al. 1999, Georges et al. 2000, Goebel et al. 2000, Field et al. 2001, Guinet et al. 2001, Lea and Dubroca 2003, Staniland and Boyd 2003, Beauplet et al. 2004). Static (e.g., bathymetry) and dynamic environmental variables (e.g., chlorophyll a; sea surface temperature, SST; and sea surface height, SSH) have both been integrated with animal movement data at varying temporal and spatial scales providing insights into the oceanic features influencing foraging behavior (Fedak et al. 2002, Lydersen et al. 2002). The ecological significance of such an approach is influenced by the scale of movements and the temporal and spatial resolution of environmental parameters (Bradshaw et al. 2004). For example, seasonal directed migrations of thousands of kilometers made by southern elephant seals *(Mirounga leonina)* across the open ocean can be effectively tracked with satellite telemetry (McConnell et al. 2002). In contrast, juvenile Steller sea lions *(Eumetopias jubatus)* often conduct short trips (<15 km) in coastal regions (Raum-Suryan et al. 2004). At these scales the precision of data provided by conventional satellite telemetry (Stewart et al. 1989, Raum-Suryan et al. 2004) is insufficient to fully understand the relationships between individual movements and the features encountered on these smaller scale foraging trips.

An alternative to satellite telemetry involves using tracking equipment in much closer proximity to the animal. Equipment may be fixed or mobile depending on the circumstances. Fixed gear can include arrays of radio or acoustic receivers that register the presence and location of individuals nearby (Wartzok et al. 1992, Hammond et al. 1993, Harcourt et al. 2000, Hindell et al. 2002). Fixed equipment methodologies are ideal if the range of the tagged animals is known a priori. However, if the animals are more mobile then it may be necessary to use a moving platform to follow tagged individuals, a technique known as "active" tracking (Holland et al. 2001). Under these conditions, the platform (usually a boat) carries the receiving gear and is moved relative to the location of the target animal.

Active techniques, including VHF and acoustic telemetry, have proven successful in fish (Holland et al. 1992, 1999, 2001; Block et al. 1997; Meyer et al. 2000; Voegeli et al. 2001), and whale studies (Goodyear 1993, Watkins et al. 1993, Baird et al. 2002) over short time periods (<3 days). These boat-based techniques also have been used to track grey seals *(Halichoerus grypus)* and harbor seals *(Phoca vitulina)* (Fedak et al. 1988, Thompson et al. 1991, Hammond et al. 1993, Thompson and Fedak 1993, Bjørge et al. 1995, Suryan and Harvey 1998), while northern fur seals *(Callorhinus ursinus)* have been radio-tracked using fixed wing aircraft (Ragen et al. 1995). Active tracking methods offer several advantages over more remote techniques. Besides providing data to produce a high-resolution two-dimensional path, active methods provide the opportunity to collect ancillary data such as an animal's behavior at sea (e.g., behavioral state, dive durations), physiological state (e.g., cardiac rate, Thompson and Fedak 1993) or more broadly, the physical and biological context in which the behaviors occurred.

Recent Steller sea lion telemetry research efforts have focused on the behavior of juvenile animals (Loughlin et al. 2003, Raum-Suryan et al. 2004), partly because of the logistic challenges in capturing adults (Loughlin 1998, Andrews et al. 2002), but primarily because of the importance of reduced juvenile survival in influencing the dramatic decline in population numbers (Pascual and Adkison 1994, York 1994, Trites and Larkin 1996). Here we describe the techniques that we applied to actively track juvenile Steller sea lions from a boat during the winter and spring of 2003-2004 in Southeast Alaska. Our aim was to determine where the sea lions went on their trips to sea and how these trips were executed. Study methods were chosen that did not necessitate recapturing individuals to retrieve archival tags. Additionally the lack of road access in Southeast Alaska precluded active VHF tracking from land (Tollit et al. 1998). We tested the efficacy of a variety of techniques (including boat-based VHF and acoustic telemetry) and show for the first time that it is possible to track sea lions at sea, both in daylight and darkness, and under a range of sea conditions. We outline both problematic and successful methods.

Materials and methods

Young Steller sea lions were captured during October 2003 and February 2004 at three haul-out sites (Benjamin Island, 58.560ºN, 134.916ºW; Little Island, 58.542ºN, 135.045ºW; and Gran Point, 59.132ºN, 135.239ºW) in

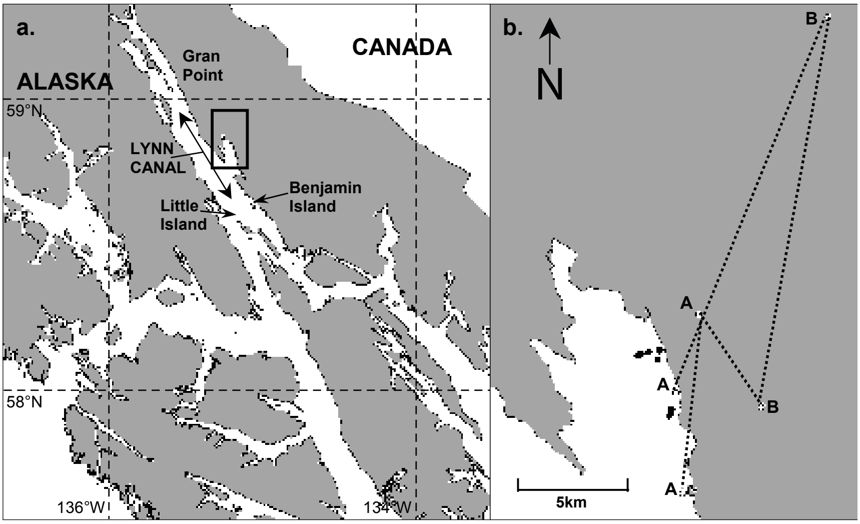


Figure 1. a. Study area and sea lion capture sites, Southeast Alaska. b. The VHF telemetry locations (●) during an 8 hour period and all Argos satellite (○, class A and B) for that day are plotted for a 35 month old female Steller sea lion in Berners Bay, 24 April 2004.

Lynn Canal, Southeast Alaska (Fig. 1a), as part of ongoing studies of Steller sea lion biology by the Alaska Department of Fish and Game (ADFG). Sea lions were captured using the underwater dive capture technique and moved to a larger boat for immobilization and processing (ADFG, Anchorage, unpubl.; Raum-Suryan et al. 2004). The combination of tag(s) that each sea lion received was scaled such that the smaller animals were not burdened by multiple or bulky tags. All animals received VHF transmitters (MM300 Series, 30 ms pulse length, reinforced stainless steel antennas, frequency range 150-152 Mhz (Advanced Telemetry Systems [ATS], Isanti, Minnesota, USA). Two of these instruments were mounted on the back with whip antennas lying along the animal's back, whereas the remaining 19 were mounted on the head with vertical antennas. Nine animals also received back-mounted satellite transmitters (three Kiwisat tags, Sirtrack Pty Ltd., Havelock Nth, New Zealand providing locations; and six series-7000 satellite relayed data loggers [SRDL], Sea Mammal Research Unit, St Andrews, Scotland, UK, providing locations and diving information). Six of the satellite-tagged Steller sea lions also carried a back-mounted acoustic transponder (VX32TP CHAT tags, VEMCO, Shad Bay, Nova Scotia, Canada).

Nylon mesh with a radius approximately 1.5 cm larger than the transmitters was attached to the bottom of each tag and then glued to the fur of the Steller sea lions using Devcon® 10-minute, clear epoxy (ITW Devcon®, Danvers, Massachusetts, USA). Back-mounted tags were placed on the dorsal mid-line slightly anterior of the shoulder blades. Following tag attachment, Steller sea lions were allowed to regain mobility and return to the water unassisted. Steller sea lions were actively tracked during 7 November–3 December 2003, 29 February–13 March 2004, and 1-30 April 2004, for a total of 10 weeks.

VHF tracking protocol

To track animals we traveled to an area highlighted by previous satellite fixes. One of two approaches was then used to detect and track animals at sea: (1) the boat approached within VHF range of the nearest haul-out site and tagged sea lions were monitored until they entered the water; or (2) VHF signals were listened for on a 4-8 s scrolling cycle while the boat was at sea engaged in other operations. Detected sea lions were then located and tracked.

We used an 18 m single propeller motor yacht fitted with an inboard diesel engine. VHF antennas were mounted on the wheelhouse roof at a height of 10.5 m above sea level (ASL). An omni-directional antenna (ATS) connected to an SRX-400 VHF receiver (Lotek Wireless Inc., Newmarket, Ontario, Canada) was used when manually searching for tagged Steller sea lions. After a signal was detected, bearings to the signal were determined using an arrangement of four directional ATS Yagi antennae mounted in a horizontal-cross formation routed to an automatic direction finder (ADF; ATS). The ADF unit compared the output from the antennas to give a display of signal strengths on a corresponding LED display. To improve the performance of the ADF, we used VHF tags with relatively long pulse lengths. Bearings were obtained from single VHF pulses using the combination of ADF and tags. The derived bearings were then drawn, in real time, as lines on a chart plotter display (Nobeltec Visual Series 2.0). This mapping software showed the position and heading of the boat on either a standard navigation chart or a high-resolution aerial photograph of the region. The boat's position on the chart was obtained from a GPS (Garmin International Inc., Olathe, Kansas, USA) and updated once each second. As the boat moved, sequential bearings to the tagged sea lion were plotted. The sea lion position was then estimated using triangulation from two or more of these bearings. Bearings from adjacent surfacings and at angles at around 90° to each other were preferred. Fixing the location of stationary animals was relatively straightforward. Moving animals were more challenging and were most easily tracked by keeping pace with them (i.e., maintaining bearings abeam and at a relatively constant angle) then periodically moving to cross their track from behind to obtain a cross bearing on their trajectory. The field VHF-derived sea lion positions were given a subjective quality rating to allow subsequent filtering. These scores ranged from 1 (excellent cross bearings and sea lion sighted) to 3 (unreliable estimate of location).

In areas of strong currents, or if the boat was stationary, the GPS system could not produce accurate estimates of the boat's heading. On these occasions, landmarks were used to determine the correct heading. Visual observations were made during the day, while RADAR was used at night. Because we were concerned that our presence might disturb the animals we were tracking, we aimed to maximize our distance to the animal while maintaining sufficient proximity to be able to see the sea lion with binoculars.

Because VHF radio waves travel well through air but not through seawater we were able to use the pauses in the VHF pulses to register the animal's diving activity. The tags transmitted approximately one pulse per second and pulses were logged manually with event recording software. The human ear is typically more sensitive than electronic signal detection systems. Though tedious, this approach also ensured that a constant vigil was kept on the strength of the radio signal. In so doing, signal loss and radio interference were dealt with immediately and any periods of known loss could be noted for exclusion in later analyses.

When tracking, attempts were made to estimate the animal's position at least four times an hour. Periods of tracking were terminated when (1) the weather deteriorated; (2) we felt that our presence might be disturbing the animal; (3) the boat was required for other studies; (4) the sea lion hauled out; or (5) the signal was lost. Two tracking crews and skippers (when available) were rotated so that 24-hour effort could be maintained.

Acoustic telemetry

Tracking studies necessarily assume that the methods used to track the animals do not overtly impact the behavior of their subjects. Disturbances stem from multiple sources including handling, the subsequent researcher presence, and the tracking devices themselves. While VHF and satellite transmitters rely on seemingly imperceptible radio waves, the high frequency acoustic transmitters that have been used to study a variety of fish and marine mammals (Hawkins et al. 1974, Holland et al. 1992, Goodyear 1993, Thompson and Fedak 1993, Dewer et al. 1999) may well be perceptible to some species. Most acoustic telemetry studies use constantly emitting acoustic tags; however, in regions inhabited by acoustically sensitive predators or prey the possibility of impact on the tagged animal needs to be considered. Killer whales *(Orcinus orca)* represent significant predators for many marine animals, including Steller sea lions, and studies of captive killer whales have shown that they can reliably hear at frequencies used by most acoustic tags (Szymanski et al. 1999). Thus, the researcher using these tags is faced with two options: (1) using purpose-made tags emitting at frequencies too high for these predators

(>150 kHz) with consequent losses in signal transmission distances or (2) using transponders which, because they are responsive, only broadcast when they themselves receive a signal from an onboard receiver. Thus these tags can be silenced if the tags are under the temporal control of the researchers and so can remain silent if predators are present.

The acoustic transponder tags we used were VEMCO CHAT tags (VX32TP; Voegeli et al. 2001) which transmitted at 32.8 kHz (163 dB) when signals (27 kHz) were received from a boat-based VR-28T set and towed hydrophones (VH-41) mounted on a fiberglass fin (VFIN, see Block et al. 1997). One cycle of transmission and reception lasted approximately 19±3 s ($n = 25$). The hydrophones were connected to the receiver by an 18 m hairy, fared Kevlar conducting cable (Cortland Cable, Cortland, New York), which permitted the towing of the VFIN at approximately 1 m depth off an outrigger. The "chatting" communication between the transponder and the towed directional hydrophones enabled range and direction to be calculated. Sensors on the tag also recorded depth and temperature data, which were transmitted as a coded acoustic signal to the receiver.

The limited data on the auditory capabilities of Steller sea lions (Kastelein et al. 2005) suggested that the broadcast frequency of the CHAT tags (32.8 kHz) might be near the high frequency limit of the hearing range of this species. To test whether these tags might cause measurable disturbances to Steller sea lions, we carried out trials on two captive animals in July 2003 at a University of British Columbia/Vancouver Aquarium facility. The trained female sea lions (aged 4 and 6 years old) were housed in a floating mesh pen with surrounding pontoons that allowed them to haul out at will. The pen was moored in a sheltered bay, floating several meters over a soft mud bottom. An active CHAT tag was lowered into the water next to the pen and the behavior of the swimming sea lions was monitored. In a second trial, the active tag was placed in a harness on the back of the sea lions and their behavior was again observed.

Behavioral context

While tracking in daylight we were able to observe the focal sea lion and collect additional data with respect to behavior. Parameters measured included the presence of other sea lions, humpback *(Megaptera novangliae)* and killer whales, foraging birds, fishing boats, and specifics of the habitat and water conditions (tidal fronts etc). Night-vision binoculars (Generation 3, ITT Industries, White Plains, New York, USA) enabled us to observe the presence of other sea lions, foraging birds, and whales.

Real-time, fine-scale animal movement data were combined with simultaneous acoustic surveys of prey distribution to provide the three-dimensional context for at-sea behavior (MacClennan and Simmonds 1992). To identify and quantify potential prey we used a fin-mounted SIMRAD EK60 scientific echosounder (Kongsberg Maritime Inc., Lynnwood, Washington, USA) towed from an outrigger on the research vessel. To examine the behavior of the sea lion in context with the prey field we conducted acoustic surveys at two spatial scales. The first were large transects encompassing Benjamin Island and Favorite Channel in Lynn Canal, Southeast Alaska, and the second were smaller transects targeting, in real time, the areas used by the tagged sea lions. The results of these analyses will be presented elsewhere.

The majority of animals in this study regularly used the Benjamin Island haul-out site in Lynn Canal (58.560°N, 134.917°W, Fig. 1). To retrospectively determine their use of the haul-out before and after our tracking sessions we placed an automatic VHF receiving station (R2100 VHF receiver and D5041A Data Collection Computer, ATS) directly behind the haul-out, which recorded the presence or absence of the seal lion VHF tags for 15-30 s every 15-30 minutes depending on the season. All hauled-out sea lions hauled out were within 150 m of the receiving station antenna, located ~20 m ASL. The receiving station operated successfully under adverse weather conditions on 12 V external deep-cycle batteries.

Results

Twenty-one juvenile sea lions (5 females, 16 males), ranging from 5 to 29 months in age and weighing 50 to 206 kg (Table 1), were fitted with either a VHF tag (n = 13), or a VHF/satellite transmitter combination (n = 8). Six of the satellite-tracked individuals also carried a back-mounted acoustic CHAT tag.

VHF tracking

Initial trials confirmed that we were able to detect and localize sea lions using the VHF telemetry equipment. The "running fix" technique proved highly effective. The ADF/VHF tag combination was able to produce bearings from single VHF pulses to within approximately 15° of the true bearing. In a blind trial, with a hidden stationary tag using typical tracking effort, we were able to estimate its position to within 50 m of the actual location. Wild, particularly moving, animals were harder to track than stationary ones but we were frequently able to validate the precision of the technique by estimating the sea lion positions and then directing a rooftop observer to visually confirm the presence of the tagged animal. This was sufficiently effective that we were able to spot the tagged animals for half of all the VHF derived locations in 2004 (49.8%, n = 801).

Using the VHF tracking equipment we followed 15 individual sea lions on 37 occasions (Table 1). Tracks ranged in duration from 12 minutes to 57 hours with the median track lasting a little over 3 hours. During these efforts we followed sea lions over a total distance of 482 km and kept a median distance between animal and boat of 522 m (n = 548 fixes). It proved possible to track animals leaving the haul-out and also to follow them on their return.

Table 1. Sex, mass, age, and radio-tracking duration of juvenile Steller sea lions tagged and actively tracked in this study.

Age (months)	Male *n*	Female *n*	Mass range (kg)	No. of tracks	Duration (min)
5	1	1	53-71	2	265
8	2	1	79-97	1	25
17	6	2	101-146	14	2,460
20	5	–	115-149	6	2,515
29	2	1	140-206	14	7,021
Total	16	5	120 ± 33[a]	37	12,286

All captures were made in October 2003 or February 2004 in Lynn Canal, Southeast Alaska. Morphometric data courtesy of Alaska Department of Fish and Game.

[a] Mean value ± sd.

Undamaged VHF tags were audible at up to 13 km on calm days and we could obtain useful bearings within 5 km of the sea lion. Head-mounted tags provided clear signals when the animal surfaced to breathe, whereas back-mounted tags were generally only audible during a small portion of each surfacing event, and the reliability of their reception was potentially dependent on the behavior of the animal at the surface. During tracking, care had to be taken in areas with steep cliffs or rock outcrops as these structures tended to interfere with signal detection. Meteorological state, wave height, and the condition of the tag all influenced the range over which we were able to track animals. For the shipboard antennas, freezing rain, sea spray, and corrosion reduced reliability, while strong auroras substantially impacted the noise level on the receivers. It was possible to work in waves up to 2 meters in height with our vessel but fixes became inaccurate in greater sea states. The greatest influence, however, was the condition of the tags. Within two months of tag deployment, the whip antennas of the VHF tags began to break off at the base with the epoxy housing leaving an antenna stump of approximately three to five cm. We were still able to track animals with these damaged antennae, but the range of detection was considerably reduced (<2 km).

Satellite/VHF precision comparisons

During the twenty occasions that we tracked satellite tag-equipped sea lions, only forty-four concurrent at-sea satellite locations were obtained during ten focal follows periods. The proportion of quality ranked sea lion fixes at sea was 2% class 3, 11% class 2, 5% class 1, 2% class 0, 30%

Table 2. A comparison of mean great circle distances between concurrent VHF and satellite-derived (SAT) positions for juvenile Steller sea lions actively tracked in Southeast Alaska.

SAT location class	Distance (km), <20 min elapsed time	*n*	Distance (km), 20-45 min elapsed time	*n*	Distance (km), combined elapsed time (<45min)	*n*
3	1.8	1	–	–	1.8	1
2	1.3 (0.6)	3	1.3 (0.5)	2	1.3 (0.5)	5
1	–	–	1.9 (1.6)	2	1.9 (1.6)	2
0	1.7	1	–	–	1.7	1
A	6.7 (6.7)	13	–	–	6.7 (6.7)	13
B	16.3 (19.3)	21	13.9	1	16.2 (18.9)	22

Distances are displayed by satellite location class and are compared by time elapsed between SAT and VHF locations. Standard deviations in parentheses.

class A, and 50% class B. The distance between satellite-derived and VHF-derived positions was subsequently compared (1) for locations obtained within 20 minutes of each other (*n* = 39) and (2) for those locations obtained up to 45 minutes of each other (*n* = 5). The best agreement in location between satellite and VHF locations was obtained for the few location class 0-3 fixes obtained within 20 minutes of each other (Table 2). On these occasions satellite locations were, on average, within 1.3 to 1.8 km of the sea lion (*n* = 9). However, 80% of satellite fixes for moving sea lions were the lower quality A and B location classes. Figure 1b illustrates the large differences (4-8 km) in location between satellite derived A and B quality fixes and the actual location of the sea lion during one VHF tracking and visual observation period. Only two of the satellite locations received during the 8-hour tracking period were in the water and only one location was within the area actually used by the sea lion. The level of precision derived from the satellite tags was therefore insufficient for the fine-scale focus of this study; however, these tags did allow us to narrow down a search area to find tagged animals and focus the VHF/acoustic tracking efforts.

Acoustic telemetry

Captive trials

The 6 year old female Steller sea lion showed no overt responses to the sound emitted by the CHAT tag, when lowered into the pen or carried in a harness. The 4 year old female, however, exited the water on 5 of 15 transmitter emissions. The responses of the younger animal were ambigu-

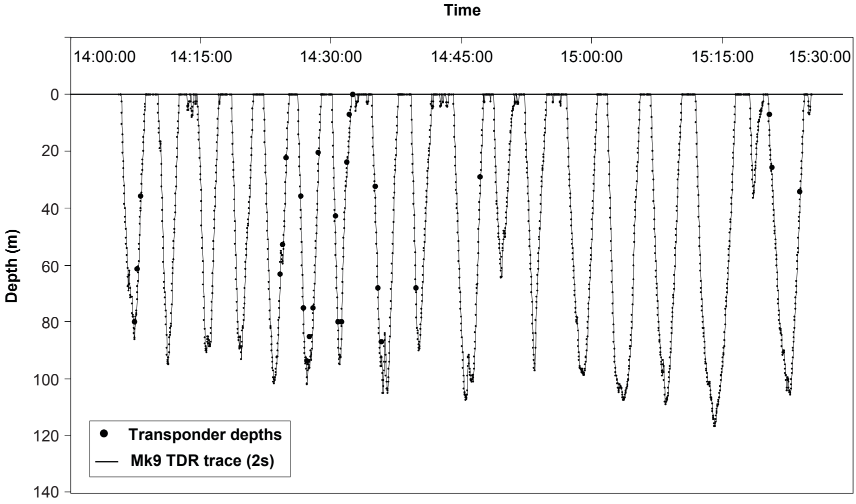


Figure 2. The two-dimensional record of a 29 month old female Steller sea lion on 10 November 2004, retrieved from an Mk9 time depth record (Wildlife Computers, Redmond, USA). Depth was recorded every 2 seconds for 6 months. Larger black dots represent those depths also identified simultaneously by the acoustic transponder (CHAT, VEMCO, Canada).

ous and suggested that if she could perceive the tag she did not show a consistent or severe response.

Field trials

Acoustic tracking of young sea lions using CHAT tags was successful at distances up to 800 m. We found that engine and propeller noise of the tracking boat could reduce this distance, probably by masking reception of the acoustic pulses returning from the tag. The engine was therefore engaged intermittently or when possible the vessel was allowed to simply lie stationary. This approach also had the effect of reducing potential acoustic disturbance for the sea lion. Onboard echosounders of similar operating frequencies (e.g., SIMRAD EK60 at 38 kHz) also produced acoustic interference.

One 29 month old female sea lion was tracked acoustically underwater for 1.5 hours on 10 November 2003; the transmitted real-time dive profiles are shown in tandem with archival time depth recorder data (Wildlife Computers) retrieved after the study (Fig. 2). The maximum dive depths (60-94 m) coincided with the depths of dense, overwintering herring schools *(Clupea pallasii)*. No obvious changes in behavior occurred in response to the acoustic transmissions for either the individual or members of the associated group of ~20 adult and juvenile sea lions. However, we suspect that the acoustic transmissions were altering her behavior on two subsequent occasions. In these instances the sea lion either changed from long to short dives or broke her diving sequence to surface immediately after the acoustic signal was transmitted from the vessel.

Two separate attempts were also made with a 30 month old male and an 18 month old female. In both instances we observed apparent responses to the acoustic tracking equipment from both the tracked individual and surrounding sea lions. In one case, a group resting at the surface startled and immediately dived. During several other occasions the group surfaced with splashing and commotion immediately after the CHAT tag was signaled. Due to concerns that this equipment disturbed the natural behavior of the tagged sea lion and those around it, and the potential that the sea lions might associate these sounds with the presence of our boat, no further transmissions were conducted.

Behavioral context

During the VHF tracking, we maintained a near continuous chronicle of the VHF tag pulses. These data provided records of 157 hours of the tracked sea lions' presence above and below the surface of the water. The temporal occurrence of the VHF pulses was variable, which when combined with contextual and behavioral data were valuable in describing the activity states of juvenile sea lions on their foraging trips.

Being in physical proximity to the focal sea lion made it possible to observe a wide variety of associated events. Tracked sea lions were observed alone and with other sea lions. Group sizes ranged from a few individuals to groups greater than a hundred. On several occasions our focal individuals were seen in close association with an adult, possibly its mother. Inter-specific interactions with humpback whales and seabirds were also witnessed. Sea lions were seen bringing fish to the surface and one track was cut short when killer whales attacked another sea lion in close proximity. Observations were heavily influenced by the weather, distance from the animal, and time of day. On two clear nights while tracking an individual Steller sea lion it was possible to also observe the presence of other sea lions and humpback whales using night vision goggles.

Discussion

In this study, we assessed the feasibility of actively tracking the movements and behavior of Steller sea lions at sea. Using the methods outlined, it proved possible to follow tagged individuals over extended periods (up to 57 hours), through darkness and adverse weather conditions. Using a combination of ADF and VHF equipment, and a moving platform, we were able to obtain real-time fixes on animals carrying head-mounted VHF tags with sufficient precision that in calm weather conditions we could see them with binoculars on their subsequent surfacings. Surface and dive durations recorded while tracking individuals showed discrete patterns, which may indicate specific behavior classes (e.g., foraging, shore navigation, and open water crossings). Dive duration data collected in this way augments and informs information collected by remote studies of foraging behavior and the ontogeny of diving. The surface interval of seal lions was often short (<3 seconds), so alternative VHF tracking methods that rely on physically maneuvering single or paired antennae to determine the best signal strength would have been unsuccessful during this study.

While at sea, the individuals we tracked spent the majority of their time underwater. We tested acoustic transmitters and found them to work over ranges insufficient to initially locate animals, but certainly sufficient to track animals within 800 m. We selected acoustic transponder tags, rather than continually broadcasting tags for this study because of concerns for potentially elevated killer whale predation risk. An additional advantage of responsive tags was that they also provided a range in addition to a bearing. Because the location of the boat was known, the position of the sea lion could be calculated. By combining this with the coded depth information from the tag, it was possible to produce a three-dimensional location for the sea lion.

The hearing capabilities of Steller sea lions are little known; however, recent underwater audiograms of a captive 8 year old male Steller sea lion and a 7 year old female indicated that hearing sensitivity rapidly declined above 16 kHz and 25 kHz respectively (Kastelein et al. 2005). Similar studies of California sea lions *(Zalophus californianus)* indicate their hearing thresholds drop off quickly above 28 kHz with an upper threshold at 34 kHz (Schusterman and Moore 1978), close to the transmission frequency of CHAT tags (32.8 kHz). Trials of CHAT tags near and attached to captive sea lions elicited few overt responses. However, our observations of startle reactions in the wild suggested otherwise. The ultrasonic tags, therefore, appear to be within the upper limit of juvenile Steller sea lion hearing range. Whether the higher behavioral sensitivity of the wild sea lions was due to better high-frequency hearing among these younger animals or simply a more flighty response to sounds of unknown origin is unknown. However, as a result of the observable responses by the wild animals we discontinued use of these tags. Given the ease of tracking animals using these tags, the future development of acoustic transponder tags that operate at frequencies clear of the hearing range of these animals could provide a valuable tool for future studies using active tracking techniques.

The choice of research platform and crew for these tracking techniques had a considerable impact on the results. Larger platforms provide a more stable working platform, better equipment protection, opportunities for elevated antennae, the capacity for larger crews, the capacity for longer at-sea endurance and operating ranges, and the capability to withstand adverse weather. However, larger platforms also have higher operating costs, are often electrically more complicated, and so are prone to electrical interference. Their physical presence, engine exhaust, and noise may also have a greater likelihood of disturbing the target animals or their prey. As a precaution, in this study we attempted to maximize our distance from the focal animal while maintaining our ability to observe context. However, we cannot exclude the possibility that our presence disturbed the animals. To assess any disturbance it might be possible to use data from other remote telemetry devices to identify unusual sea lion behavior. We therefore tested our fine-scale tracking results against the data derived from the satellite tags but these analyses only served to emphasize the inaccuracy of satellite derived positions for fine-scale studies of sea lion behavior at sea.

As with other telemetry studies, we were limited to relatively small sample sizes given the finances and effort invested. This problem was further accentuated because it was only possible to track one sea lion at a time. With smaller sample sizes, the selection of sea lions in which to invest tracking effort becomes critical to the objective of the study. For example, searching for swimming sea lions in the immediate vicinity of haul-out sites could bias the tracking data away from individuals that make long-range trips. The comparison of the individuals included in the active-tracking data with the range of behaviors exhibited in the satellite telemetry data offers one opportunity to validate this.

The value of real time tracking methods for a particular species is dependent upon several factors relating to the foraging environment and behavior of the species. We found that active tracking was successful with juvenile Steller sea lions in Southeast Alaska. The sheltered nature of the region undoubtedly increased the number of days within which we could work compared to the more exposed coasts occupied by the species elsewhere. Furthermore, the frequent islands and fjords constrained the sea lion movement paths and in so doing, made our searches easier for animals once they had left the haul-out. Because movements were generally localized (1-20 km) we were able to minimize our search time and validate the accuracy of concurrent satellite derived locations. Sea lions that forage in pelagic environments would pose greater, but not insurmountable, logistical problems unless tracked exclusively from a haul-out.

The study also provided a rare opportunity to assess the precision of satellite-derived locations for sea lions at sea through comparisons with concurrently recorded VHF locations. Very few high quality Argos locations (classes 3-0) were recorded for animals at sea, with 80% of locations being from the poorer quality A and B classes. Consequently mean errors of 6.7-16.2 km (range 0.6-74.5 km) were recorded for the majority of satellite-estimated locations at sea (Table 2). Only nine high precision locations (classes 3-0), accurate to within ~1.5-2 km, were recorded. This level of precision, however, while acceptable for large, trans-oceanic migrations, is still insufficient to elucidate direct relationships between prey dynamics and predator behavior, particularly for patchy, highly mobile prey such as herring.

Geographic Positioning System (GPS) tags, however, may provide an alternative to conventional satellite tags for high-resolution tracking studies. A recent study evaluating the use of satellite-linked GPS tags on Pacific walrus *(Odobenus rosmarus divergens)* indicated that infrequent and short surface intervals, and the proximity of cliffs limited the success of this technique (Jay and Garner 2002). However, the faster signal detection and alternative processing strategies of GPS-Fastloc (Wildtrack Telemetry Systems, UK) has radically improved the effectiveness of GPS in marine mammal tracking. Recent development and trials of Fastloc-GSM tags [Sea Mammal Research Unit, UK]) on grey seals in the North Sea have proved successful, providing an average of 40 locations per day at sea over a period of 100 days (B. McConnell, Sea Mammal Research Unit, UK, pers. comm.). However, if we are to understand the behavior of foraging marine mammals at the scales relevant to their decision processes and the factors influencing them, then fine-scale active tracking is necessary. One of the greatest advantages active tracking offers is the opportunity to put the behavior of individual animals in the context of their often highly dynamic prey and predators, at temporal and spatial scales that are generally unobtainable through the use of remote telemetry, or archival tags.

Acknowledgments

This work was funded by NOAA and the Alaska Fisheries Development Foundation, through the North Pacific Marine Science Foundation, to the North Pacific Universities Marine Mammal Research Consortium. Captures were conducted under NOAA Permit No. 358-1564-06 by the Alaska Department of Fish and Game. We thank A. Trites (University of British Columbia [UBC]); T. Gelatt, K. Pitcher, and the ADFG sea lion capture team; M. Sigler and D. Csepp (NMFS Auke Bay Lab); G. Hastie and trainers (UBC Open Water facility); Laura Reichle (ATS); RL&L Environmental Consultants; Captain D. Rogers and crew (MV *Alaska Adventurer*) and assistants: S. Thalmann, M. Dougherty, R. Lu, M. Melnychuk, R. Munro, J. Scott-Ashe, K. Soto, G. Sharam, K. Willis, and L. Wilson. We are also grateful to Rob Harcourt, Gordon Hastie, Dom Tollit, Tom Gelatt, and two anonymous reviewers who provided useful comments on the manuscript.

References

Andrews, R.D., D.G. Calkins, R.W. Davis, B.L. Norcross, K. Peijnenberg, and A.W. Trites. 2002. Foraging behavior and energetics of adult female Steller sea lions. In: D. DeMaster and S. Atkinson (eds.), Steller sea lion decline: Is it food II. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 19-22.

Baird, R.W., J.F. Borsani, M.B. Hanson, and P.L. Tyack. 2002. Diving and night-time behavior of long-finned pilot whales in the Ligurian Sea. MEPS 237:301-305.

Beauplet, G., L. Dubroca, C. Guinet, Y. Cherel, W. Dabin, C. Gagne, and M. Hindell. 2004. Foraging ecology of subantarctic fur seals *(Arctocephalus tropicalis)* breeding on Amsterdam Island: Seasonal changes in relation to maternal characteristics and pup growth. MEPS 273:211-225.

Bjørge, A., D. Thompson, P. Hammond, M.A. Fedak, E. Bryant, H. Aarefjord, R. Roen, and M. Olsen. 1995. Habitat use and diving behavior of harbor seals in a coastal archipelago in Norway. In: A.S. Blix, L. Walløe, and Ø. Ultang (eds.), Whales, seals, fish and man, Elsevier Science, Amsterdam, pp. 211-223.

Block, B.A., J.E. Keen, B. Castillo, H. Dewar, E.V. Freund, D.J. Marcinek, R.W. Brill, and C. Farwell. 1997. Environmental preferences of yellowfin tuna *(Thunnus albacares)* at the northern extent of its range. Mar. Biol. 130:119-132.

Boyd, I.L., I.J. Staniland, and A.R. Martin. 2002. Distribution of foraging by female Antarctic fur seals. MEPS 242:285-294.

Bradshaw, C.J.A., J. Higgins, K.J. Michael, S.J. Wotherspoon, and M.A. Hindell. 2004. At-sea distribution of female southern elephant seals relative to variation in ocean surface properties. ICES J. Mar. Sci. 61:1014-1027.

Dewer, H., M. Deffenbaugh, G. Thurmond, K. Lashkari, and B.A. Block. 1999. Development of an acoustic telemetry tag for monitoring electromyograms in free-swimming fish. J. Exp. Biol. 202:2693-2699.

Fedak, M.A., M.R. Pullen, and J. Kanwisher. 1988. Circulatory responses of seals to periodic breathing: Heart rate and breathing during exercise and diving in the laboratory and open sea. Can. J. Zool. 66:53-60.

Fedak, M.A., P. Lovell, B.J. McConnell, and C.J. Hunter. 2002. Overcoming the constraints of long range radio telemetry from animals: Getting more useful data from smaller packages. Integr. Comp. Biol. 42:3-10.

Field, I., M. Hindell, D.J. Slip, and K. Michael. 2001. Foraging strategies of southern elephant seals *(Mirounga leonina)* in relation to frontal zones and water masses. Antarct. Sci. 13:371-379.

Georges, J.-Y., F. Bonadonna, and C. Guinet. 2000. Foraging habitat and diving activity of lactating subantarctic fur seals in relation to sea-surface temperatures at Amsterdam Island. MEPS 196:279-290.

Goebel, M.E., D.P. Costa, D.E. Crocker, J.T. Sterling, and D.A. Demer. 2000. Foraging ranges and dive patterns in relation to bathymetry and time-of-day of Antarctic fur seals, Cape Shirreff, Livingston Island. In: W. Davidson, C. Howard-Williams, and P. Broady (eds.), Antarctic ecosystems: Models for wider ecological understanding. New Zealand Natural Sciences, Christchurch, pp. 47-50.

Goodyear, J.D. 1993. A sonic/radio tag for monitoring dive depths and underwater movements of whales. J. Wildl. Manag. 57:503-513.

Guinet, C., L. Dubroca, M.-A. Lea, S.D. Goldsworthy, Y. Cherel, G. Duhamel, F. Bonadonna, and J.P. Donnay. 2001. Spatial distribution of foraging in female Antarctic fur seals Arctocephalus gazella in relation to oceanographic variables: A scale dependant approach using geographic information systems. MEPS 219:251-264.

Hammond, P., B.J. McConnell, and M.A. Fedak. 1993. Grey seals off the east coast of Britain: Distribution and movements at sea. In: I.L. Boyd (ed.), Marine mammals: Advances in behavioral and population biology. Clarendon Press, Oxford, pp. 211-224.

Harcourt, R., and L.S. Davis. 1997. The use of satellite telemetry to determine fur seal foraging areas. In: M. Hindell and C. Kemper (eds.), Marine mammal research in the Southern Hemisphere: Status, ecology and medicine. Surrey Beatty and Sons Ltd., Chipping Norton, pp. 137-142.

Harcourt, R.G., M.A. Hindell, D.G. Bell, and J.R. Waas. 2000. Three dimensional dive profiles of free-ranging Weddell seals. Polar Biol. 23:479-486.

Hawkins, A.D., D.N. MacLennan, G.G. Urquhart, and C. Robb. 1974. Tracking cod, Gadus morhua, in a Scottish sea loch. J. Fish Biol. 6:225-236.

Hindell, M., R.G. Harcourt, J.R. Waas, and D. Thompson. 2002. Fine-scale three-dimensional spatial use by diving, lactating female Weddell seals *Leptonychotes weddellii*. MEPS 242:275-284.

Hindell, M.A., B.J. McConnell, M.A. Fedak, D.J. Slip, H.R. Burton, J.H. Reijnders, and C.R. McMahon. 1999. Environmental and physiological determinants of successful foraging by naive southern elephant seal pups during their first trip to sea. Can. J. Zool. 77:1807-1821.

Holland, K.N., C.G. Lowe, J.D. Peterson, and A. Gill. 1992. Tracking coastal sharks with small boats: Hammerhead shark pups a case study. Aust. J. Mar. Freshw. Res. 43:61-66.

Holland, K.N., B.W. Wetherbee, C.G. Lowe, and C.G. Meyer. 1999. Movements of tiger sharks *(Galeocerdo cuvier)* in coastal Hawaiian waters. Mar. Biol. 134:665-673.

Holland, K.M., A. Bush, C.G. Meyer, S. Kajiura, B.W. Wetherbee, and C.G. Lowe. 2001. Five tags applied to a single species in a single location: The tiger shark experience. In: J.R. Sibert and J.L. Nielsen (eds.), Electronic tagging and tracking in marine fisheries. Kluwer Academic Publishers, The Netherlands, pp. 236-247.

Jay, C.V., and G.W. Garner. 2002. Performance of satellite-linked GPS on Pacific walruses *(Odobenus rosmarus divergens)*. Polar Biol. 25:235-237.

Kastelien, R.A., van Schie, R., Verboom, W.C., and D. de Haan. 2005. Underwater hearing sensitivity of a male and a female Steller sea lion *(Eumetopias jubatus)*. J. Acoust. Soc. Am. 118:1820-1829.

Lea, M.-A., and L. Dubroca. 2003. Fine-scale linkages between diving behavior of Antarctic fur seals and oceanographic features in the southern Indian Ocean. ICES J. Mar. Sci. 60:1-13.

Loughlin, T.R. 1998. The Steller sea lion: A declining species. Biosph. Cons. 1:91-98.

Loughlin, T.R., W.J. Ingraham Jr., N. Baba, and B.W. Robson. 1999. Use of surface-current model and satellite telemetry to assess marine mammal movements in the Bering Sea. In: T.R. Loughlin and K. Ohtani (eds.), Dynamics of the Bering Sea. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 615-630.

Loughlin, T.R., J.T. Sterling, R.L. Merrick, J.L. Sease, and A.E. York. 2003. Diving behavior of immature Steller sea lions *(Eumetopias jubatus)*. Fish. Bull. U.S. 101:566-582.

Lydersen, C., O.A. Nøst, P. Lovell, B.J. McConnell, T. Gammelsrød, C.J. Hunter, M.A. Fedak, and K.M. Kovacs. 2002. Salinity and temperature structure of a freezing arctic fjord, monitored by white whales *(Delphinapterus leucas)*. Geophys. Res. Lett. 29:34-1–34-4.

MacClennan, D.N., and J.E. Simmonds. 1992. Fisheries acoustics. Chapman and Hall, London, 325 pp.

McConnell, B.J., C. Chambers, and M.A. Fedak. 1992a. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. Antarct. Sci. 4:393-398.

McConnell, B.J., C. Chambers, K.S. Nicholas, and M.A. Fedak. 1992b. Satellite tracking of grey seals *(Halichoerus grypus)*. J. Zool. (Lond.) 226:271-282.

McConnell, B., M. Fedak, H.R. Burton, G.H. Engelhard, and P.J.H. Reijnders. 2002. Movements and foraging areas of naive, recently weaned southern elephant seal pups. J. Anim. Ecol. 71:65-78.

Meyer, C.G., K.M. Holland, B.W. Wetherbee, and C.G. Lowe. 2000. Movement patterns, habitat utilization, home range size, and site fidelity of whitesaddle goatfish, *Paupeneus porphyreus*, in a marine reserve. Environ. Biol. Fish. 59:235-242.

Pascual, M.A., and M.D. Adkison. 1994. The decline of the Steller sea lion in the Northwest Pacific: Demography, harvest or environment? Ecol. Appl. 4:393-403.

Ragen, T.J., G.A. Antonelis, and M. Kiyota. 1995. Early migration of northern fur seal pups from St. Paul Island, Alaska. J. Mammal. 76:1137-1148.

Raum-Suryan, K.L., M. Rehberg, G.W. Pendleton, K.W. Pitcher, and T.S. Gelatt. 2004. Development of dispersal, movement patterns, and haul-out use by pup and juvenile Steller sea lions (*Eumetopias jubatus*) in Alaska. Mar. Mamm. Sci. 20:823-850.

Schusterman, R.J., and P. J. Moore. 1978. The upper limit of underwater auditory frequency discrimination in the California sea lion. JASA 63:1591-1595.

Staniland, I.J., and I.L. Boyd. 2003. Variation in the foraging location of Antarctic fur seals *(Arctocephalus gazella)* and the effects on diving behavior. Mar. Mamm. Sci. 19:331-343.

Stewart, B.S., S. Leatherwood, P.K. Yochem, and M.-P. Heide-Jorgensen. 1989. Harbor seal tracking and telemetry by satellite. Mar. Mamm. Sci. 5:361-375.

Stewart, B.S., P.K. Yochem, T.S. Gelatt, and D.B. Siniff. 2000. First-year movements of Weddell seal pups in the western Ross Sea, Antarctica. In: W. Davidson, C. Howard-Williams, and P. Broady (eds.), Antarctic ecosystems: Models for wider ecological understanding. New Zealand Natural Sciences, Christchurch, pp. 71-76.

Suryan, R.M., and J.T. Harvey. 1998. Tracking harbor seals *(Phoca vitulina richardsi)* to determine dive behavior, foraging activity, and haul-out site use. Mar. Mamm. Sci. 14:361-372.

Szymanski, M.D., D.E. Bain, K. Kent, S. Pennington, S. Wong, and K.R. Henry. 1999. Auditory brainstem response and behavioral audiograms. JASA 106:1134-1141.

Thompson, D., and M.A. Fedak. 1993. Cardiac responses of grey seals during diving at sea. J. Exp. Biol. 174:139-164.

Thompson, D., P.S. Hammond, K.S. Nicholas, and M.A. Fedak. 1991. Movements, diving and foraging behavior of grey seals *(Halichoerus grypus)*. J. Zool. (Lond.) 224:223-232.

Tollit, D.J., A.D. Black, P.M. Thompson, A. Mackay, H.M. Corpe, B. Wilson, S.M. Van Parijs, K. Grellier, and S. Parlane. 1998. Variations in harbor seal *Phoca vitulina* diet and dive-depths in relation foraging habitat. J. Zool. (Lond.) 244:209-222.

Trites, A.W., and P.A. Larkin. 1996. Changes in the abundance of Steller sea lions *(Eumetopias jubatus)* in Alaska from 1956 to 1992: How many were there? Aquat. Mamm. 223:153-166.

Voegeli, F.A., M.J. Smale, D.M. Webber, Y. Andrade, and R.K. O'Dor. 2001. Ultrasonic telemetry, tracking and automated monitoring technology for sharks. Environ. Biol. Fish. 60:267-281.

Wartzok, D., S. Sayegh, H. Stone, J. Barchak, and W. Barnes. 1992. Acoustic tracking system for monitoring under-ice movements of polar seals. JASA 92:682-687.

Watkins, W.A., M.A. Daher, K.M. Fristrup, T.J. Howald, and G. Notarbartolo di Scara. 1993. Sperm whales tagged with transponders and tracked underwater by sonar. Mar. Mamm. Sci. 9:55-67.

York, A.E. 1994. The population dynamics of northern sea lions, 1975-1985. Mar. Mamm. Sci. 10:38-51.

Three-Dimensional Diving Behavior of a South American Sea Lion (*Otaria flavescens*)

Gabriele Müller
Leibniz-Institut für Meereswissenschaften, Kiel, Germany

Rory P. Wilson
University of Wales Swansea, School of Biological Sciences, Institute of Environmental Sustainability, Swansea, UK

Flavio Quintana and Claudio Campagna
Centro Nacional Patagonico (CONICET), Puerto Madryn, Argentina

Abstract

Even though the use of time-depth-recorders (TDRs) has dramatically increased knowledge about pinniped diving behavior, recent studies have shown the limitations of two-dimensional plots of time and depth in interpretation of animal activity. Recently, new technologies have become available allowing collection of more dive parameters so that dives can be depicted in three dimensions. This study uses information collected by a multiple-channel dead reckoner (tracking recorder) to provide detailed information on movements in space of a male South American sea lion (*Otaria flavescens*) in Patagonia, Argentina. The information was analyzed using an area-interest-index (AII), which reflects the directionality of movement. The AII was calculated for a complete foraging trip where the middle part showed the highest values, indicative of foraging activity. Activity estimations based on three-dimensional dive profiles (four dimensions with speed) showed good agreement with the calculated AII. The use of the AII is thus a promising tool for the determination of activity of marine animals over varying spatial scales.

Introduction

Determination of animal activity at sea has generally been hindered by the lack of information on animal movement in three-dimensional space so that behaviors cannot be assigned to specific areas. However, in recent years advances in technology have allowed collection of information that allows animal movements to be determined in more than the conventional two dimensions of depth over time (Harcourt et al. 2000; Davis et al. 2001, 2003, 2004; Hindell et al. 2002; Mitani et al. 2003).

Relatively little is known about the distribution at sea and diving behavior of the South American sea lion (*Otaria flavescens*), knowledge to date being almost exclusively limited to lactating females equipped with satellite tags and time-depth recorders (Werner and Campagna 1995, Campagna et al. 2001). We hypothesized that use of a compass together with measures of speed and dive depth would allow a much more comprehensive insight into dive behavior than the standard dive depth versus time approach. This study details recent investigations on a single male sea lion using a dead reckoner (tracking recorder) to reconstruct the three-dimensional route during a foraging trip, to detail the applicability of the method as well as to provide insights as to what types of behaviors can be elucidated by this approach. An activity index based on analysis of track tortuosity was created and applied to the route. Individual three-dimensional dive profiles are also provided to exemplify specific activities observed at different stages of the trip.

Methods

As part of a larger project studying the foraging ecology of South American sea lions conducted at Peninsula Valdés, Chubut, Argentina, eight subadult males from the breeding colony of ca. 250 males at Punta Norte were equipped with dead reckoners (Driesen and Kern GmbH, Bad Bramstedt, Germany) in November 2003. Animals were immobilized using a combination of tiletamine and zolazepam (Telazol®), which was delivered intramuscularly by darting the animals. A detailed description of this procedure is in Campagna et al. 2001. Approval for this procedure was given by the Dirección de Fauna and Subsecretaría de Turismo de la Provincia del Chubut. Although five units were recovered (see Müller et al. 2005), we only managed to obtain appropriate data for the complete foraging trip from a single animal. This is important for dead reckoning applications because the start and end positions must be known to correct for drift (Wilson et al. 2002). As a result, we will only consider further the data from this single animal. The recovered device recorded time, depth, swim speed, compass heading (in three dimensions), and tilt angle (pitch and roll, 0-70 degrees off the horizontal) at a sampling interval of 10 seconds. This relatively low sampling rate was chosen to try and ensure that the complete foraging trips could be recorded before the memory was full. Animal speed was determined by using two medium-separated 20 bar pressure transducers, one that recorded hydrostatic pressure directly and another that recorded hydrostatic pressure plus an additional component derived from the pressure produced by the forward motion of the animal underwater. For this a small paddle projected into the water from the device. The paddle was linked via an axle to another arm, set at 90 degrees to it, running longitudinally up the length of the device. The end of this second arm articulated with a small plate that rested on the medium-separating membrane of one of the pressure transducers. Water pressure from the front as the animal swam caused the paddle to be pushed back and thus, via the axle, caused the plate to be pushed with more force down onto the membrane (cf. Wilson et al. 2004). This resulted in a higher pressure being recorded from one pressure transducer than the other. Subtracting the value of one transducer from the other produced an output that was proportional to swim speed. This was calibrated in situ by plotting the pressure sensor's swim component against the known speed when the animal dived or returned to the surface; simple trigonometry allowed us to calculate this using rates of change of depth and pitch angle. The resulting regression was then used to derive swim speed when the animal swam horizontally. The compass used was a solid-state system sensing tri-axial magnetic field strength. Methods for determination of heading are based on known pitch and roll angle and are detailed in Mitani et al. (2003). The three-dimensional route could be determined using the stored data and was reconstructed using custom-written software (MT-Route from Jensen Software Systems, Laboe, Germany). The route was corrected for drift using two procedures, by incorporating the known start and end point of the trip and by correcting for depth inconsistencies. In a first iteration of the route, the known start and end points were made to accord with the calculated positions by assuming that any errors were due to drift resulting from a constant current displacing the animal to the extent shown over the full course of the foraging trip (R.P. Wilson et al. unpubl.). We then used bathymetry data, with a resolution of 10 m, and superimposed the first iteration onto the map, noting where the maximum depth reached by the animal exceeded that of the seabed. The nearest likely point for the animal to be, in terms of depth, was then allocated to that position and all subsequent positions corrected to accord as if the error occurred due to drift (see above).

An area-interest-index (AII) was used to describe animal activity at sea (Fig. 1). It relates the total horizontal distance traveled between two points ("a" through to "e") to the direct distance between the first and the last point (F):

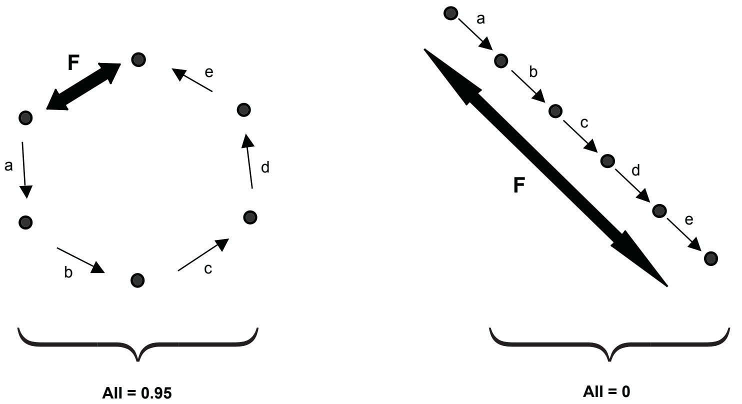


Figure 1. Calculation of the area-interest-index (AII) over six successive points illustrating concentrated movement in a small area (left) and highly directional movement (right).

A high AII value corresponds to a convoluted track whereas low values indicate more directional movements. Because of the long duration of the trip the data were thinned out so only every tenth data point was included in the calculation of the AII, which spanned five successive points and thus was calculated over a time interval of 360 seconds. In order to see the change in AII over time the trip was divided into intervals, each covering 5% of the total time, and an inverse polynomial curve was fitted to the means of the AII for each interval.

Results

During the 16 day foraging trip the sea lion made 2,163 dives, of which 1,849 (85.5%) were square (U-shape) dives (cf. Le Boeuf et al. 1988). The mean dive depth was 62.5 m (SD 29.1 m) with mean duration being 4.7 min (SD 1.6 min). From Punta Norte the animal headed eastward toward the shelf break, turning north just before reaching the 100 m depth contour, and finally turning southwest on return to the colony (Fig. 2). The AII was highly variable, but an inverse polynomial curve fit through the means of each time interval showed that the index increased over time reaching a maximum at about five days into the trip and then declining again toward the end of the trip (Fig. 3). AII values less than 0.2 were found in the first 10% and the last 25% of the trip with the middle part showing greater AII values.

A selection of individual dives considered to be typical of three different parts of the foraging trip is shown in Figs. 4-6. All two-dimensional

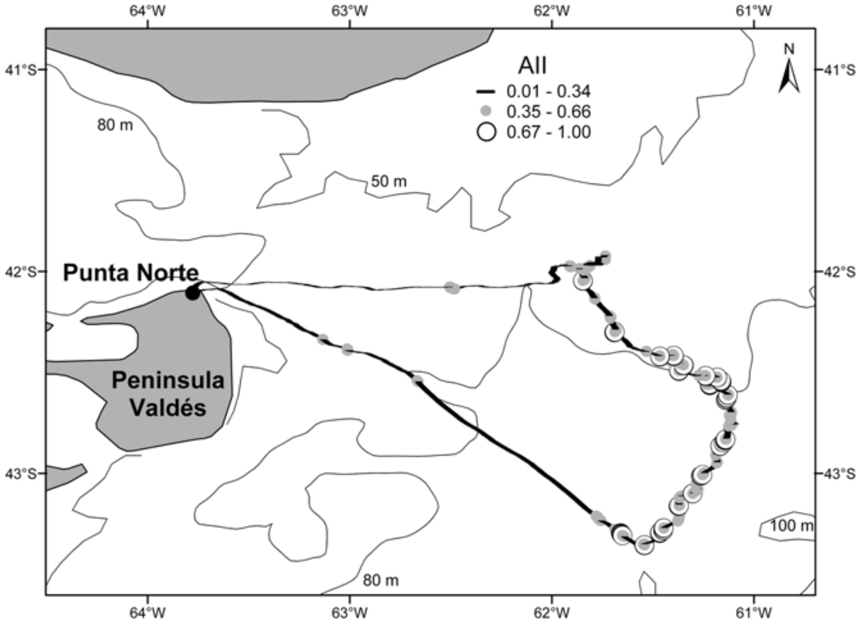


Figure 2. **Map showing the route of the foraging trip performed by a male South American sea lion. For each dive only one AII value (corresponding to the start time of the dive) is depicted. The AII was calculated over five successive points with only every tenth data point being used in the calculation.**

time-depth profiles are similar in being U-shaped and differing only in maximum depths attained. The time-AII profiles, on the other hand, show obvious differences between these dives. The differences become even more apparent in the three-dimensional presentations of these dives. The first dive, taken from the beginning of the trip, has a low AII value of around 0.2 and shows very directional movement through all phases of the dive with a relatively constant, high speed (Fig. 4). The two dives with higher AII values from the middle part of the trip (Figs. 5 and 6) are much less directional in all phases of the dive. The last dive shows extremely convoluted movements during the bottom phase (Fig. 6). In the latter two dives the speed during the bottom phase is much slower and more variable than in the first dive.

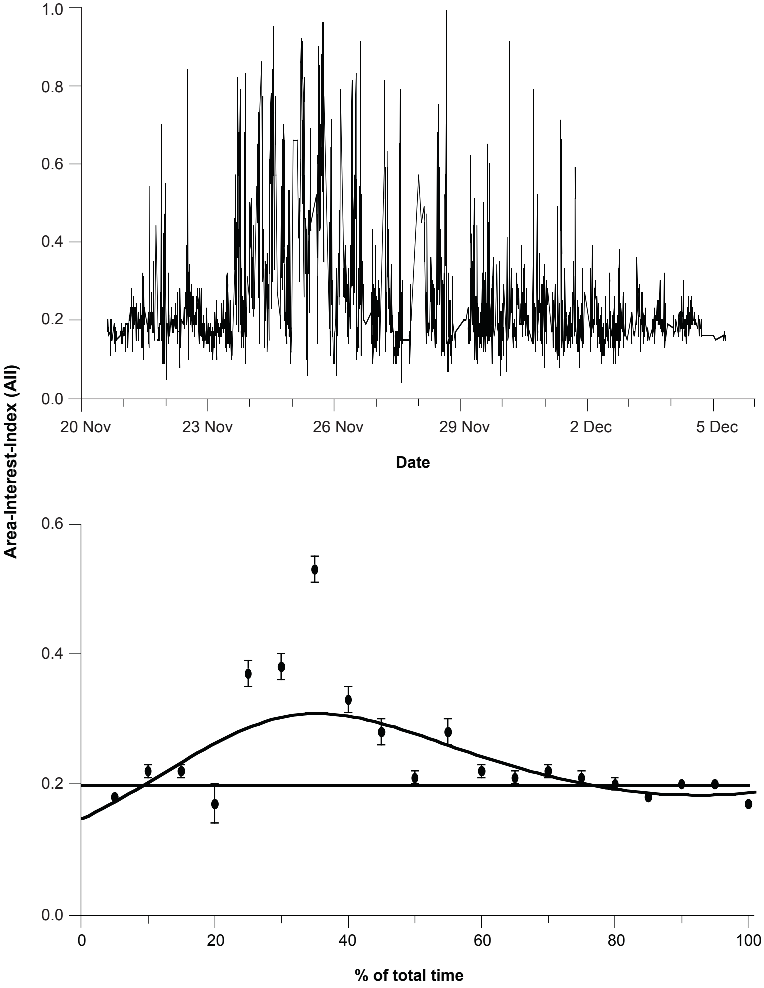


Figure 3. The change in area-interest-index (AII) over the course of the complete foraging trip (above) and AII means for time intervals (each covering 5% of total time) with an inverse polynomial curve fit ($y = 1/(6.8017923 - 0.2313366x + 0.0045242x^2 - 0.0000024x^3)$, $r^2 = 0.5$, below).

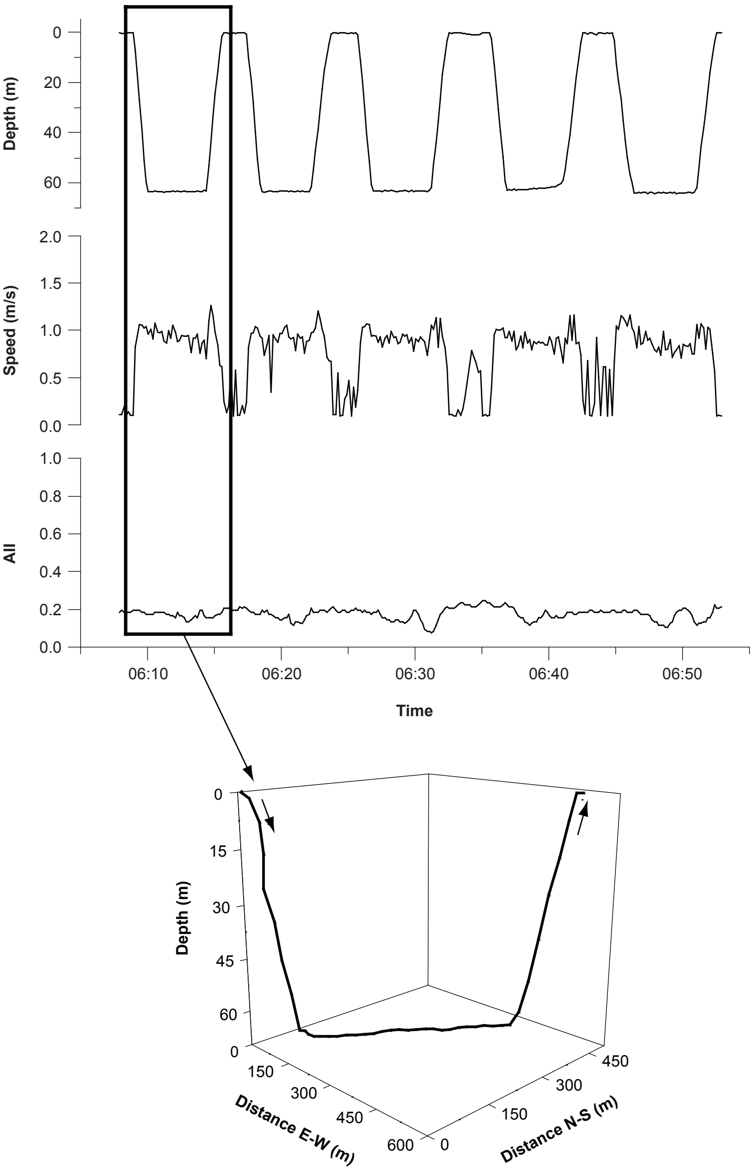


Figure 4. Example of dives from the beginning of the foraging trip with relatively constant speed throughout the dives and low AII values. The three-dimensional dive path of the framed dive is depicted below.

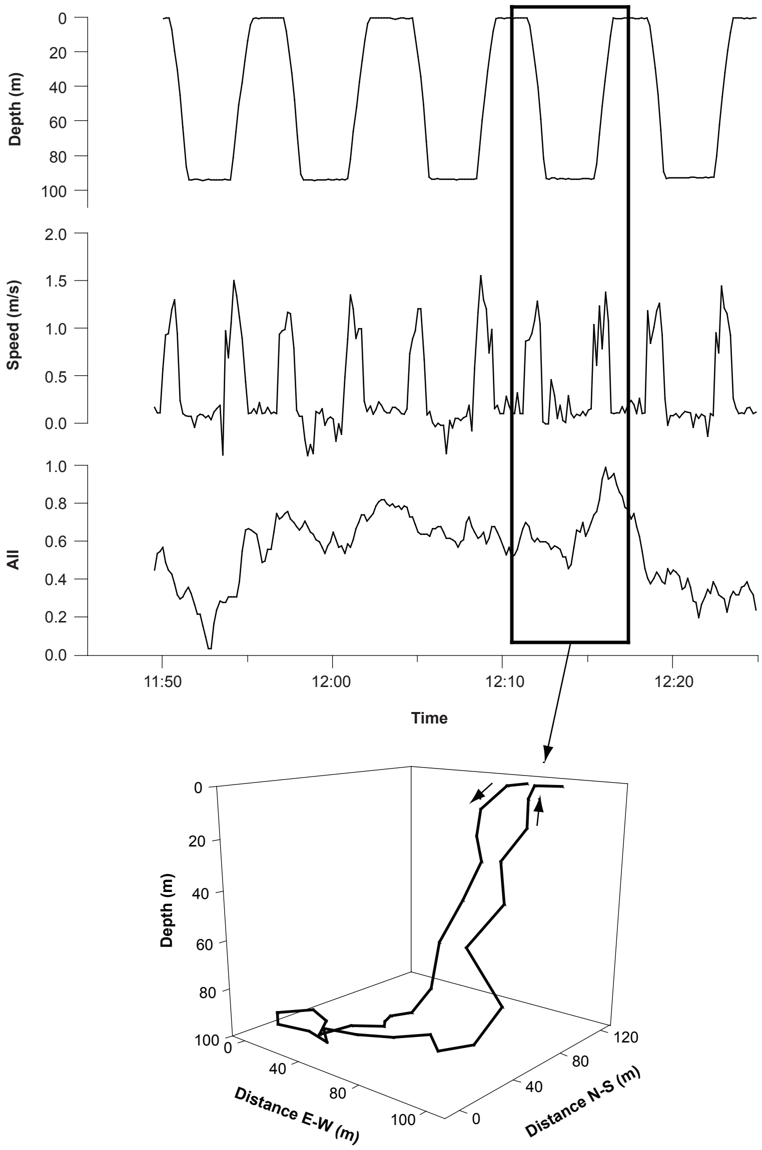


Figure 5. Example of dives from the middle part of the foraging trip with slow speed throughout the dives and variable AII values. The three-dimensional dive path of the framed dive is depicted below.

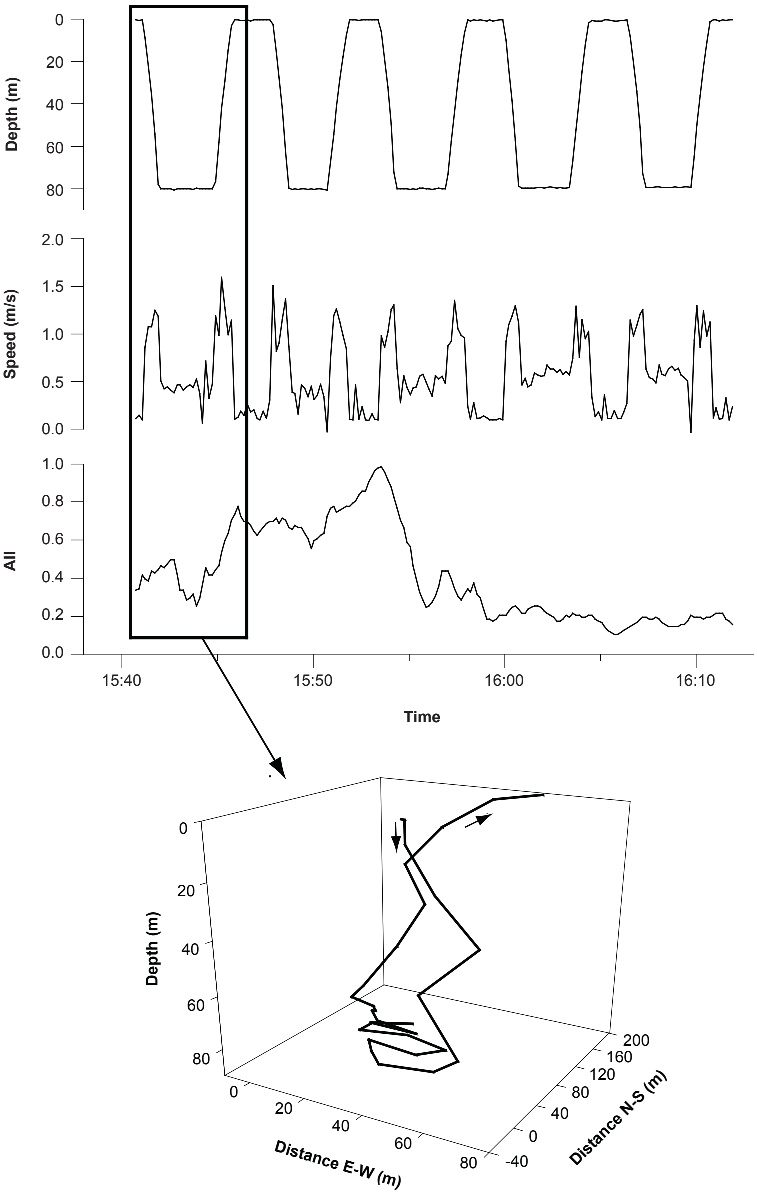


Figure 6. **Example of dives from the middle part of the foraging trip with variable speed and AII values throughout the dives. The three-dimensional dive path of the framed dive is depicted below. Note the convoluted path in the bottom phase of the dive.**

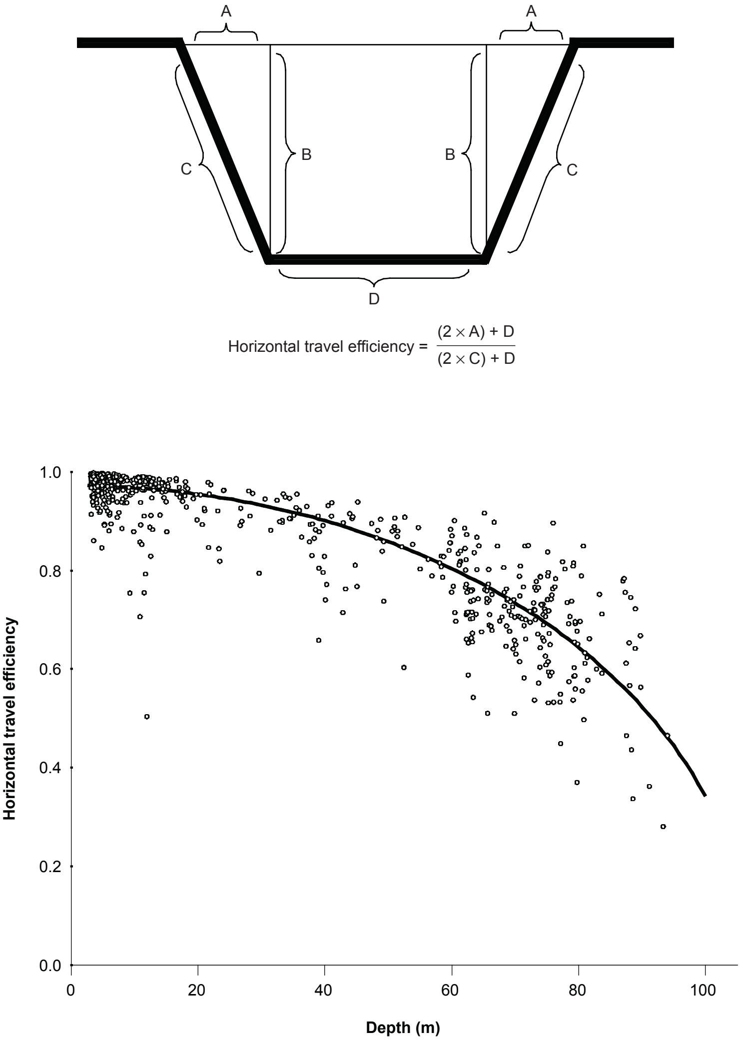


Figure 7. Calculation of the horizontal travel efficiency of a dive (above) where C and D are the actual distances traveled (including the vertical component), A is the horizontal distance covered during the descent and ascent phases, and B is the depth of the dive. Actual data from the trip made by the sea lion are given below.

Discussion

The results of this study highlight the advantage of incorporating information on three-dimensional behavior and movements in the determination of animal activity at sea and the association of these activities with specific areas. The sea lion in this study foraged on the Patagonian shelf, as has been shown for other males from Peninsula Valdés (Campagna et al. 2001; unpubl. data). The combination of position and area-interest-index shows that only the middle part of the trip (in terms of distance covered) is characterized by consistently high AII values. Both the outward and inward legs of the trip show mainly low AII values (indicative of directional movement), but each covers approximately the same distance as the middle part, suggesting that the sea lion employs a strategy of comparatively fast and directional travel to foraging grounds in order to maximize the time available for foraging. This division of time at sea into distinct travel and foraging phases has also been noted in southern elephant seals (*Mirounga leonina*) (McConnell and Fedak 1996) and Antarctic fur seals (*Arctocephalus gazella*) (Bonadonna et al. 2000). The travel function of these parts of the trip is further supported by inspection of individual three-dimensional dive profiles. During these apparent travel dives the animal shows very straight movements during all phases of the dive, with only minor changes in speed during the entire dive. The reduction in speed at the surface does not necessarily reflect the actual swim speed of the animal, as the device was located on the sea lion's head and therefore was not able to measure speed at the surface. In addition, the location of the device led to a high variability in speed measurements, as movements of the head do not necessarily reflect movements of the body. Therefore the measured speed might not always correspond to the actual swim speed, although the overall changes in speed are assumed to be generally correct.

High AII values are a reflection of localized movements and thus depict areas that are of particular interest to the animal. For the South American sea lion, these areas are most likely foraging spots. Again, the three-dimensional dive profiles support this, as the observed movements, especially during the bottom phase, can be highly convoluted. This suggests that the animal dives down to the bottom (at approximately the same speed as during travel dives) and then slows down in order to search for prey. The slow speed supports earlier studies which showed that South American sea lions mainly feed on benthic-demersal prey (George-Nascimiento et al. 1985, Koen Alonso et al. 2000). However, as the sampling interval increases, the probability of recording short events such as speed bursts during pursuit of fast-moving prey will decrease (see Ropert-Coudert and Wilson 2004 for a discussion of the errors involved in this). Thus, data logging devices sampling at high frequencies would be beneficial for a detailed study of the pursuit and capture of prey (Davis et al. 1999, Williams et al. 2004).

The time-depth profiles in combination with the AII imply that the sea lion at least partially performs square dives while traveling. Because the movement during a dive can be divided into a horizontal and a vertical component, the most efficient strategy for travel dives in which the horizontal component is to be maximized would be to make shallow parabolic dives as observed in, e.g., penguins (Wilson 1995). For a constant dive duration the horizontal distance traveled will decrease with increasing depth, as a greater proportion of the dive is allocated to the vertical component of the movement. This can be illustrated by calculating the horizontal travel efficiency, which is the horizontal distance actually traveled divided by the total distance traveled, including the vertical component (Fig. 7). As the vertical component increases with depth, the horizontal efficiency decreases because the horizontal movement along the bottom becomes a smaller fraction of the total movement. Such a reduction in efficiency not only leads to a loss of time for the animal but also to an apparently unnecessary expenditure of energy. However, swimming along the bottom may confer advantages that cannot be easily measured. It may allow the animal to feed on an opportunistic basis, if prey is encountered, which could be of particular importance after long periods of fasting on land when the foraging grounds are far from land. In addition, if a sea lion is close to the seabed it may reduce the risk of being detected by predators such as sharks, as these often approach and attack their prey from below and behind (Tricas and McCosker 1984, Crespi-Abril et al. 2003, Lucifora et al. 2005). Ultimately, however, the possible advantages of swimming along the bottom will be eventually limited by the animals' diving capacity and the bathymetry.

In conclusion, the analysis of a sea lion foraging trip using an index of activity showed that, in terms of distance covered, the major part of the trip was spent traveling. However, more than half the time was spent performing more localized movements at lower speed, suggesting foraging activity. This is supported by the three-dimensional dive profiles that reveal substantial differences in movements during travel and foraging dives. The obtained results emphasize that incorporation of three-dimensional data on movements is particularly useful for determining activity of animals at sea as well as inferring the function of different dive types.

Acknowledgments

This study was supported by the Deutsche Forschungsgemeinschaft (Wi 1023/10-1) and the Wildlife Conservation Society. The help of M. Uhart, B. Raphael, P. Calle, and D. A. Albareda with the anesthesia of the sea lions, and of V. Ramos and P. Ledesma in recovering the dead reckoners, is gratefully acknowledged. Permission to carry out the work was granted by the Dirección de Fauna and Subsecretaría de Turismo de la Provincia del Chubut, Argentina.

References

Bonadonna F., M.A. Lea, and C. Guinet. 2000. Foraging routes of Antarctic fur seals (*Arctocephalus gazella*) investigated by the concurrent use of satellite tracking and time-depth recorders. Polar Biol. 23:149-159.

Campagna, C., R. Werner, W. Karesh, M.R. Marín, F. Koontz, R. Cook, and C. Koontz. 2001. Movements and location at sea of South American sea lions (*Otaria flavescens*). J. Zool. (Lond.) 257:205-220.

Crespi-Abril, A.C., N.A. García, E.A. Crespo, and M.A. Coscarella. 2003. Consumption of marine mammals by broadnose sevengill shark *Notorynchus cepedianus* in the northern and central Patagonian shelf. LAJAM 2:101-107.

Davis, R.W., W. Hagey, and M. Horning. 2004. Monitoring the behavior and multidimensional movements of Weddell seals using an animal-borne video and data recorder. Mem. Natl. Inst. Polar Res., Special Issue 58:148-154.

Davis, R.W., L.A. Fuiman, T.M. Williams, and B.J. Le Boeuf. 2001. Three-dimensional movements and swimming activity of a northern elephant seal. Comp. Biochem. Physiol. Part A 129:759-770.

Davis, R.W., L.A. Fuiman, T.M. Williams, M. Horning, and W. Hagey. 2003. Classification of Weddell seal dives based on 3-dimensional movements and video-recorded observations. Mar. Ecol. Prog. Ser. 264:109-122.

Davis, R.W., L.A. Fuiman, T.M. Williams, S. Collier, W. Hagey, S.B. Kanatous, S. Kohin, and M. Horning. 1999. Hunting behavior of a marine mammal beneath the Antarctic fast-ice. Science 283:993-996.

George-Nascimiento, M., R. Bustamante, and C. Oyarzun. 1985. Feeding ecology of the South American sea lion *Otaria flavescens*: Food content and selectivity. Mar. Ecol. Prog. Ser. 21:135-143.

Harcourt, R.G., M.A. Hindell, D.G. Bell, and J.R. Waas. 2000. Three-dimensional dive profiles of free-ranging Weddell seals. Polar Biol. 23:479-487.

Hindell, M.A., R. Harcourt, J.R. Waas, and D. Thompson. 2002. Fine-scale three-dimensional spatial use by diving, lactating female Weddell seals *Leptonychotes weddellii.* Mar. Ecol. Prog. Ser. 242:275-284.

Koen Alonso, M., E.A. Crespo, S.N. Pedraza, N.A. García, and M.A. Coscarella. 2000. Food habits of the South American sea lion, *Otaria flavescens*, off Patagonia, Argentina. Fish. Bull. U.S. 98:250-263.

Le Boeuf, B.J., D.P. Costa, A.C. Huntley, and S.D. Feldkamp. 1988. Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris.* Can. J. Zool. 66:416-458.

Lucifora, L.O., R.C. Menni, and A.H. Escalante. 2005. Reproduction, abundance and feeding habits of the broadnose sevengill shark *Notorynchus cepedianus* in north Patagonia, Argentina. Mar. Ecol. Prog. Ser. 289:237-244.

McConnell, B.J., and M. Fedak. 1996. Movements of southern elephant seals. Can. J. Zool. 74:1485-1496.

Mitani, Y., K. Sato, S. Ito, M.F. Cameron, D.B. Siniff, and Y. Naito. 2003. A method for reconstructing three-dimensional dive profiles of marine mammals using geomagnetic intensity data: Results from two lactating Weddell seals. Polar Biol. 26:311-317.

Müller, G., N. Liebsch, and R.P. Wilson. 2005. A new shot at a release mechanism for devices attached to free-living animals. Wildl. Soc. Bull. 33:337-342.

Ropert-Coudert, Y., and R.P. Wilson. 2004. Subjectivity in bio-logging science: Do logged data mislead? Mem. Natl. Inst. Polar Res., Special Issue 58:23-33.

Tricas, T.C., and J.E. McCosker. 1984. Predatory behavior of the white shark, *Carcharodon carcharias*, with notes on its biology. Proc. Calif. Acad. Sci. 14:221-238.

Werner, R., and C. Campagna. 1995. Diving behaviour of lactating southern sea lions (*Otaria flavescens*) in Patagonia. Can. J. Zool. 73:1975-1982.

Williams, T.M., L.A. Fuiman, M. Horning, and R.W. Davis. 2004. The cost of foraging by a marine predator, the Weddell seal (*Leptonychotes weddellii*): Pricing by the stroke. J. Exp. Biol. 207:973-982.

Wilson, R.P. 1995. The foraging ecology of penguins. In: T. Williams (ed.), Penguins. Oxford University Press, Oxford, UK, pp. 81-106.

Wilson, R.P., J. Kreye, K. Lucke, and H. Urquardt. 2004. Antennae on transmitters on free-living marine animals: Balancing energy budgets on the high wire. J. Exp. Biol. 207:2649-2662.

Wilson, R.P., D. Gremillet, J. Syder, M.A.M. Kierspel, S. Garthe, H. Weimerskirch, C. Schafer-Neth, J.A. Scolaro, C.A. Bost, J. Plötz, and D. Nel. 2002. Remote-sensing systems and seabirds: Their use, abuse and potential for measuring marine environmental variables. Mar. Ecol. Prog. Ser. 228:241-261.

Nearshore Fish Assemblages in the Vicinity of Two Steller Sea Lion Haul-Outs in Southeastern Alaska

John F. Thedinga, Scott W. Johnson, and David J. Csepp
National Marine Fisheries Service, Alaska Fisheries Science Center, Auke Bay Laboratory, Juneau, Alaska

Abstract

To better understand Steller sea lion foraging ecology, information is needed on the species composition, abundance, and seasonality of prey species, especially in nearshore waters adjacent to rookeries and haul-outs. From 2001 to 2004, we examined nearshore fish assemblages in summer and winter in the vicinity of two Steller sea lion haul-outs, Benjamin Island and The Brothers Islands, in southeastern Alaska. Fish were captured in nearshore waters (<115 m deep, <350 m from shore) by beach seining and hand-jigging; we also observed fish assemblages with a remotely operated vehicle (ROV). Total catch by seining and jigging for all sampling periods was 201,331 fish and 559 fish; 58 species were identified in summer and 44 species in winter. Seine catches were dominated by young-of-the-year walleye pollock, Pacific herring, and Pacific sand lance in summer, and salmon fry, armorhead sculpin, and rock sole in winter. Jig catches were dominated by armorhead sculpin, Pacific cod, and two rockfish species in summer and winter. Twenty-seven species were observed with the ROV; seven of these species were not captured by seining or jigging. Catch and number of fish species were greater in summer than in winter and greater at The Brothers Islands than at Benjamin Island. Most fish captured by seining were too small (median fork length [FL] <81 mm) to be consumed by Steller sea lions, whereas most fish captured by jigging or observed with the ROV were large enough (median FL >248 mm) to be consumed by Steller sea lions. Inclusive of all sampling methods, 34 of the species inventoried have been identified in Steller sea lion scat collected at either haul-out. Although the extent of Steller sea

lion foraging in nearshore waters surrounding Benjamin Island and The Brothers Islands is unclear, a diverse fish assemblage is present at both locations and may be an important prey field for Steller sea lions.

Introduction

Few studies have examined species composition, abundance, and seasonality of fish assemblages in nearshore waters close to Steller sea lion (*Eumetopias jubatus*) haul-outs, or the utilization of this prey field by Steller sea lions. Quantifying the distribution of Steller sea lion prey has been mostly limited to trawling in relatively deep areas offshore of haul-outs and rookeries for key species such as Pacific herring (*Clupea pallasii*) and walleye pollock (*Theragra chalcogramma*) (Pitcher 1981, Byrd et al. 1997, Calkins 1998). Recently, hydroacoustic surveys in conjunction with midwater trawls have been used to locate, capture, and identify prey near Steller sea lion haul-outs in southeastern Alaska (Mike Sigler, National Marine Fisheries Service, Juneau, Alaska, 2004, pers. comm.). Of the few nearshore prey studies related to Steller sea lions, most have been done in the Gulf of Alaska—Mueter and Norcross (2000) sampled juvenile fish with a bottom trawl at depths greater than 15 m close to several Steller sea lion rookeries, and Wynne et al. (2005) identified fish assemblages in shallow nearshore waters with beach and purse seines near a Steller sea lion haul-out. A diverse and abundant prey field in nearshore waters may be especially important for young Steller sea lions that have limited diving ability and tend to make shorter foraging trips from rookeries and haul-outs (Loughlin et al. 2003).

Some general distribution information is available on fish assemblages present in nearshore waters of Alaska in summer (Abookire et al. 2000; Dean et al. 2000; Johnson et al. 2003b, 2005), but no information is available for winter. Availability and diversity of fishes in nearshore waters differs seasonally—some species (e.g., Pacific herring) are present in spring or summer during spawning and move farther and deeper offshore in winter (Brown and Carls 1998). Knowledge about the seasonality of nearshore fish assemblages close to Steller sea lion haul-outs is important for understanding Steller sea lion foraging behavior.

The objective of our study was to use a suite of sampling techniques (beach seining, hand-jigging, and observations with a remotely operated vehicle [ROV]) to inventory nearshore fish assemblages in summer and winter near two Steller sea lion haul-outs in southeastern Alaska. In addition, we compared our fish catches to the frequency of prey species identified in Steller sea lion scat collected from the same two haul-outs. Identifying seasonal fish assemblages close to Steller sea lion haul-outs, and the presence or absence of these species in Steller sea lion scat, may provide important information on the value of nearshore areas in providing food resources for Steller sea lions.

Methods

Study locations

We sampled fishes in nearshore waters in the immediate vicinity of two Steller sea lion haul-outs in southeastern Alaska, Benjamin Island in Lynn Canal, and The Brothers Islands in Frederick Sound (Fig. 1). Benjamin Island is used by up to 800 Steller sea lions from October to June; in 2004 and 2005, however, an estimated 200 Steller sea lions were still observed at the haul-out in July (Jamie Womble, National Marine Fisheries Service, Juneau, Alaska, 2005, pers. comm.). The Brothers Islands are used year-round by nearly 1,500 Steller sea lions. From 2001 to 2004, we sampled each location once each summer (July) and winter (February-March). Fish were sampled by beach seining and hand-jigging, and were also observed with an ROV. For the purpose of this study, nearshore includes intertidal and subtidal habitats that extend offshore to 115 m depth and within 350 m of shore.

Seining

To sample the extreme nearshore (<5 m deep), up to 14 sites were sampled with a beach seine near each haul-out each season. One seine haul was made at each site. Sites were selected in areas that could be seined (e.g., no obstructions) and were spatially distributed throughout each study location among three habitat types. Different habitat types were sampled to account for segregation of some species based on habitat preference (Johnson et al. 2003b). Habitat types included vegetated substrates (kelp, *Laminaria saccharina*; one site with eelgrass, *Zostera marina*); non-vegetated substrates (e.g., gravel, sand, silt); and steep bedrock walls, usually with attached kelps (e.g., *L. saccharina* or *Alaria* spp.). A position was taken at the center of each seine site with global positioning system (GPS) technology so that it could be re-sampled in subsequent years.

The beach seine was a 37 m long, variable-mesh seine that tapered from 5 m wide at the center to 1 m wide at the ends. Outer panels were each 10 m of 32 mm stretch mesh, intermediate panels were each 4 m of 6 mm square mesh, and the bunt was 9 m of 3.2 mm square mesh. We set the seine as a “round haul” by holding one end on the beach, backing around in a skiff with the other end to the beach about 18 m from the start, and pulling the seine onto shore. The seine had a lead line and a float line so that the bottom contacted the substrate and the top floated.

Fish captured with the seine were identified to species and enumerated. For large catches, the number of fish was estimated gravimetrically. A random subsample of approximately 500 fish was removed from the total catch, and the remaining fish were collectively weighed to the nearest 0.1 kg. Fish in the subsample were weighed to the nearest gram and counted

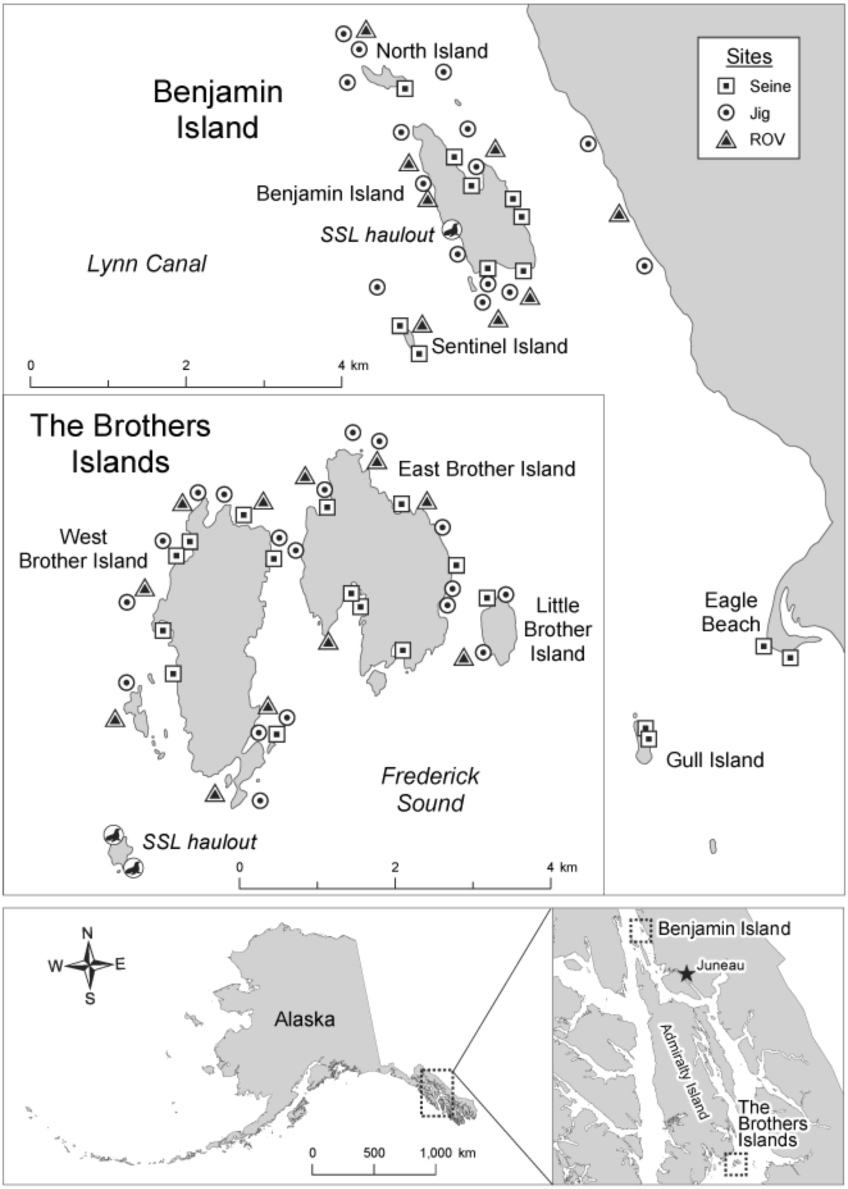


Figure 1. **Location of sites sampled for fish assemblages near two Steller sea lion (*Eumetopias jubatus*) haul-outs (Benjamin Island and The Brothers Islands) in southeastern Alaska, 2001-2004. Sampling methods included beach seining, hand-jigging, and observations with a remotely operated vehicle (ROV).**

by species. A mean weight of fish determined from the subsample was used to estimate the number of fish in the total catch. The proportion of each species in the subsample was also used to determine the species composition of the total catch. Fork length (FL) was measured to the nearest millimeter for up to 50 individuals of select species, primarily species important in the diet of Steller sea lions (e.g., walleye pollock, Pacific herring). Fish were anesthetized in a mixture of 1 part carbonated water to 2 parts seawater for identification and measurement; a more dilute mixture (1:7) was used for some sensitive species (e.g., Pacific cod, *Gadus macrocephalus*). Smaller individuals (<40 mm FL) of some families of fish (e.g., Cottidae, Hexagrammidae) that could not be easily identified to species in the field were grouped and recorded as juvenile cottids or juvenile greenling.

Hand-jigging

Up to 18 sites were sampled by hand-jigging at each location each season. Sites were selected throughout the depth range of 5 to 115 m and were spatially distributed throughout each study location. A GPS position was taken at each site so that it could be re-sampled in subsequent years. Three people jigged for 15 minutes at each site, one person with a 6-hook herring jig, and two people with 170 g dart lures. Captured fish were placed in a holding tank until jigging was finished at each site, and then each fish was identified and measured for FL.

ROV

An ROV was used to survey and identify fish not captured by seining or jigging. Near each haul-out, up to 11 ROV dives were completed each season. Dive sites were randomly selected to spatially cover each study location. Each ROV dive was perpendicular to shore, beginning at a maximum depth of 85 m (limit of umbilical cord) and ending close to shore at a depth of about 1 m. A GPS position was taken at the start and end of each dive so that the dive site could be re-sampled in subsequent years. A more complete description of the ROV and its operation is reported in Johnson et al. (2003a).

Data analysis

Seine catch data were standardized to catch per haul by dividing the total catch of selected species by the total number of seine hauls for both locations and all sampling periods. Jig catch was standardized by dividing the total catch of selected species by the total number of rod hours for both locations and all sampling periods. Differences in total seine and jig catches between locations, seasons, and among years were tested with a general linear model ANOVA. Data were log-transformed prior to analysis. Significance for all tests was at $P \leq 0.05$. We used box plots to show the wide distribution of FL data. For comparison of mean catches and FL, we combined all species of the Salmonidae (five species), Cottidae (four species), Pleuronectidae (six species), Scorpaenidae (five species), and Hexagrammidae (two species) into salmon, sculpin, flatfish, rockfish, and greenling groups.

Results

Seine catch

A total of 156 seine hauls yielded 201,331 fish representing 45 species (Table 1). Total catch for all sampling periods and both locations in summer was dominated by walleye pollock, Pacific herring, and Pacific sand lance (*Ammodytes hexapterus*) (Table 1). No walleye pollock or Pacific herring, and few Pacific sand lance, were captured in winter at either location. The most frequently occurring species in summer were northern sculpin (*Icelinus borealis*) at Benjamin Island and walleye pollock at The Brothers Islands; these species were captured in 53% and 85% of all seine hauls. The most frequently occurring species in winter were rock sole (*Lepidopsetta* spp.) at Benjamin Island, and pink salmon (*Oncorhynchus gorbuscha*) at The Brothers Islands; these species were captured in 33% and 60% of all seine hauls.

Catch was greater in summer than in winter at both locations and was significantly greater ($P < 0.05$) at The Brothers Islands than at Benjamin Island. A total of 12,355 fish representing 29 species were captured at Benjamin Island in summer compared to 187,613 fish representing 37 species at The Brothers Islands (Table 1). Similarly, 376 fish representing 23 species were captured at Benjamin Island in winter compared to 987 fish representing 24 species at The Brothers Islands (Table 1). Mean catch per seine haul for all species and sampling periods ranged from a low of 3 fish at Benjamin Island in winter 2003 to a high of 6,119 fish at The Brothers Islands in summer 2003. For known Steller sea lion prey species (Pitcher 1981, Calkins 1998), mean catch per haul for both locations combined was greatest for young-of-the-year (YOY) walleye pollock in summer (1,844 fish) and salmon in winter (2 fish) (Fig. 2).

Catch also varied by year, especially in summer, because of the strong year-class strength of some species. For example, at The Brothers Islands, mean catch per haul of YOY walleye pollock ranged from 5,878 fish in summer 2001 to only 727 fish in summer 2002. Because of the variability in catch among sites at each location, the only significant difference ($P < 0.05$) in catch per seine haul among years was at Benjamin Island in winter.

Regardless of season or location, most fish captured by seining were juveniles. For example, median size of walleye pollock, Pacific herring, salmon, Pacific sand lance, and Pacific cod was ≤80 mm FL (Fig. 3).

Jig catch

A total of 559 fish, representing 22 species, were captured by hand-jigging (Table 2). Total catch for all sampling periods was dominated by armorhead sculpin (*Gymnocanthus galeatus*), Pacific cod, and dusky rockfish (*Sebastes ciliatus*). The most frequently occurring species in summer were armorhead sculpin (44%) at Benjamin Island and Pacific cod (62%) at The Brothers Islands (Table 2). Armorhead sculpin was the most frequently occurring (>20%) species in winter at both locations. Few walleye pollock and no Pacific herring were captured by jigging.

More fish were captured by jigging in summer (406) than in winter (153) (Table 2). At Benjamin Island, 140 fish representing 19 species were captured in summer and 56 fish representing 12 species in winter (Table 2). At The Brothers Islands, 266 fish representing 14 species were captured in summer and 97 fish representing 13 species in winter. Catch per rod hour was significantly greater ($P < 0.01$) at The Brothers Islands than at Benjamin Island in summer, but did not differ in winter ($P = 0.12$). Mean catch per rod hour for all species in summer ranged from 3 to 6 fish at Benjamin Island and from 6 to 9 fish at The Brothers Islands. At both locations in winter, mean catch per rod hour for all species ranged from 1 to 3 fish. For known Steller sea lion prey species, mean catch per rod hour for both locations combined was greatest for sculpins and Pacific cod, about 1.8 fish in summer and 0.6 fish in winter (Fig. 2).

Fish captured by jigging were larger than those captured by seining. Median size of sculpin, flatfish, Pacific cod, rockfish, and greenling was ≥249 mm FL, and more than 95% of all fish captured by jigging were ≥170 mm FL (Fig. 3).

ROV observations

A total of 26 fish species in summer and 14 species in winter were observed with the ROV at both locations. Species commonly observed with the ROV were juvenile gadids, Pacific sand lance, dusky rockfish, and snake pricklebacks (*Lumpenus sagitta*). Only seven species observed with the ROV were not captured by seining or jigging: Atka mackerel (*Pleurogrammus monopterygius*), Puget Sound rockfish (*Sebastes emphaeus*), silvergray rockfish (*S. brevispinis*), tiger rockfish (*S. nigrocinctus*), yelloweye rockfish (*S. ruberrimus*), rex sole (*Glyptocephalus zachirus*), and Alaska skate (*Bathyraja parmifera*). Mean depth of observation and length of fish observed with the ROV were 43 m and 290 mm FL.

Discussion

A diverse fish assemblage is present in nearshore waters surrounding Benjamin Island and The Brothers Islands. We identified 58 fish species in summer and 44 species in winter at both locations—34 of the species that

Table 1. Total catch and frequency of occurrence (%) of fish captured by beach seining near two Steller sea lion (*Eumetopias jubatus*) haul-outs in southeastern Alaska, 2001-2004.

	Benjamin Island				The Brothers Islands			
	Summer		Winter		Summer		Winter	
Common name	Catch	% n = 38	Catch	% n = 39	Catch	% n = 39	Catch	% n = 40
Walleye pollock	2,096	37	0	0	138,637	85	0	0
Pacific herring	4,362	34	0	0	20,362	28	0	0
Pacific sand lance	4,544	18	0	0	16,839	56	49	3
Pacific cod	187	39	1	3	4,716	82	0	0
Chum salmon[a]	53	13	6	8	4,303	46	75	25
Pacific sandfish	20	5	0	0	1,027	31	1	3
Snake prickleback	389	16	0	0	140	23	0	0
Pink salmon[a]	0	0	64	28	13	10	401	60
Crescent gunnel	42	45	3	8	387	67	5	10
Silverspotted sculpin	20	24	3	8	371	82	8	20
Juvenile cottid	154	53	13	21	214	15	2	5
Rock sole	83	37	105	33	70	26	71	28
Armorhead sculpin	1	3	123	23	13	10	63	28
Tubesnout	1	3	2	5	0	0	191	10
Northern sculpin	44	53	8	13	86	46	4	8
Juvenile greenling	5	8	0	0	125	51	2	5
Juvenile flatfish	77	18	3	3	44	10	2	3
Dolly Varden	117	26	0	0	6	8	0	0
Great sculpin	12	16	11	13	45	49	23	23
Buffalo sculpin	20	29	17	31	28	23	10	18
Coho salmon[a]	43	26	0	0	10	13	0	0
Tubenose poacher	1	3	1	3	34	31	5	10
Sturgeon poacher	21	11	3	3	9	5	3	8
Lingcod	0	0	0	0	32	28	0	0
Arctic shanny	4	8	1	3	16	10	9	8
Capelin	0	0	0	0	1	3	28	5
Tidepool sculpin	0	0	1	3	28	3	0	0

Table 1. (continued.)

	Benjamin Island				The Brothers Islands			
	Summer		Winter		Summer		Winter	
Common name	Catch	% n = 38	Catch	% n = 39	Catch	% n = 39	Catch	% n = 40
Leister sculpin	8	13	1	3	13	10	5	5
Juvenile gadid	20	5	0	0	0	0	0	0
Crested sculpin	2	5	0	0	3	8	11	13
Sockeye salmon[a]	0	0	0	0	1	3	0	0
Steelhead trout[a]	1	3	0	0	0	0	0	0
Additional species[b]	28	–	10	–	40	–	19	–
Total catch	12,355		376		187,613		987	

Summer = July, Winter = February or March.
n = total number of seine hauls for 3 years.

[a] Salmon species were combined into a salmon group for comparison of mean catches and fork length with other Steller sea lion prey species.

[b] Additional species include at least 17 species of fish that were captured in low numbers; frequency of occurrence was not determined for these species.

we captured by seining or jigging, or observed with an ROV, are known to be consumed by Steller sea lions. Some of the most abundant species that we captured also had a high frequency of occurrence in Steller sea lion scat collected at these two haul-outs; walleye pollock, Pacific herring, sculpins, Pacific cod, and rockfish were abundant in our seine or jig catches and occurred in 5% to more than 90% of Steller sea lion scats (Andrew Trites, Univ. of British Columbia, Vancouver, 2004, pers. comm.; J. Womble, 2004, pers. comm.).

Some of the most abundant species that we captured by seining (e.g., walleye pollock, Pacific herring) were mostly YOY and likely too small to be targeted by Steller sea lions. Only 2% of the fish captured by seining were greater than 170 mm FL, an approximate minimum size threshold for entry into the prey field of Steller sea lions (A. Trites, 2004, pers. comm.). Steller sea lions consume a wide size range of walleye pollock (40-780 mm FL), but most walleye pollock that they consume are between 200 and 600 mm long (Tollit et al. 2004, Zeppelin et al. 2004). Thus, at the time of sampling, most of the fish captured by seining were probably not an important component of Steller sea lion diets, but likely contribute to their diet the following winter.

Conversely, most fish captured by jigging (95%) or observed with the ROV were within the size range for entry into the Steller sea lion prey field. Immature Steller sea lions may benefit most from this nearshore

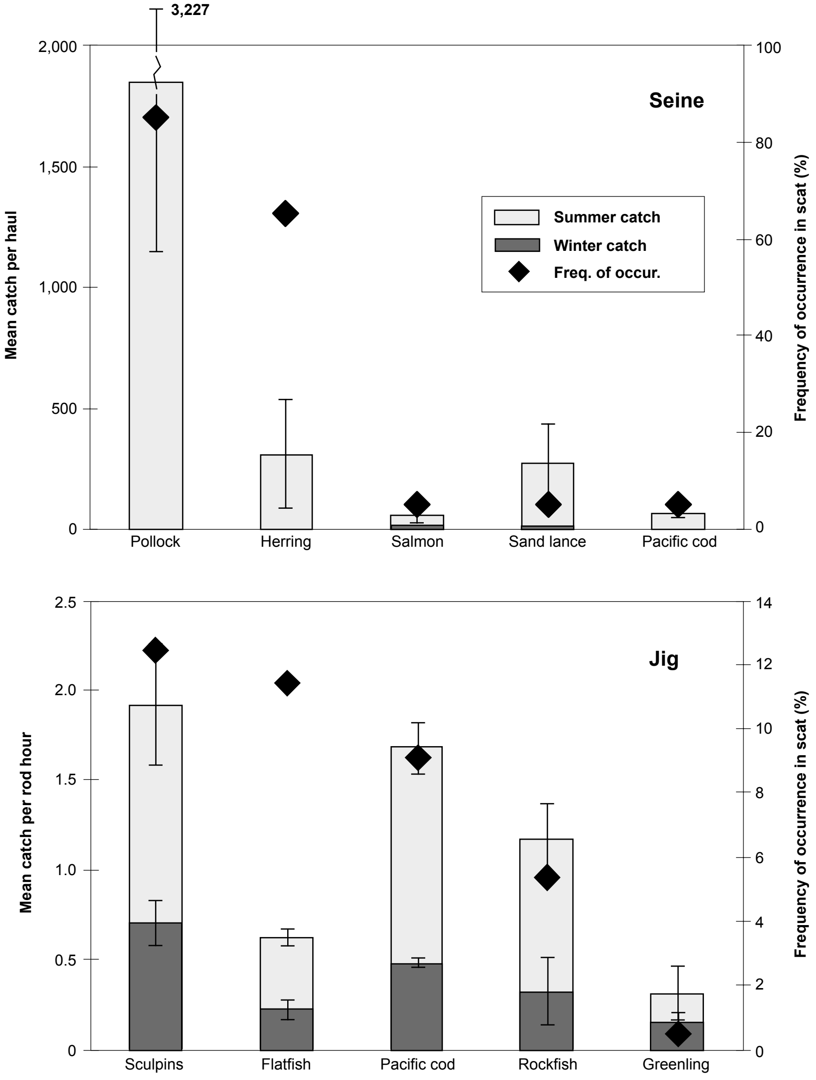


Figure 2. Mean catch per seine haul and per rod hour (with 95% confidence intervals) of prey species captured by beach seining and hand-jigging near two Steller sea lion (*Eumetopias jubatus*) haul-outs in southeastern Alaska, 2001-2004. Diamonds are estimates of the frequency of occurrence of prey in Steller sea lion scat from Benjamin Island and The Brothers Islands (Andrew Trites, Univ. of British Columbia, Vancouver, 2004, pers. comm.; Jamie Womble, National Marine Fisheries Service, Juneau, Alaska, 2004, pers. comm.). Salmon, sculpins, flatfish, rockfish, and greenling consist of numerous species listed in Tables 1 and 2.

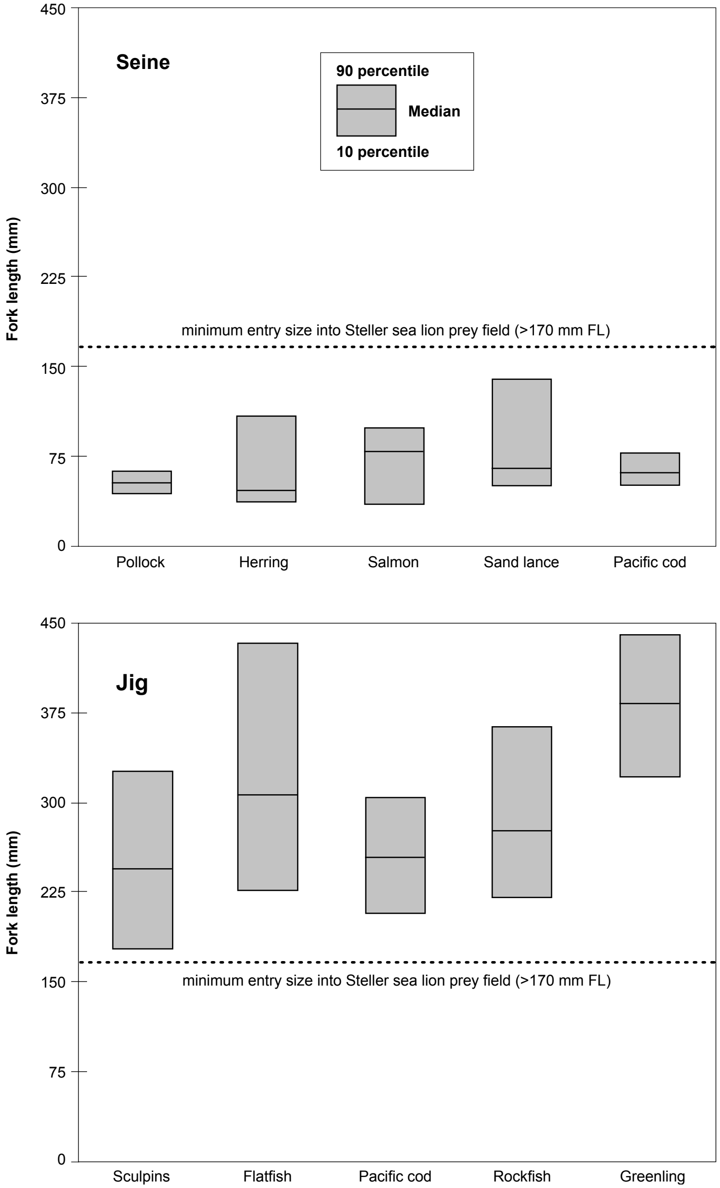


Figure 3. Box plots of fork lengths (FL) of fish captured by beach seining and hand-jigging near two Steller sea lion (*Eumetopias jubatus*) haul-outs in southeastern Alaska, 2001-2004. The dotted line represents the approximate minimum entry size for prey to be consumed by Steller sea lions (Andrew Trites, Univ. of British Columbia, Vancouver, 2004, pers. comm.). Salmon, sculpins, flatfish, rockfish, and greenling consist of numerous species listed in Tables 1 and 2.

Table 2. Total catch and frequency of occurrence (%) of fish captured by hand-jigging near two Steller sea lion (*Eumetopias jubatus*) haul-outs in southeastern Alaska, 2001-2004.

	Benjamin Island				The Brothers Islands			
	Summer		Winter		Summer		Winter	
Common name	Catch	% n = 45	Catch	% n = 43	Catch	% n = 46	Catch	% n = 46
Armorhead sculpin[a]	51	44	18	21	62	38	21	29
Pacific cod	23	29	7	12	87	62	24	24
Dusky rockfish[b]	2	4	5	5	50	36	15	11
Searcher	2	4	1	2	25	33	10	16
Quillback rockfish[b]	14	20	1	2	5	9	1	2
Rock sole[c]	6	13	3	7	8	13	3	7
Yellowfin sole[c]	12	16	7	9	0	0	0	0
Great sculpin[a]	6	11	4	2	6	13	2	4
Kelp greenling[d]	1	2	0	0	6	13	11	18
Walleye pollock	3	4	6	7	6	7	1	2
Red Irish lord[a]	1	2	0	0	3	7	5	11
Pacific halibut[c]	4	7	0	0	3	7	1	2
Alaskan ronquil	2	2	1	2	0	0	2	4
Whitespotted greenling[d]	5	9	0	0	0	0	0	0
Redstripe rockfish[b]	1	2	0	0	3	4	0	0
Flathead sole[c]	3	2	0	0	0	0	0	0
Harlequin rockfish[b]	1	2	0	0	1	2	1	2
Arrowtooth flounder[c]	2	4	0	0	0	0	0	0
Rougheye rockfish[b]	0	0	2	2	0	0	0	0
Dolly Varden	1	2	0	0	0	0	0	0
Roughspine sculpin[a]	0	0	0	0	1	2	0	0
Slender sole[c]	0	0	1	2	0	0	0	0
Total catch	140		56		266		97	

Summer = July, Winter = February or March.
n = total number of jig sites sampled in 3 years.

[a]Sculpin, [b]rockfish, [c]flatfish, and [d]greenling species were each combined into single groups for comparison of mean catches and fork length.

prey field because of their shorter and shallower diving capabilities (Merrick and Loughlin 1997, Loughlin et al. 2003). In addition, a prey field adjacent to haul-outs may be critical to the survival of young Steller sea lions as they remain close to shore while foraging skills are being developed (Raum-Suryan et al. 2004). Whether Steller sea lions utilize this nearshore prey field is difficult to determine because most foraging behavior studies have used satellite telemetry (Merrick and Loughlin 1997, Loughlin et al. 2003, Raum-Suryan et al. 2004), which lacks the fine scale resolution needed to determine the amount of time that Steller sea lions spend in the nearshore. Very high frequency (VHF) tagging studies near Benjamin Island, however, were able to estimate Steller sea lion position within 50 m of actual position and showed that juvenile Steller sea lions often remain close to shore in winter, possibly for access to shallow prey or to reduce the risk of predation (Ben Wilson, Univ. of British Columbia, Vancouver, 2004, pers. comm.).

Lower catches in winter than in summer may indicate seasonal movement of fish (e.g., YOY walleye pollock) from our sampling areas. Turbulence with the onset of fall and winter storms, and seasonal declines in water temperature and food availability, are likely cues for fish to migrate from shallow water habitats to alternate habitats (Love et al. 1991). Lower jig catches in winter than in summer may be the result of fish feeding less because of cooler water temperatures, and fish may seek areas of greater cover (e.g., rocky cracks, crevices, holes), making them less vulnerable to capture.

Jigging was the most effective method for sampling demersal or semi-demersal fish in the size range consumed by Steller sea lions. Although jig catches (3-9 fish per rod hour) were relatively low compared to seine catches (3-2,003 fish per seine haul), all 22 species captured by jigging are known Steller sea lion prey. Jigging also allowed sampling in areas (e.g., rocky bottoms) that could not be effectively sampled by seining or trawling. Jigging was particularly effective for catching Pacific cod (mean FL = 259 mm) in shallow waters (<10 m deep) in summer, and often in dense kelp (*Alaria fistulosa*) beds. At one of our jig sites near kelp, we witnessed a Steller sea lion catch a Pacific cod in summer. Hand-jigging has been successfully used in other studies for sampling fish (Richards et al. 1985, Rutecki and Meyers 1992). Similar to jigging, an ROV can be particularly effective in identifying fish use of habitats where the substrate is too rough to sample with a seine or trawl (Johnson et al. 2003a).

Nearshore waters in the vicinity of Benjamin Island and The Brothers Islands provide a summer nursery area for many important Steller sea lion prey species. For example, at The Brothers Islands, walleye pollock was the highest occurring species in Steller sea lion scat (85%) (A. Trites, 2004, pers. comm.), and the most abundant species captured in summer by seining. Based on mean annual seine catch from summer 2001 to 2003, the area sampled per seine haul, and the total perimeter of the islands, an estimated 706 million YOY walleye pollock may rear in nearshore waters surrounding The Brothers Islands. Eventually, YOY walleye pollock move offshore, and at that time they likely enter the Steller sea lion prey field. For example, at The Brothers Islands, YOY walleye pollock were captured in mid-water trawls more than 800 m offshore at depths from 40 to 265 m in September 2001 (M. Sigler, 2004, pers. comm.). Changes in the nearshore environment from human or natural disturbances, therefore, could have direct effects on nursery areas of Steller sea lion prey and the long-term abundance of prey.

Not all Steller sea lion prey species were caught or observed in nearshore waters surrounding Benjamin Island and The Brothers Islands. Some species such as skates (Rajidae) had a high frequency of occurrence in Steller sea lion scats collected from these haul-outs (20-25%, A. Trites, 2004, pers. comm.; J. Womble, 2004, pers. comm.), but were absent in our catches or were observed in very low numbers (1) with the ROV. We observed only one skate with the ROV; skates were likely in deeper waters than we sampled. Skates were caught offshore of The Brothers Islands with longline gear (M. Sigler, 2005, pers. comm.). This suggests that Steller sea lions are foraging in areas away from the nearshore for some species (e.g., skates). Similarly, Pacific herring had a high frequency of occurrence (>90%) in Steller sea lion scat collected from Benjamin Island in winter; however, no herring were captured or observed in the nearshore in winter, but large schools of herring were identified in hydroacoustic and mid-water trawl surveys offshore of Benjamin Island in winter (M. Sigler, 2004, pers. comm.).

Regardless of season, Pacific herring and walleye pollock were the two most frequently occurring species identified in Steller sea lion scat at either haul-out (A. Trites, 2004, pers. comm.; J. Womble, 2004, pers. comm.). In nearshore waters, however, these two species were mostly too small to be targeted by Steller sea lions, or were absent or not abundant at the time we sampled. Many known Steller sea lion prey species that we identified in nearshore waters, however, were of sufficient size in summer and winter (e.g., Pacific cod, rockfish, Pacific sand lance), and could be important in the diet of Steller sea lions. Nearshore prey close to Steller sea lion haul-outs does provide a source of food that could reduce foraging effort and could be especially important in winter when energy requirements for Steller sea lions are high (Winship et al. 2002). The question remains, to what extent do Steller sea lions forage in nearshore waters; this will require additional, fine-scale tagging (VHF) studies to monitor Steller sea lion foraging behavior close to haul-outs.

We have identified that a diverse assemblage of fish are present in nearshore waters close to two Steller sea lion haul-outs in summer and winter. Methods that we used were successful in capturing or identifying many known Steller sea lion prey species (e.g., Pacific sand lance by seining; Pacific cod by jigging). The best approach to identify the prey field available to Steller sea lions near haul-outs and rookeries is a combination of sampling nearshore methods similar to our techniques and offshore sampling methods of hydroacoustic surveying, mid-water trawling, and longlining.

Acknowledgments

We thank Mary D. Courtney, Wyatt Fournier, Pat Harris, Lee Hulbert, Neil Muirhead, and Cedar Stark for assistance with fieldwork. Darcie Neff assisted with fieldwork and with preparation of the figures and tables of this manuscript. Randy Gregg, captain of the F/V *Patriot* provided winter vessel charters. Adam Moles reviewed an earlier draft of this manuscript.

References

Abookire, A.A., J.F. Piatt, and M.D. Robards. 2000. Nearshore fish distributions in an Alaskan estuary in relation to stratification, temperature and salinity. 2000. Estuar. Coast. Shelf Sci. 51:45-59.

Brown, E.D., and M.G. Carls. 1998. Pacific herring: *Clupea pallasii*. Restoration Notebook, *Exxon Valdez* Oil Spill Trustee Council. *Exxon Valdez* Oil Spill Trustee Council, Anchorage, Alaska. www.evostc.state.ak.us/Habitat/fish.htm.

Byrd, G.V., R.L. Merrick, J.F. Piatt, and B.L. Norcross. 1997. Seabird, marine mammal, and oceanography coordinated investigations near Unimak Pass, Alaska. In: Forage fishes in marine ecosystems. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 351-364.

Calkins, D.G. 1998. Prey of Steller sea lions in the Bering Sea. Biosphere Conservation 1:33-44.

Dean, T.A., L. Haldorson, D.R. Lauf, S.C. Jewett, and A. Blanchard. 2000. The distribution of nearshore fishes in kelp and eelgrass communities in Prince William Sound, Alaska: Associations with vegetation and physical habitat characteristics. Environ. Biol. Fish. 57:271-287.

Johnson, S.W., M.L. Murphy, and D.J. Csepp. 2003a. Distribution, habitat, and behavior of rockfishes, *Sebastes* spp., in nearshore waters of southeastern Alaska: Observations from a remotely operated vehicle. Environ. Biol. Fish. 66:259-270.

Johnson, S.W., A.D. Neff, and J.F. Thedinga. 2005. An atlas on the distribution and habitat of common fishes in nearshore waters of southeastern Alaska. NOAA Tech. Memo. NMFS-AFSC-157. 89 pp.

Johnson, S.W., M.L. Murphy, D.J. Csepp, P.M. Harris, and J.F. Thedinga. 2003b. A survey of fish assemblages in eelgrass and kelp habitats of southeastern Alaska. NOAA Tech. Memo. NMFS-AFSC-139. 39 pp.

Loughlin, T.R., R.L. Merrick, J.L. Sease, and A.E. York. 2003. Diving behavior of immature Steller sea lions (*Eumetopias jubatus*). Fish. Bull. U.S. 101:566-582.

Love, M.S., M.H. Carr, and L.J. Haldorson. 1991. The ecology of substrate-associated juveniles of the genus *Sebastes.* Environ. Biol. Fish. 30:225-243.

Merrick, R.L., and T.R. Loughlin. 1997. Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. Can. J. Zool. 75:776-786.

Mueter, F.J., and B.L. Norcross. 2000. Species composition and abundance of juvenile groundfishes around Steller sea lion *Eumetopias jubatu*s rookeries in the Gulf of Alaska. Alaska Fish. Res. Bull. 7:33-43.

Pitcher, K.W. 1981. Prey of the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska. Fish. Bull. U.S. 79:467-472.

Raum-Suryan, K.L., M. Rehberg, G.W. Pendleton, K.W. Pitcher, and T.S. Gelatt. 2004. Development of dispersal, movement patterns, and haul-out use by pup and juvenile Steller sea lions (*Eumetopias jubatus*) in Alaska. Mar. Mamm. Sci. 20:823-850.

Richards, L.J., A.J. Cass, J.R. Selsby, R. van den Broek, and S.D. Loynachan. 1985. A summary of research catch and effort data for nearshore reef-fishes collected during 1984 in MSA 15 and 16 of the Strait of Georgia. Can. Manuscr. Rep. Fish. Aquat. Sci. 1833. 69 pp.

Rutecki, T.L., and T.R. Meyers. 1992. Mortality of juvenile sablefish captured by hand-jigging and traps. N. Am. J. Fish. Manag. 12:836-837.

Tollit, D.J., S.G. Heaslip, and A.W. Trites. 2004. Sizes of walleye pollock (*Theragra chalcogramma*) consumed by the eastern stock of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska from 1994 to 1999. Fish. Bull. U.S. 102:522-532.

Winship, A.J., A.W. Trites, and D.A.S. Rosen. 2002. A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA. Mar. Ecol. Prog. Ser. 229:291-312.

Wynne, K.M., R. Foy, and L. Buck. 2005. Gulf apex predator-prey study (GAP). Final Report FY2001-2003. University of Alaska Fairbanks, School of Fisheries and Ocean Sciences, Kodiak, Alaska. 241 pp. www.sfos.uaf.edu/gap/publications/annual_reports.htm.

Zeppelin, T.K., D.J. Tollit, K.A. Call., T.J. Orchard, and C.J. Gudmundson. 2004. Sizes of walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*) consumed by the western stock of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1998 to 2000. Fish. Bull. U.S. 102:509-521.

Movements of a Juvenile Southern Sea Lion in La Plata River Estuary (Argentina-Uruguay)

Diego Rodríguez and Ricardo Bastida
CONICET and Universidad Nacional de Mar del Plata, Facultad de Ciencias Exactas y Naturales, Departamento de Ciencias Marinas, Mar del Plata, Argentina

Donald G. Calkins
Alaska SeaLife Center, Seward, Alaska

Randall W. Davis
Texas A&M University, Department of Marine Biology, Galveston, Texas

Abstract

A southern sea lion (*Otaria flavescens*) juvenile male (50 kg) was instrumented with a location-only satellite telemeter and released in December 2003 in the southern margin of the La Plata River estuary (Argentina-Uruguay). The animal was tracked for 28 days, with an average of 3.7 (SD 1.76; range 1-8) daily locations. The total distance traveled was 1,383 km, at a mean transit speed of 0.9 ± 0.55 m s^{-1}. The sea lion spent 90% of the time at sea in characteristic shallow areas (<50 m), with two short periods at the breeding rookeries of Cabo Polonio and Isla de Lobos (Uruguay). At-sea locations were concentrated in the outer area of the estuary, coinciding with a thermohaline surface front, an area reported to be an important spawning ground for several southern sea lion prey. Travel distances, transit speed, and trip durations were similar to those reported for adults. The La Plata River estuary has a high potential importance as a foraging area, especially for the breeding population in Uruguay. For unknown reasons, southern sea lion stocks that inhabit the central southwestern Atlantic have shown a steady decline during the past twenty years, possibly caused by a decrease in prey availability or increasing competition with fisheries and other top predators. These preliminary results indicate that satellite telemetry can improve our understanding of preferred habitats of southern sea lions and aid in designing conservation strategies for the future.

Introduction

Southern sea lions (*Otaria flavescens* [Shaw 1800]) breed and range throughout the coastal temperate waters of South America, from southern Brazil to central Peru, including the Malvinas-Falkland Islands. This species was heavily exploited mainly for oil, with current populations representing a small fraction of historical levels (Hamilton 1934, 1939; Carrara 1952). Although southern sea lions are protected in all South American countries, many populations have never recovered from intense sealing performed during the first half of the twentieth century.

The coastal area of northern Buenos Aires Province (Argentina) is located between southern sea lion populations that are decreasing in Uruguay (Páez 1996) and a stable population in northern Patagonia (Crespo and Pedraza 1991, Reyes et al. 1999). An increasing number of sea lions in northern Buenos Aires Province has been recorded since the mid 1980s, with the establishment of permanent non-breeding colonies (Rodríguez 1996). In northern Argentina and Uruguay, sea lions feed on a variety of fish and squid, most of them part of expanding commercial fisheries (Vaz Ferreira 1982a, Chaijale 1999, Rivero et al. 1999, Naya et al. 2000). This area is also inhabited by South American fur seals (*Arctocephalus australis*) and the Franciscana dolphin (*Pontoporia blainvillei*), both of them preying on many of the same fish and squid species as southern sea lions (Vaz Ferreira 1982b; Rodríguez et al. 1996, 2002; Rivero et al. 1999; Naya et al. 2002). Competition between these top predators and human fisheries may have contributed to the decline of southern sea lions in Uruguay.

The study of marine mammal movements and diving behavior at sea has improved with the use of satellite telemetry. The data provided by these animal-borne instruments have been used to locate foraging areas and to monitor diving behavior in relation to food availability and distribution (Costa et al. 1989, Boyd and Arnbom 1991, Costa 1993, Costa and Gales 2000, Block et al. 2003). This technology has been used in sea lions, but only to a very limited extent with southern sea lions. Werner and Campagna (1995) instrumented six lactating female southern sea lions with time-depth recorders (TDR) in Patagonia, and Campagna et al. (2001) attached satellite telemeters to 20 lactating females and two adult males instrumented in the same area. Thompson et al. (1998) studied a single lactating female in the Malvinas-Falkland Islands. These studies confirmed that southern sea lion foraging trips are confined to the continental shelf, most of them in coastal waters less than 100 m in depth.

The goal of this preliminary study was to track the movements of a juvenile southern sea lion male in the La Plata River estuary (Argentina-Uruguay) using satellite telemetry. Previous studies have focused on adult southern sea lions, so this is the first study to focus on a juvenile. Although our sample size is small, the results show the potential of this approach to increase our understanding of the movements and habitat use of young sea lions, an age class that may be the most vulnerable to mortality.

Materials and methods

A location-only satellite telemeter (SPOT2, 5 cm × 5 cm × 1 cm; Wildlife Computers) was glued (5 min Epoxy, Devcon Inc., Danvers, MA, USA) to the head of a young-of-the-year southern sea lion male (50 kg) before being released from the Fundación Mundo Marino Rehabilitation Center in San Clemente del Tuyú (Argentina) in December 2003. The animal had come ashore on a local beach and had been kept for observation for one week. However, veterinary evaluation showed that the animal was healthy and should be released. The satellite telemetry was programmed to provide geographical location continuously, with transmission suspended after 12 hours on land. Location classes were determined by the Argos satellite system (Service Argos Inc., USA). Only location classes B, A, 0, 1, 2, and 3 were used. Consecutive locations with transit speeds exceeding 2 m s^{-1} were rejected following previous studies on *Otaria flavescens* (Thompson et al. 1998, Campagna et al. 2001); Z-quality locations were also excluded. Mean transit speed was calculated as the average from individual velocities between two consecutive locations. Filtered locations represented 66.4% of total locations recorded. Distance traveled, distance from land, and haul-out locations were determined using Garmin MapSource 3.02 software.

Results

The sea lion was tracked for 28 days, with an average of 3.7 (SD 1.76; range 1-8) usable locations per day (location classes = [A = 19%]; [0 = 2%]; [1 = 47%]; [2 = 24%]; [3 = 9%]; 87 total locations). The total distance traveled was 1,383 km at an average transit speed of 0.9 ± 0.55 m s^{-1} (Fig. 1); the most common rate was less than 0.5 m s^{-1} (32.2% of the trips), with decreasing frequencies with increasing speed. The locations were mainly recorded during night hours, with 84.3% received between 20:00 and 04:00 local time (Fig. 2). Daily distance traveled averaged 57.6 km (SD 32.22; range 3.2-124.1), with an average distance and time between locations of 15.89 ± 24.73 km and 6.69 ± 9.81 h, respectively.

The sea lion spent 90% of the time at sea, with a two-day haul-out period at the colony near Cabo Polonio (34º20'54"S, 54º44'45"W). The first

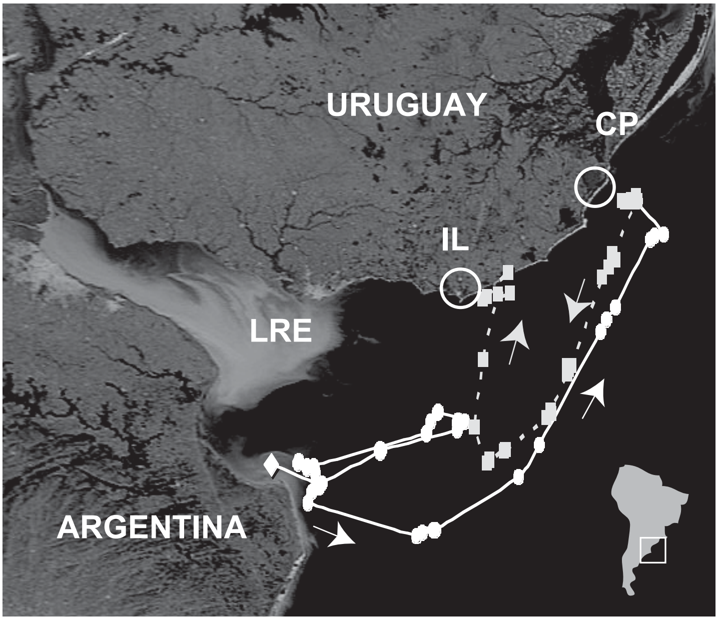


Figure 1. Locations of trips performed by a southern sea lion juvenile male in the La Plata River Estuary (LRE), December 2003-January 2004. Diamond indicates the release location; white track with circles indicates the first trip, and dashed track with squares represents the second trip. Large circles indicate southern sea lion colonies on Isla de Lobos (IL) and Cabo Polonio (CP).

trip, from release to haul-out at Cabo Polonio, lasted 11 days and covered 802 km, whereas the second part after hauling-out lasted 14 days and covered 577 km. The sea lion also visited the area near the colony on Isla de Lobos (35º01'50"S, 54º53'00"W), but there is no indication that it hauled out on land. Nearly all locations were recorded in coastal waters (<50 m deep), half of them less than 30 m deep. Average distance from shore was 60.8 km (SD 52.96; max 150 km).

Discussion

The data presented here are the first describing the movements of a juvenile southern sea lion, as previous studies focused on lactating females (Thompson et al. 1998, Campagna et al. 2001) or adult males (Campagna et al. 2001). The juvenile sea lion in this study remained in shallow (<50 m) waters within the La Plata river estuary, with a maximum range from the location of release of ca. 400 km. The movements of this animal

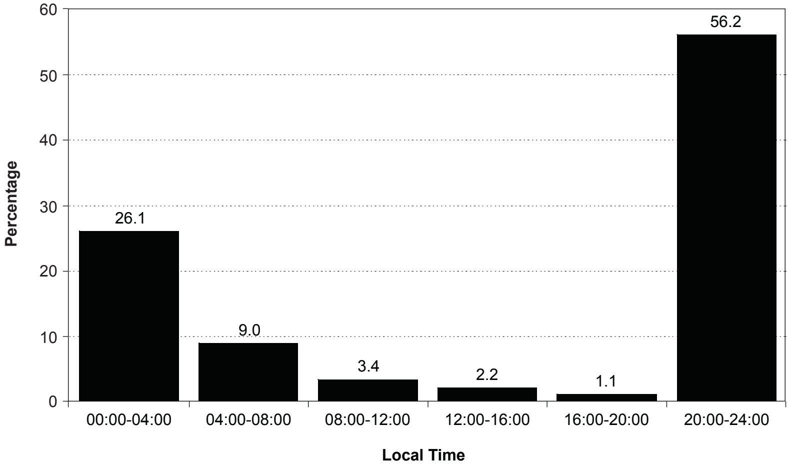


Figure 2. Frequency of satellite locations received at 4 hour intervals of local time.

indicate the potential importance of this estuarine habitat for young southern sea lions.

Maximum travel distances (803 and 577 km) between haul-out and average transit speed were similar to those reported for adult sea lions in Patagonia, but trip duration was longer than those reported by Campagna et al. (2001) (2-4 days for lactating females during the breeding season and 4-9 days in males during the foraging period prior to the breeding season). The shorter maximum distance from shore reported here (150 km) suggests that juveniles may not travel long distances offshore compared to adults (300-500 km).

The tendency of a more frequent nocturnal reception of satellite locations may reflect a higher proportion of time present at surface or differences in satellite pass frequency or reception.

The La Plata river estuary drains the second fluvial basin of South America. With a surface of about 30,000 km^2, this shallow funnel-shaped estuary outflows 22,000 m^3 s^{-1} of freshwater into coastal marine waters, creating a highly dynamic and productive environment that dominates the northern coast of Argentina, Uruguay and southern Brazil (Boschi 1988, Mianzan et al. 2001). Semi-permanent surface and bottom thermohaline salinity fronts have been identified, and have a strong influence on the distribution and abundance of fish stocks (Lasta 1995, Nion 1997, Acha 1999). At-sea locations in the present study indicate that foraging activity in the outer area of the estuary coincide with a thermohaline surface front. This area is reported to be an important summer spawning ground for several southern sea lion prey species, especially the striped weakfish (*Cynoscion guatucupa*, Macchi et al. 1996, Macchi 1998, Macchi and Acha 1998, Acha 1999), which is the most important prey item of sea lions at both Isla de Lobos (Uruguay; Naya et al. 2000) and Puerto Quequén (Argentina; Rivero et al. 1999). To implement effective conservation strategies for southern sea lions, we need to improve our knowledge on foraging ecology in areas of high fishing effort, such as occurs in coastal northern Argentina and Uruguay. Monitoring the foraging behavior of southern sea lions in a highly dynamic area as La Plata River estuary will help us to understand the trophodynamics of this species and the potential overlapping with fisheries and other marine mammals of the region. The effects of commercial fisheries should be a concern for the future of sea lions in northern Argentina, as the most important fish prey (i.e., *Cynoscion guatucupa*, *Micropogonias furnieri*, and *Macrodon ancylodon*) show early signs of overfishing (Cordo 1986a,b).

Acknowledgments

We wish to express our gratitude to directors and staff of Fundación Mundo Marino (Argentina) for their support and assistance in the instrumentation procedure.

References

Acha, E.M. 1999. Estrategia reproductiva de la sacara, *Brevoortia aurea* (Spix and Agassiz, 1829), en el estuario del Río de la Plata. Tesis doctoral, Universidad Nacional de Mar del Plata. 253 pp.

Block, B.A., D.P. Costa, G.W. Bohelert, and R.E. Kochevar. 2003. Revealing pelagic habitat use: The Tagging of Pacific Pelagics Program. Oceanol. Acta 25:255-266.

Boschi, E.E. 1988. El ecosistema estuarial del Rio de la Plata. Anales del Instituto de Ciencias del Mar y Limnologia de la Universidad Nacional Autonoma de Mexico 15:159-182.

Boyd, I.L., and T. Arnbom. 1991. Diving behavior in relation to water temperature in the southern elephant seal: Foraging implications. Polar Biol. 11:259-266.

Campagna, C., R. Werner, W. Karesh, M.R. Marin, F. Koontz, F. Cook, and C. Koontz. 2001. Movements and location at sea of South American sea lions (*Otaria flavescens*). J. Zool. 257:205-220.

Carrara, I.S. 1952. Lobos marinos, pingüinos y guaneras de las costas del litoral maritimo e islas adyacentes de la Republica Argentina. Publicación Especial del Ministerio de Educación, Facultad de Ciencias Veterinarias, Universidad Nacional de La Plata, Argentina. 235 pp.

Chaijale, N. 1999. Feeding ecology of southern sea lions in Mar del Plata harbour. Undergraduate thesis, Facultad de Ciencias Exactas, Fisicas y Naturales, Universidad Nacional de Cordoba (Argentina). 99 pp. (In Spanish.)

Cordo, H.D. 1986a Estudios biológicos sobre peces costeros con datos de dos campañas de investigación realizadas en 1981. III Pescadilla de red (*Cynoscion striatus*). Publicación de la Comisión Técnica Mixta Argentino-Uruguaya 1:15-27.

Cordo, H.D. 1986b. Estudios biológicos sobre peces costeros con datos de dos campañas de investigación realizadas en 1981. IV Pescadilla real (*Macrodon ancylodon*). Publicación de la Comisión Técnica Mixta Argentino-Uruguaya 1:47-52.

Costa, D.P. 1993. The secret life of marine mammals: New tools for studying their behavior and movements at sea. Oceanography 6:120-128.

Costa, D.P., and N.J. Gales. 2000. Foraging energetics and diving behavior of lactating New Zealand sea lions, *Phocarctos hookeri*. J. Exp. Biol. 203:3655-3665.

Costa, D.P., M. Kretzmann, and P.H. Thorson. 1989. Diving patterns and energetics of the Australian sea lion, *Neophoca cinerea*. Am. Zool. 29:71-75.

Crespo, E.A., and S.N. Pedraza. 1991. Current status and population trends of the norpatagonian population of southern sea lions (*Otaria flavescens*). Ecol. Austral 1:87-95. (In Spanish.)

Hamilton, J.E. 1934. The southern sea lion, *Otaria byronia* (de Blainville). Discov. Rep. 8:269-318.

Hamilton, J.E. 1939. A second report on the southern sea lion *Otaria byronia* (de Blainville). Discov. Rep. 19:121-164.

Lasta, C.A. 1995. La Bahía Samborombón: Zona de desove y crianza de peces. Tesis Doctoral, Universidad Nacional de La Plata (Argentina). 304 pp.

Macchi, G.J. 1998. Preliminary estimate of the spawning frequency and batch fecundity of the striped weakfish, *Cynoscion striatus*, in the coastal waters off Buenos Aires province. Fish. Bull. U.S. 96:375-381.

Macchi, G.J., and E.M. Acha. 1998. Aspectos reproductivos de las principales especies de peces de la Zona Común de Pesca y en El Rincón. In: C.A. Lasta (ed.), Resultados de una campaña de evaluación de recursos demersales costeros de la Provincia de Buenos Aires. Informe Técnico del Instituto Nacional de Investigación y Desarrollo Pesquero 21:67-89.

Macchi, G.J., E.M. Acha, and C.A. Lasta. 1996. Desove y fecundidad de la corvina rubia, *Micropogonias furnieri* Desmarest, 1823, del Estuario del Río de la Plata, Argentina. Boletín del Instituto Español de Oceanografía 12:99-113.

Mianzan, H., C. Lasta, E. Acha, R. Guerrero, G. Macchi, and C. Bremec. 2001. The Rio de la Plata Estuary, Argentina-Uruguay. In: U. Seelinger and B. Kjervje (eds.), Coastal and marine environments of Latin America. Springer-Verlag, Berlin, pp. 185-204.

Naya, D.E., M. Arim, and R. Vargas. 2002. Diet of South American fur seals (*Arctocephalus australis*) in Isla de Lobos, Uruguay. Mar. Mamm. Sci. 18:734-745.

Naya, D.E., R. Vargas, and M. Arim. 2000. Preliminary analysis of southern sea lion (*Otaria flavescens*) diet in Isla de Lobos, Uruguay. Boletin de la Sociedad Zoologica del Uruguay (2da Epoca) 12:14-21. (In Spanish.)

Nion, H. 1997. Fishes of the Rio de la Plata and some aspects of their ecology. In: P.G. Wells and G.R. Daborn (eds.), The Rio de la Plata: An environmental overview. Eco-Plata Project background report. Dalhousie University, Halifax, Nova Scotia, Canada, pp. 163-184.

Páez, E. 1996. Simulaciones estocásticas en la población de *Otaria flavescens* en Uruguay. Abstracts 7ma Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur, Viña del Mar, Chile, p. 116. (In Spanish.)

Reyes, L.M., E.A. Crespo, and V. Szapkievich. 1999. Distribution and population size of the southern sea lion (*Otaria flavescens*) in central and southern Chubut, Patagonia, Argentina. Mar. Mamm. Sci. 15:478-493.

Rivero, L., R. Bastida, D. Rodriguez, and G. Westergaard. 1999. Southern sea lion feeding habits in Puerto Quequen, Argentina. Resúmenes Expandidos del VIII Congreso Latinoamericano de Ciencias del Mar I:265-266. (In Spanish.)

Rodriguez, D. 1996. Biology and ecology of pinnipeds from northern Argentina. Ph.D. thesis, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina. 351 pp. (In Spanish.)

Rodriguez, D., L. Rivero, and R. Bastida. 2002. Feeding ecology of the Franciscana dolphin (*Pontoporia blainvillei*) in marine and estuarine waters of Argentina. Latin American Journal of Aquatic Mammals 1:77-94.

Rodriguez, D., R. Bastida, L. Rivero, and S. Moron. 1996. Preliminary results on the diet of South American fur seals, *Arctocephalus australis*, in coastal waters of northern Argentina. Abstracts 7ma Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur, Viña del Mar, Chile. (In Spanish.)

Thompson, D., C.D. Duck, B.J. McConnell, and J. Garrett. 1998. Foraging behavior and diet in lactating southern sea lions (*Otaria flavescens*) in the Falkland Islands. J. Zool. 246:135-146.

Vaz Ferreira, R. 1982a. *Otaria flavescens* (Shaw), South American sea lion. Mammals in the seas, Vol. IV. FAO Fish. Ser. 5, pp. 477-496.

Vaz Ferreira, R. 1982b. *Arctocephalus australis* (Zimmermann). South American fur seal. Mammals in the seas, Vol. IV. FAO Fisheries Series 5, pp. 497-508.

Werner, R., and C. Campagna. 1995. Diving behavior of lactating southern sea lions (*Otaria flavescens*) in Patagonia. Can. J. Zool. 73:1975-1982.

Estimating Diet Composition in Sea Lions: Which Technique to Choose?

Dominic Tollit and Susan Heaslip
University of British Columbia, Marine Mammal Research Unit, Fisheries Centre, Vancouver, British Columbia, Canada

Bruce Deagle
University of Tasmania, Zoology Department, Hobart, Australia

Sara Iverson
Dalhousie University, Biology Department, Halifax, Nova Scotia, Canada

Ruth Joy, David Rosen, and Andrew Trites
University of British Columbia, Marine Mammal Research Unit, Fisheries Centre, Vancouver, British Columbia, Canada

Abstract

Reliable estimates of diets are vital to monitor impacts of sea lion populations on their ecosystems and their interactions with fisheries, and to understand the role of food to animal nutrition and health. Approaches include using (1) prey remnants in stomach contents, spews and scats; (2) prey DNA in scats; (3) fatty acid signatures in blubber; and (4) stable isotope ratios in predator's tissue. Each methodology has particular advantages and limitations, many of which can be assessed and improved through controlled captive feeding trials. Analysis of prey remnants from captive sea lion scats have shown significant variability in digestion between and within prey species, which, coupled with preferential regurgitation and enumeration biases, can confound accurate diet quantification, but does not prevent spatial or temporal comparisons. Correction for partial digestion and use of additional structures besides otoliths can provide reliable prey size estimates. Prey DNA can be consistently isolated from soft remains in scats from captive sea lions, and with further development this approach may allow quantification of diet. Genetic methods can be expensive and representative of only one to two days foraging (like prey remnant analysis), but may be less affected by differential digestion and can identify prey in scats that could not be identified through structural remnants. Validation of fatty acid signature analysis to quantify diet at longer temporal scales in sea lions is ongoing. This new technique promises to be particularly useful to assess biases in traditional methods, identify the onset of weaning, and highlight the prey that most contribute to lipid reserves. Stable isotope analysis of predator tissues gives only trophic level data, but can provide data on diet changes on many temporal scales. Remote video monitoring of foraging events and lavage/enema techniques can provide valuable diet information, but, like many newer techniques, animal capture is required. Ideally a suite of techniques should be used to study diet. While methods and correction factors developed for Steller sea lions can likely be applied to the other five sea lion species, they should be verified experimentally.

Introduction

Reliable estimates of diets are vital to monitor impacts of sea lion populations on their ecosystems and their interactions with fisheries, and to understand the role of food to animal nutrition and health. The traditional approach was to examine stomach contents. More recent methods include using hard remains in scats and spews, isolating prey DNA from scats, fatty acid signatures in blubber, stable isotope ratios in predators' tissues, and direct video observation. All methods of estimating diet have pros and cons (Table 1), many of which can be assessed and improved through controlled captive feeding trials.

Methods

Captive feeding studies with 2-5 year old female Steller sea lions at the Vancouver Aquarium Marine Science Centre have assessed three different methods to quantify diet. In this review, we summarize the findings of these studies, complement them with results from additional captive studies with sea lions, and discuss the benefits and drawbacks of alternate techniques presently being used to study sea lion diet (Table 1).

1. Prey remains found in scats

The analysis of prey skeletal structures found in scats (feces) is now the most widely used technique for estimating the diet of pinnipeds, with sagittal otoliths being the most commonly used identifying structure (Frost and Lowry 1980, Olesiuk et al. 1990, Bowen et al. 1993, Tollit and Thompson 1996). However, there remain a number of well recognized problems related to identifying prey without hard remains, differential rates of digestion (hence, recovery), and choice of skeletal structures used to identify prey (see reviews by Pierce and Boyle 1991, Bowen 2000).

Table 1. Pros and cons of different methods used to estimate diet in otariids.

Method to estimate diet	Impact on individual	Impact on group	Dietary time period	Prey size estimate	Additional limitations
Scats, hard remains	No	Moderate	Short	Yes	Differential prey digestion and retention. Requires presence of prey hard parts. Special identification skills often required.
Spews, hard remains	No	Moderate	Short	Yes	Differential prey digestion and retention. Requires presence of prey hard parts. Special identification skills often required.
Scats, DNA remains	No	Moderate	Short	No	New technique, relatively untested. Lack of genetic data for many prey.
Lavage (enema)	Moderate (low)	Low-moderate	Short	Yes	Capture and sample size issues. Empty stomachs (colons) reduce sample size.
Stomach samples	Extreme	Moderate-high	Short	Yes	Differential prey digestion and retention. Empty stomachs reduce sample size.
Stable isotopes	Moderate	Low-moderate	Moderate-long	No	Capture and sample size issues. Only trophic level quantification.
Fatty acid signatures	Moderate	Low-moderate	Moderate-long	No	Capture and sample size issues. New technique, relatively untested. Current prey library required.
Head camera	Moderate	Low-moderate	Short	Possible	Capture and sample size issues. High cost and unit recovery required. Low number of feeding events captured.
Direct observation	No	Low	Immediate	Possible	Limited to prey brought to surface. Limited mainly to nearshore interactions.

Recent captive studies (e.g., Gales and Cheal 1992, Orr and Harvey 2001, Cottrell and Trites 2002, Staniland 2002, Tollit et al. 2003) were designed to provide numerical and size correction factors to account for the effects of digestion, and to assess the use of different structures and diet indices in describing diet. More recently, multiple bones in addition to otoliths have been used for prey identification from scat, a technique that requires highly specialized identification skills and a complete reference collection. Nevertheless, the technique was believed to significantly reduce the problems associated with differential digestion (Olesiuk et al. 1990). Our captive studies have therefore concentrated on assessing this new approach by feeding both individual single species meals (see Tollit et al. 2003 for methods) as well as replicated meals of mixed and varying species composition.

A total of three replicated meal feeding trials were undertaken at the Vancouver Aquarium Marine Science Centre in the summer of 2003. As in the single species meal feeding trials, experimental meals were preceded and followed by 3 days of herring fillets. Each trial fed for 15 days the same four species (herring, walleye pollock, coho salmon, and capelin) at the same time (~10:15 and ~15:15), in the same quantity (7.5% body mass per day), but in three different prey ratios (scenario 1, 67.5%, 22.5, 7.5%, 2.5% respectively; scenario 2, 22.5%, 67.5%, 2.5%, 7.5% respectively, and scenario 3, 25% of each species). Other than during tank drains for scat collections, animals had full access to water. The number of fish represented by all recovered structures was estimated using a "minimum number of individuals" technique (Tollit et al. 2003) for each drain and scat recovered over days 2-16. Diet fed (proportion by mass) was compared with diet estimated using both the split sample frequency of occurrence (SSFO) method (Olesiuk et al. 1990) and a simple biomass reconstruction (BR) method, in which it was assumed prey size egested was identical to that ingested and each drain/scat contributed a variable quantity of prey biomass (Laake et al. 2002). Reconstructed biomass estimates were compared when using the "all structure" technique and when using only otoliths.

2. Prey soft remains identified in scats using genetic techniques

Using molecular genetic scatology to study diet is a relatively new and involved technique (Jarman et al. 2004), but it has been successfully utilized to classify morphologically unidentifiable hard parts of salmon from harbor seal scats (Purcell et al. 2004). Many of the biases associated with hard remnant analysis could potentially be investigated using DNA techniques to identify prey from soft material, making this approach very appealing. Our recent collaborative captive study (Deagle et al. 2005) aimed to assess whether prey DNA could reliably be detected from soft remains in scats and whether DNA in scats might be useful in quantifying diet. In this study, we collected scats from two female Steller sea lions. The first animal (#F97HA, mean mass 146 kg, 6 years old) was in the feeding trial for 48 days; and the second animal (#F00NU, mean mass 131 kg, 3 years old) for 24 days. Four species of prey were fed consistently in the trial: Pacific herring (*Clupea pallasii*), surf smelt (*Hypomesus pretiosus*), sockeye salmon (*Oncorhynchus nerka*), and Californian market squid (*Loligo opalescence*). The basic daily diet (7-8 kg per day, ~5.5% of body mass) was fed in two meals (at ~9:30 and 14:30) and consisted of herring (47% by mass), smelt (34%), sockeye (13%), and squid (6%). This diet was initiated at least 4 days before the first scats were collected. Small subsamples were taken from each scat and the remaining material blended and then also sampled. DNA was extracted and identified to species using polymerase chain reaction (PCR) and denaturing gradient gel electrophoresis. In a preliminary investigation into quantifying diet, proportions of fish DNA present in six scats were evaluated through the screening of PCR clone libraries. See Deagle et al. (2005) for full details of DNA detection and cloning methodology.

3. Fatty acid signature analysis

Fatty acid signatures have been shown to be useful in documenting qualitative variations in diet across species, age, and sex class (e.g., Beck et al. 2005) as well as space and time (e.g., Iverson et al. 1997, Walton and Pomeroy 2003). Quantified fatty acid signature analysis (QFASA) is based on an optimization model that has been developed to estimate the species composition of marine mammal diets by matching the fatty acid (FA) signatures of their blubber with those of their potential prey (Iverson et al. 2004). We conducted captive feeding studies (1-9 months each) on seven juvenile female Steller sea lions to evaluate QFASA's ability to identify known mixed-prey diets and to provide information on FA turnover time and deposition rates down the core of the biopsy. For each animal, 2-9 sequential full-depth blubber biopsies were collected mid-flank, following various periods of controlled diet, including 1-4 week pulses of salmon, capelin, eulachon, walleye pollock, or Atka mackerel. Changes in mass and body composition (using D_20) were also measured (Tollit et al. 2003). A key prerequisite of QFASA are the FA calibration coefficients (FA-CCs), which aim to account for the differential deposition and synthesis of fatty acids during lipid metabolism. These are typically calculated by using FA signatures in blubber after feeding a long-term diet of pure herring. FA-CCs are available for two species of phocid (Iverson et al. 2004), but none are available for otariids. To assess possible differences in fatty acid metabolism across pinnipeds, blubber biopsies were taken from five Steller sea lions after they were fed pure herring diets for 7-9 months. After lipid extraction, flame ionization detector (FID) gas chromatography was used to assess contributions of 68 fatty acid signatures (see Iverson et al. 2004 for a full methodology).

Results

1. Prey hard remains found in scats

Use of multiple bones (versus only otoliths) increased percent prey recovery (Fig. 1), particularly for salmon. Despite the use of the "all structure" technique, significant differences across prey species in percent recovery (more than tenfold) and passage time (twofold) was documented. Bones in scats were found to consist of a composite of meals eaten 2-148 hours earlier (longer than many phocids) and a single day feeding event was distributed across 1-6 scats (Tollit et al. 2003).

Beaks from the small (~40 g) squid fed were typically found in scats 1-2 days following ingestion, but were also sometimes recovered more than 3 weeks later. A number of meals were subsequently regurgitated, which dramatically reduced the overall recovery of bones in scats, most notably for pollock and salmon. Use of other cranial bones (in addition to otoliths), grading the degree of observed digestion, and the application of experimentally derived grade-specific digestion correction factors (Fig. 2) are fundamental to correctly estimating prey size eaten by Steller sea lions (see also Tollit et al. 2004a,b; Zeppelin et al. 2004).

Regurgitations in scenario 3 of the replicated mixed meal study resulted in fed diets being ~12% pollock and ~29% for the remaining species, not 25% for each species as planned. Analysis of the repeated mixed meal study showed that, despite low contributions of capelin and salmon in scenarios 1 and 2, their presence in subsequent scats was almost always detected when using the "all structure" technique. Consequently, the frequency of occurrence model could not discern the different mixed diet scenarios actually fed. In this particular set of scenarios, the biomass reconstruction (BR) models provided better predictions of the actual amount fed of each species. The BR model using "all structures" did, however, exhibit consistent biases, with capelin consistently underestimated, and salmon and pollock consistently overestimated (Fig. 3). The use of only otoliths to estimate diet resulted in a number of improvements (e.g., salmon) over the "all structure" technique, but also resulted in some poorer predictions (e.g., herring). Capelin, the smallest prey consumed, remained consistently underestimated (Fig. 3).

2. Prey soft remains identified in scats using genetic techniques

Our results show prey DNA can be successfully isolated from soft remains, even in cases when the scats were left out in the sun for a number of days. Detection rates (i.e., frequencies of prey DNA occurrence) were extremely high (98%) when scats were blended together and sampled. When scats were simply subsampled, the detection rates were significantly lower (but still relatively high—89%). Different prey species were generally detected equally despite the large differences in the amount

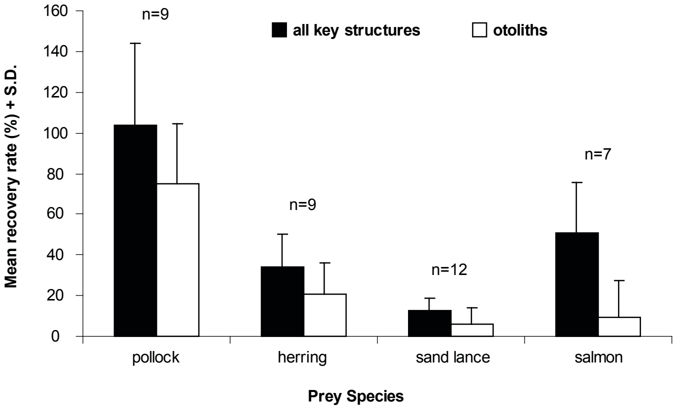


Figure 1. Between-species comparison of mean prey recovery (%), when using multiple bones (all key structures) versus otoliths only. Data represent multiple feeding trials (n) with two female captive Steller sea lions in which meals containing regurgitated material have been excluded. Adapted from Tollit et al. (2003).

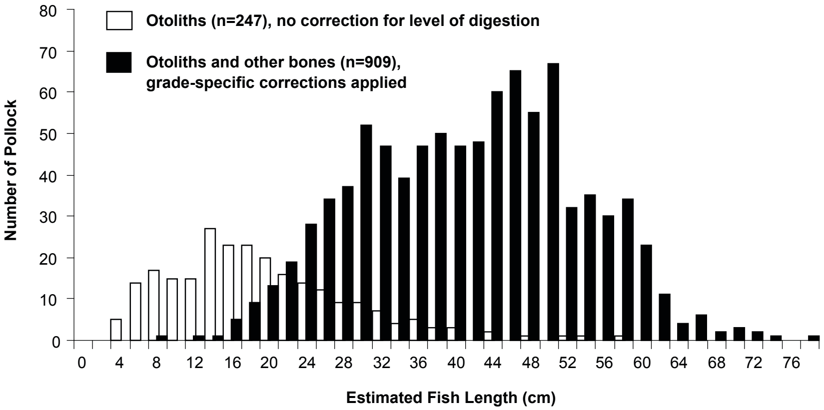


Figure 2. Comparison of two methods to estimate the size of walleye pollock recovered in Steller sea lion scats collected in the field (Southeast Alaska 1993-1999). Fish length predicted from all otoliths regardless of digestive state (mean FL = 20.2 cm) are compared with estimates using six additional cranial structures besides otoliths, of which all are in good or fair condition and to which experimentally derived grade-specific correction factors have been applied to account for level of digestion (mean FL = 42.4 cm).

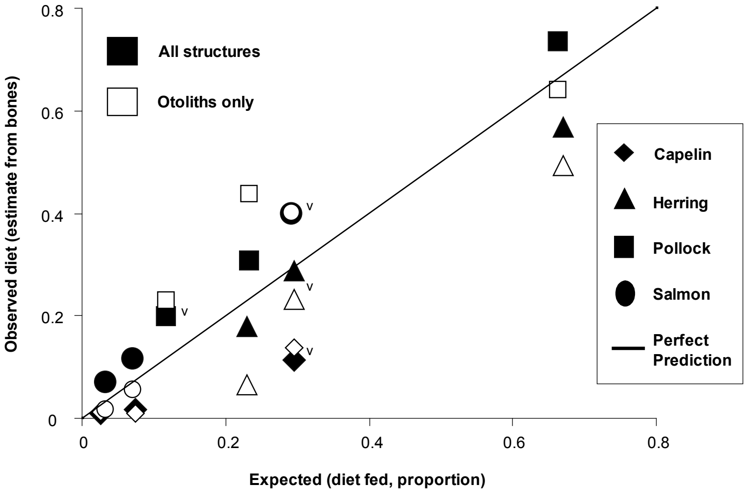


Figure 3. Comparison of using the "all structure" technique versus only otoliths in estimating diet using a biomass reconstruction method (observed diet). Captive Steller sea lions were fed meals of mixed and variable prey composition consistently for 15 days (diet fed). V denotes data points that include evidence of regurgitated hard remains in 36% of scats/tank drains.

Figure 4. Fatty acid calibration coefficients shown for three pinniped species, including Steller sea lions (SSL). Fatty acids (n = 41) ranging from C12.0 to C24.1w9 are shown, with the line at 1 indicating the proportion found in the diet was identical to that found in the blubber sample (no synthesis or deposition). Data for grey and harp seals are taken from Iverson et al. (2004).

of each fed. Proportions of fish DNA present in six scat samples were roughly proportional to the mass of prey consumed, but directional biases were apparent. For example, herring (fed at 50% of the total fish component) and salmon (fed at 14%) were both slightly overestimated (clone predictions: herring, 56-72%; salmon, 16-28%), while smelt (fed at 36%) was underestimated somewhat, with predictions from clones ranging from 12% to 32%.

3. Fatty acid signature analysis

Optimization of the QFASA model using data from captive animal studies is still ongoing. To date QFASA results were promising, but did result in false identifications of prey, and were dependent on which modeling parameters were used (FA-CCs, number of FAs included, etc.). Preliminary results also showed Steller sea lion FA-CCs were comparable to but not interchangeable with those previously obtained from phocid seals (Fig. 4). Overall, where differences were apparent, Steller sea lion FA-CCs were lower than for those observed for gray and harp seals for fatty acids: C14.1w5, C15.1w8, C16.1w11, C17.0, C17.1, C16.4w1, C18.1w11, C18.1w9, C18.3w3, C18.4w3, C20.5w3, C22.2w6 and C22.5w3; and higher for fatty acids: C14.1w7, C15.1w6, C20.0, C22.1w7, C22.1w9, C22.1w11, C22.4w6, C24.1w9.

Discussion

Scat collections may disturb animals resting on land, but they are otherwise noninvasive. Importantly, they typically provide definitive prey species identification and can often be collected in large numbers. Analysis of prey remnants in scats presently remains the best method for assessing prey size, provided levels of digestion are taken into account (Jobling and Breiby 1986). Low recovery of otoliths in sea lion scats has been shown in a number of species (e.g., Dellinger and Trillmich 1988, Gales and Cheal 1992, Tollit et al. 2003), therefore other techniques are needed to supplement dietary data. For example, the use of alternate bones (as well as accounting for the amount of digestion) was demonstrated to be crucial in assessing the extent of overlap between sizes of pollock taken by Steller sea lions compared to that taken by the commercial fishery (Fig. 2, Tollit et al. 2004a). However, while the use of multiple bones increases species recovery rates, species differences (hence potential biases) are not eliminated and enumeration becomes problematic (see Tollit et al. 2003). This is mainly a result of fish bones from single feeding events being spread over multiple (1-6) scats and consequently resulting in the double counting of the same fish. Counting the most numerous paired bone available or the development of new bone-counting techniques to estimate prey numbers eaten may circumvent this particular problem. However, it is important to note that captive feeding studies often report information by collapsing data for all scats collected after a meal. A more logical (realistic?) approach would be to provide information at the level of individual scats. For example, while pollock recovery per feeding event was relatively high overall (Fig. 1), it was also distributed across a large number of scats. Nevertheless, the extended scat output we observed in Steller sea lions, and seen also in southern sea lions (D. Rodriguez, CONICET, Mar del Plata, Argentina, pers. comm.), does challenge the assumption that scats necessarily represent just nearshore or recent foraging.

Provided sample sizes are sufficient (estimated for biomass reconstruction to be around 100 samples by Hammond and Rothery [1996]), it is reasonable to assume inherent biases are consistent, permitting comparisons of the relative importance of prey species across time periods or geographical areas. Use of correction factors can negate some biases associated with differential digestion, but regurgitation and crushing by gastroliths or stomach rocks of larger bones confound their easy application. Clearly, given the high intraspecific variability observed, multiple experiments are required to produce useful correction factors and the experiment must be designed to be as realistic as possible. Gastroliths in the Australian sea lion may have been a factor in the low otolith recovery observed in captive feeding studies (Gales and Cheal 1992), as well as from scats collected in the wild. In species that are known to regularly regurgitate material (e.g., California sea lion, Steller sea lion, northern fur seal, Galapagos fur seal), it is important to analyze regurgitate material (either from lavage or from land-based regurgitates) to assess possible biases in size and species consumed, compared to assessments solely from scats (Fea and Harcourt 1997, Kiyota 1999). Apparent biases in exclusively using scat data include underestimating large cephalopods and large fish such as gadoids. Data on at-sea feeding episodes and regurgitation rates (using head-mounted cameras) would be useful in this assessment (see Bowen et al. 2002).

Frequency of occurrence indexes can quickly provide useful dietary information, particularly with large sample sizes (Olesiuk 1990, Sinclair and Zeppelin 2002). Our replicated mixed meal study highlighted the reliability of the "all structure" technique in identifying the presence of four prey fed regularly in widely varying proportions (2.5%-67.5%), leading to the split sample frequency of occurrence index (SSFO) to predict all prey were eaten in approximately equal quantities. Olesiuk et al. (1990) recognized SSFO captures the occurrence component of diet and suggested a volume-weighted version. Our results concur that a prey biomass/volume approach is required if fine level diet estimates are required at small scales and within narrow time frames, especially when sample sizes are limited. Thus, while biomass reconstruction generally gave improved predictions of the actual amount fed of each species, systematic biases were observed (Fig. 3), that confirm previous studies (e.g., Harvey 1989; Tollit et al. 1997, 2003) that highlight the need for species-specific numerical correction factors. The drawbacks of reconstructing prey biomass include the need for prey remains to be enumerated and measured and the need for bone size to fish size regressions. In addition to captive studies, the use of Monte Carlo diet simulations can provide useful information on the biases of each method and to assess the success of possible solutions (Hammond and Rothery 1996, Arim and Naya 2003), such as the use of numerical correction factors to account for species variability in bone recovery rates.

Analysis of prey hard remains clearly can provide useful dietary information that is difficult to obtain using alternate methods. Time permitting, and if suitable regression equations and digestion correction factors exist, then biomass/volume reconstructions are recommended. Further captive studies are required to assess if prey in individual scats should be considered a random and therefore variable subsample of diet or if the contribution of each scat should be fixed to a predetermined constant (e.g., daily mass consumption or calorific requirement)(Laake et al. 2002). For the sake of comparison, it is important to present results using a variety of indices, including percent numbers, frequency of occurrence, and some measure of contribution by mass. Potentially, an index of relative importance (Harvey 1987) can be calculated combining these indices, whereby species are merely ranked, as opposed to supplying a point estimate that may be potentially biased (see discussion by Laake et al 2002).

While isolating prey DNA from scats and using PCR techniques to identify species is clearly involved and presently more expensive than traditional analysis of prey remnants in scats, it does not require prey hard parts and therefore is likely to be less affected by differential bone retention and digestion. The captive feeding study described (see Deagle et al. 2005 for full details) clearly highlights that further investment is warranted; particularly in determining new genetic markers for prey species of interest, trialing the technique on field collected scat samples, and assessing alternate techniques for quantifying DNA in scats (such as Real Time PCR). Like prey remnant analysis, this approach only reflects short-term dietary history. Nevertheless, the technique may prove very useful in studies where prey have fragile bones (such as salmonids), where prey have hard parts that are regurgitated (e.g., large cephalopods), where prey have few or no hard parts, or in species such as Australian sea lions in which bones are poorly represented in scats (Gales and Cheal 1992). We note that DNA methods can also provide information on the predator, including animal sex, species (e.g., Reed et al 1997), and theoretically individual identification information.

Animal capture (if possible) clearly provides useful demographic information and dietary data at the individual level, that can be collected on many temporal scales (long term—vibrissae stable isotope analysis; medium term—QFASA muscle and skin stable isotope analysis, short term—lavage, enema, cameras). Stable isotope ratio analysis of predator tissues presently provides only trophic level data, but the technique allows one to follow diet changes through time and at different temporal scales (Kurle 2002). Fatty acid signatures have also been useful in documenting both species, as well as spatial and temporal variations in diet (Iverson et al. 1997). While the validation of the QFASA model to quantify diet in Steller sea lions is continuing, preliminary results of this new technique are promising and worth pursuing, particularly to assess biases in traditional methods, the onset of weaning, and the prey that most contribute to lipid reserves. QFASA ideally requires a current and full prey base as well as fatty acid calibration coefficients (FA-CCs). Preliminary results of our study showed Steller sea lion FA-CCs were comparable to but not interchangeable with those previously obtained from phocid seals (Iverson et al. 2004, Fig. 4). Thus it appears either otariid or species-specific FA-CCs are needed or alternatively the comparatively shorter time period herring was fed in the two phocid studies did not result in the full turnover of lipid reserves (i.e., some trace of previous diet remained). Collections of blubber from animals difficult to capture can be obtained remotely using various dart projectors (Barrett-Lennard et al. 1996), but further information is needed to assess if signatures vary around the body and along the length of the blubber core (if only partial samples are collected). Animal capture also allows the ability to deploy cameras. Cameras need to be recovered and are presently somewhat limited by memory capacity, but they can provide useful foraging information, including profitability rates (Bowen et al. 2002), prey types, and search patterns (e.g., benthic, pelagic). Foraging success (intensity) can also be addressed using stomach temperature sensors and, more recently, magnet-based mandibular sensors (Wilson et al. 2002). Overall, while the analysis of prey remnants remains the obvious first step, ideally a suite of techniques should be used to study diet to ensure important components are not missed. Methods and correction factors developed for Steller sea lions can likely be applied to the other four sea lion species, but they should be verified experimentally.

Acknowledgments

Funding for this project was provided to the North Pacific Universities Marine Mammal Research Consortium by the National Oceanic and Atmospheric Administration and the North Pacific Marine Science Foundation. We would like to thank the marine mammal trainers and staff of the Vancouver Aquarium Marine Science Centre, the contribution of personnel of the Marine Mammal Research Unit, National Marine Mammal Laboratory, Dalhousie University and also S. Crockford of Pacific IDentifications Inc., Victoria. We would also like to express gratitude to the organizations and companies that have donated fish to the project. Work was undertaken in accordance with UBC Animal Care Committee guidelines.

References

Arim, M., and D.E. Naya. 2003. Pinniped diets inferred from scats: Analysis of biases in prey occurrence. Can. J. Zool. 81(1):67-73.

Barrett-Lennard, L.G., T.G. Smith, and G.M. Ellis. 1996. A cetacean biopsy system using lightweight pneumatic darts, and its effect on the behavior of killer whales. Mar. Mamm. Sci. 12:14-27.

Beck, C.A., S.J. Iverson, and W.D. Bowen. 2005. Blubber fatty acids of gray seals reveal sex differences in the diet of a size-dimorphic marine carnivore. Can. J. Zool. 83(3):377-388.

Bowen, W.D. 2000. Reconstruction of pinniped diets: Accounting for complete digestion of otoliths and cephalopod beaks. Can. J. Fish. Aquat. Sci. 57:898-905.

Bowen, W.D., J.W. Lawson, and B. Beck. 1993. Seasonal and geographic variation in the species composition and size of prey consumed by grey seals (*Halichoerus grypus*) on the Scotian shelf. Can. J. Fish. Aquat. Sci. 50:1768-1778.

Bowen W.D., D. Tully, D.J. Boness, D. Bulheier, and G. Marshal. 2002. Prey dependent foraging tactics and prey profitability in a marine mammal. Mar. Ecol. Prog. Ser. 244:235-245.

Cottrell, P.E., and A.W. Trites. 2002. Classifying prey hard part structures recovered from fecal remains of captive Steller sea lions (*Eumetopias jubatus*). Mar. Mamm. Sci. 18:525-539.

Deagle, B.E., D.J. Tollit, S.N. Jarman, M.A. Hindell, A.W. Trites, and N.J. Gales. 2005. Molecular scatology as a tool to study diet: Analysis of prey DNA in scats from captive Steller sea lions. Mol. Ecol. 14:1831-1842.

Dellinger, T., and F. Trillmich. 1988. Estimating diet composition from scat analysis in otariid seals (Otariidae): Is it reliable? Can. J. Zool. 66:1865-1870.

Fea, N., and R. Harcourt. 1997. Assessing the use of faecal and regurgitate analysis as a means of determining the diet of New Zealand fur seals. In: M. Hindell and C. Kemper (eds.), Marine mammal research in the Southern Hemisphere: Status, ecology and medicine. Surrey Beatty and Sons Ltd., Chipping Norton, pp. 143-150.

Frost, K.J., and L.F. Lowry. 1980. Feeding of ribbon seal (*Phoca fasciata*) in the Bering Sea in spring. Can. J. Zool. 58:1601-1607.

Gales, N.J., and A.J. Cheal. 1992 Estimating the diet composition of the Australian sea lion (*Neophoca cinerea*) from scat analysis: An unreliable technique. Wildl. Res. 19:447-455.

Hammond, P.S., and P. Rothery. 1996. Application of computer sampling in the estimation of seal diet. J. Appl. Stat. 23:525-533.

Harvey, J.T. 1987. Population dynamics, annual food consumption, dive behaviors, and movements of harbor seals, *Phoca vitulina richardsi*, in Oregon. Ph.D. thesis, Oregon State University, Corvallis. 168 pp.

Harvey, J.T. 1989. Assessment of errors associated with harbor seal (*Phoca vitulina*) fecal sampling. J. Zool. (Lond.) 219:101-111.

Iverson, S.J., K.J. Frost, and L.F. Lowry. 1997. Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. Mar. Ecol. Prog. Ser 151:255-271.

Iverson, S.J., C. Field, W.D. Bowen, and W. Blanchard. 2004. Quantitative fatty acid signature analysis: A new method of estimating predator diets. Ecol. Monogr. 74:211-235.

Jarman, S.N., B.E. Deagle, and N.J. Gales. 2004. Group-specific polymerase chain reaction for DNA-based analysis of species diversity and identity in dietary samples. Mol. Ecol. 13:1313-1322.

Jobling, M., and A. Breiby. 1986. The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. Sarsia 71:265-274.

Kiyota, M., C. Kawai, and N. Baba. 1999. Estimation of diet of male northern fur seals (*Callorhinus ursinus*) based on the analysis of fecal and regurgitated materials. Bull. Nat. Res. Inst. Far Seas Fish 36:1-7.

Kurle, C.M. 2002. Stable-isotope ratios of blood components from captive northern fur seals (*Callorhinus ursinus*) and their diet: Applications for studying the foraging ecology of wild otariids. Can. J. Zool. 80:902-909.

Laake, J.L., P. Browne, R.L. DeLong, and H.R. Huber. 2002. Pinniped diet composition: A comparison of estimation models. Fish. Bull. U.S. 100:434-477.

Olesiuk, P.F., M.A. Bigg, G.M. Ellis, S.J. Crockford, and R.J. Wigen. 1990. An assessment of the feeding habits of harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia, based on scat analysis. Can. Tech. Rep. Fish. Aquat. Sci. 1730. 135 pp.

Orr, A.J., and J.T. Harvey. 2001. Quantifying errors associated with using fecal samples to determine the diet of the California sea lion (*Zalophus californianus*). Can. J. Zool. 79:1080-1087.

Pierce, G.J., and P.R. Boyle. 1991. A review of methods for diet analysis in piscivorous marine mammals. Oceanogr. Mar. Biol. Ann. Rev. 29:409-486.

Purcell, M., G. Mackey, E. LaHood, H. Huber, and L. Park. 2004. Molecular methods for genetic identification of salmonid prey from Pacific harbor seal (*Phoca vitulina richardsi*) scat. Fish. Bull. U.S. 102:213-220.

Reed, Z., D.J. Tollit, P.M. Thompson, and W. Amos. 1997. Molecular scatology: The use of molecular genetic analysis to assign species, sex and individual identity to seal faeces. Mol. Ecol. 6:225-234.

Sinclair, E.H., and T.K. Zeppelin. 2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). J. Mammal. 83(4):973-990.

Staniland, I.J. 2002. Investigating the biases in the use of hard prey remains to identify diet composition using Antarctic fur seals (*Arctocephalus gazella*) in captive feeding trials. Mar. Mamm. Sci. 18:223-243.

Tollit, D.J., and P.M. Thompson. 1996. Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland. Can. J. Zool. 74:1110-1121.

Tollit, D.J., S.G. Heaslip, and A.W. Trites. 2004a. Sizes of walleye pollock consumed by the eastern stock of Steller sea lions *(Eumetopias jubatus)* in Southeast Alaska from 1994-1999. Fish. Bull. U.S. 102:522-532.

Tollit, D.J., S.J. Iverson, S.G. Heaslip, D.A.S. Rosen, and A.W. Trites. 2003. Validation studies of blubber quantitative fatty acid signature analysis (QFASA) with captive Steller sea lions (*Eumetopias jubatus*). 15th Biennial Conference on the Biology of Marine Mammals, Greensboro, NC, 14-19 December 2003, Abstract book. Society for Marine Mammalogy.

Tollit, D.J., M. Wong, A.J. Winship, D.A.S. Rosen, and A.W. Trites. 2003. Quantifying errors associated with using prey skeletal structures from fecal samples to determine the diet of the Steller sea lion (*Eumetopias jubatus*). Mar. Mamm. Sci. 19:724-744.

Tollit, D.J., S.G. Heaslip, T.K. Zeppelin, R. Joy, K.A. Call, and A.W. Trites. 2004b. Improving size estimates of walleye pollock and Atka mackerel consumed by Steller sea lions using digestion correction factors and bones recovered in scats. Fish. Bull. U.S. 102:498-508.

Tollit, D.J., M. Steward, P.M. Thompson, G.J. Pierce, M.B. Santos, and S. Hughes. 1997. Species and size differences in the digestion of otoliths and beaks: Implications for estimates of pinniped diet composition. Can. J. Fish. Aquat. Sci. 54:105-119.

Walton, M.J., and P. Pomeroy. 2003. Blubber fatty acid profiles detect inter-annual variation in the diet of grey seals (*Halichoerus grypus*). Mar. Ecol. Prog. Ser. 248:257-266.

Wilson, R.P., A. Steinfurth, Y. Ropert-Coudert, A. Kato, and M. Kurita. 2002. Lip-reading in remote subjects: An attempt to quantify and separate ingestion, breathing and vocalization in free-living animals using penguins as a model. Mar. Biol. 140:17-27.

Zeppelin, T.K., D.J. Tollit, K.A. Call, T.J. Orchard, and C.J. Gudmundson. 2004. Sizes of walleye pollock and Atka mackerel consumed by the western stock of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1999-2001. Fish. Bull. U.S. 102:509-521.

Sea Lions in Drag, Fur Seals Incognito: Insights from the Otariid Deviants

J.P.Y. Arnould
Deakin University, School of Biological and Chemical Sciences, Burwood, Victoria, Australia

D.P. Costa
University of California, Department of Ecology and Evolutionary Biology, Santa Cruz, California

Sea lions and fur seals have two broadly divergent foraging patterns. Lactating sea lions generally undertake short trips (1-2 days) foraging mostly on the benthos of continental shelf areas. In contrast, lactating fur seals generally undertake longer trips (4-23 days) foraging mostly on vertically migrating prey in oceanic frontal structures or continental shelf-edges with upwelling regions. Associated with the observed divergent trends of epipelagic and benthic foraging appear to be differences in the population dynamics of sea lions and fur seals. Populations of the various sea lion species have experienced little recovery since the sealing era, whereas fur seals have generally experienced rapid population recovery rates. The divergent patterns of foraging between the two otariid groups were originally thought to be due to the mode of insulation and diving ability. Subsequent studies, however, have shown that some fur seal species regularly forage at pelagic depths deeper and longer than some sea lions. Alternatively, the larger body size of sea lions may make foraging on small pelagic prey energy-inefficient and, hence, may explain why throughout most of their distribution sea lions have adopted the benthic foraging mode. Indeed, exceptions to the general fur seal and sea lion foraging patterns have been documented, which may be related to the productivity of their local marine habitat. California sea lions display epipelagic foraging behavior in the rich California Current, while Australian fur seals have been shown to forage exclusively over the shallow continental shelf of Bass Strait (southeast Australia), a region recognized as being an area of low oceanic productivity. Interestingly,

these uncharacteristic foraging modes are associated with population dynamics uncharacteristic for the respective phylogenetic groups: California sea lions have been steadily increasing, while the Australian fur seal has exhibited a very slow recovery in comparison to the conspecific cape fur seal which feeds epipelagically in the rich Benguela current and is now the most numerous otariid.

Introduction

Since the development in the mid-1970s of electronic time-depth recorders (TDRs) for measuring diving activity and satellite-telemetry methods for monitoring the at-sea movements of animals, there have been numerous studies investigating the foraging behavior of lactating otariid seals (e.g., Gentry and Kooyman 1986; Francis et al. 1998; Thompson et al. 1998; Costa and Gales 2000, 2003). There are nine species of fur seals (plus one subspecies) and five species of sea lions (plus one subspecies) (Reijnders et al. 1993) and these studies have revealed two broadly divergent patterns for the two groups. Lactating sea lions generally undertake short trips (1-2 days) during which they have a continuous dive pattern with no diel variation, foraging mostly on benthic or demersal prey in continental shelf areas (Costa and Gales 2000, 2003). This mode of foraging is, hereafter, referred to as "*benthic*" foraging. In contrast, lactating fur seals generally undertake longer trips (3-23 days), during which diving is mostly nocturnal (Boyd et al. 1991, Francis et al. 1998, Harcourt et al. 2001, Beauplet et al. 2004). The dives occur in bouts to the deep scattering layer, with a pronounced diel variation in depth that reflects the vertical migration of their prey (Boyd et al. 1994, Harcourt et al. 1995, Georges et al. 2000a), and foraging occurs mostly in oceanic frontal structures or continental shelf-edges with upwelling regions (Gentry and Kooyman 1986). This mode of foraging is hereafter referred to as "*epipelagic*" foraging.

Associated with the observed divergent trends of *epipelagic* and *benthic* foraging in otariid seals appear to be differences in the population dynamics of sea lions and fur seals. All species of otariid seals throughout the world were subject to extensive and, in most cases, excessive hunting pressure during the eighteenth and nineteenth centuries (Wickens and York 1997). By the late 1800s, however, most species had acquired total legislative protection or were subject to only regulated managed harvests. Despite this protection, populations of the various sea lion species have experienced very little recovery and in some cases are declining, whereas fur seal species have generally experienced rapid population recovery rates (Wickens and York 1997, Costa et al. 2006). A question these observations pose is whether there may be life-history consequences associated with the different foraging modes that might influence population

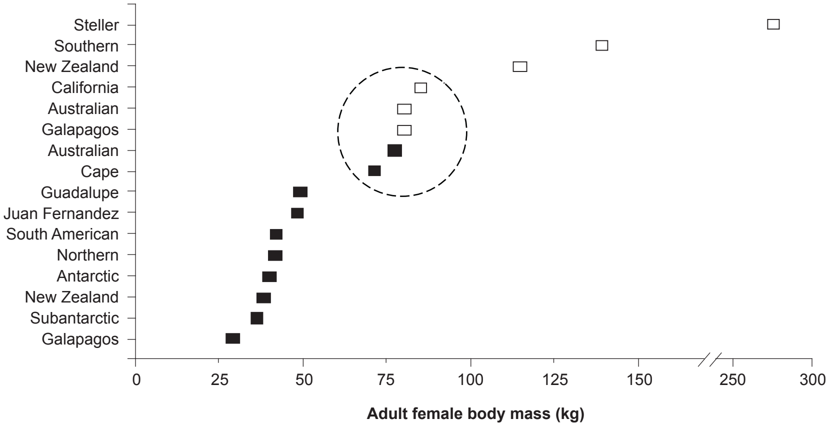


Figure 1. Mean body masses of adult female otariid seals (☐ sea lions, ■ fur seals). Circled species represent the narrow range of body masses encompassing both fur seals and sea lions that provide an opportunity for investigating the mechanisms determining foraging mode and its potential impact on life-history parameters. See review in Wickens and York (1997), Warneke and Shaughnessy (1985), Gentry and Kooyman (1986), and Costa and Gales (2000, 2003) for data sources.

dynamics (i.e., is a particular foraging mode more efficient?). However, addressing this question is problematical for several reasons.

First, life-history parameters such as litter size or reproductive rate may be phylogenetically constrained, reflecting selective pressures that may no longer apply (Calder 1984) and that may be independent of foraging mode. Second, the different insulation qualities of the integument in fur seals and sea lions may have significant physiological implications. For example, it has been suggested that the insulating feature of fur seal integument (trapped layer of air) would be inefficient at great depths preventing them from foraging as deep as sea lions (Gentry et al. 1986, Costa 1991). Third, the difference in body size between fur seals and sea lions (Fig. 1), which would have implications for metabolism and reproductive output (Heusner 1991, Blanckenhorn 2000), could also mask any effect of foraging mode on life-history parameters. For example, it has been suggested that the generally larger body size of sea lions (80-273 kg) compared to fur seals (27-76 kg) results in greater oxygen storage capabilities, enabling them to dive aerobically for longer periods and, hence, deeper (Costa 1991, Costa et al. 1998).

Fortuitously, despite the great breadth of body size within the Otariidae, there is a narrow range of adult female body masses that encompasses several fur seal and sea lion species (Fig. 1). This group of species includes the cape fur seal (*Arctocephalus pusillus pusillus*) and its subspecies the Australian fur seal (*A. p. doriferus*), and the California sea lion (*Zalophus californianus*) and its subspecies the Galapagos sea lion (*Z. c. wollebaeki*). It provides a unique opportunity to investigate the potential relationships between foraging mode and life-history parameters within the Otariidae while controlling for differences in integument and body size. The Australian sea lion (*Neophoca cinerea*) also has a similar adult female body mass to the above species, but its unique 17.5 month breeding cycle (Gales and Costa 1997) makes direct comparisons regarding life-history traits problematic.

The aims of this study, therefore, were to (1) compare and contrast the foraging behaviors of adult female cape and Australian fur seals with California and Galapagos sea lions; (2) assess whether there are any relationships between foraging mode and life-history parameters; and (3) place these findings within the context of otariids in general. An additional aim of this study was to highlight deficiencies in the information necessary for better understanding the mechanisms that determine foraging mode in otariid seals and its potential impacts on life-history parameters.

Methods

Information for the comparisons between the four focal species (cape and Australian fur seals, and California and Galapagos sea lions) and with other otariids, were obtained from published reports and unpublished sources. Due to a paucity of information on some species, data were not available for each parameter in each species.

Summary data on diving behavior and foraging mode were collated for the cape fur seal (Kooyman and Gentry 1986), Australian fur seal (Arnould and Hindell 2001), California sea lion (Costa et al. 2004), and Galapagos sea lion (Kooyman and Trillmich 1986). As a means of comparing diving performance between species, published data (Costa et al. 2004) on the ratio of mean dive duration to calculated aerobic dive limit (cADL) for individual Australian fur seals and California sea lions were compared. No comparable data are available for the cape fur seal or Galapagos sea lion, but comparisons were made with other *benthic* (Australian sea lion and New Zealand sea lion, *Phocarctos hookeri*) and *epipelagic* (Antarctic fur seal, *A. gazella*) feeding otariids (Costa et al. 2004).

The proportion of time at sea spent diving was used an index of foraging effort to compare between the four focal species (Gentry et al. 1986, Kooyman and Gentry 1986, Kooyman and Trillmich 1986, Feldkamp et al. 1989, Arnould and Hindell 2001, Costa et al. 2004) and with other otariids (Gentry et al. 1986; Thompson et al. 1998; Costa and Gales 2000, 2003; Georges et al. 2000b; Costa et al. 2001).

Numerous studies have investigated the diet of fur seals and sea lions and how it relates to foraging activity, focusing on the relative proportions of various prey species in relation to changes in food availability and diving behavior (e.g., Feldkamp et al. 1991, Boyd et al. 1994, Harcourt et al. 2002, Lea et al. 2002). There is little information, however, on how the mode of foraging relates to prey size, an important factor that will influence foraging efficiency. In the present study, information on the size of common prey item size were obtained for the Australian fur seal (Gales et al. 1993, Gales and Pemberton 1994, Hume et al. 2004), California sea lion (Antonelis et al. 1984, Weise 2000), and cape fur seal (Punt et al. 1995; de Bruyn et al. 2003; W.H. Oosthuizen, Marine and Coastal Management, South Africa, unpubl. data). Size data were collated only for the four most numerically abundant prey species identified in each diet study. Similar data were obtained for *epipelagic* Antarctic fur seals (Reid and Arnould 1996, Goldsworthy et al. 1997) and New Zealand fur seals (*A. forsteri*) (Fea et al. 1999); and *benthic* feeding Australian sea lions (Gales and Cheal 1992; R. Campbell, Dept. of Fisheries, Western Australia, unpubl. data) and New Zealand sea lions (Lalas 1997). Where necessary, fish prey mass was calculated from published length estimates using mass-length relationships available on www.fishbase.org.

There are few life-history parameters available for comparison between fur seals and sea lions. Probably the most relevant for assessing the potential influence of foraging mode on population dynamics is adult female reproductive rate as it is likely to be influenced heavily by female foraging success and have a significant impact population dynamics (Boyd 2000). Information on late gestation pregnancy rates and birth rates were obtained for the Australian fur seal (Arnould et al. 2003), cape fur seal (Guinet et al. 1998, Odendaal et al. 2002), and California sea lion (Melin 2002). Similar data are not available for the Galapagos sea lion but are available for the *benthic* foraging New Zealand sea lion (I.S. Wilkinson, Dept. of Conservation, Wellington, New Zealand, unpubl. data) and Steller sea lion (Pitcher et al. 1998); and the *epipelagic* foraging South American fur seal (*A. australis*) (Majluf 1992), subantarctic fur seal (*A. tropicalis*), and Antarctic fur seal (Wickens and York 1997).

Results

Summary information on foraging behavior for Australian and cape fur seals and California and Galapagos sea lions is presented in Table 1. Within the small mass range of the four species (71-85 kg), mean dive depth varied substantially (37-64 m) though this was not related to foraging mode. Interestingly, despite the similar body masses between the four species, differences in foraging mode were apparent within the con-

Table 1. Adult female foraging behavior of four otariid species (two sea lions and two fur seals) with similar body masses. Means ± SE are presented where indicated in the original studies.

Species	Body mass (kg)	Dive depth (m)	Dive duration (min)	Foraging mode
Australian fur seal[a]	78	63.4 ± 4.0	3.2 ± 0.4	Benthic
Cape fur seal[b,c]	71	45.0 ± 4.0	2.1 ± 0.4	Epipelagic
California sea lion[d]	85	42.2 ± 12.9	1.9 ± 0.2	Epipelagic
Galapagos sea lion[e,f]	80	37.3 ± 0.3	<2	Benthic

[a]Arnould and Hindell (2001); [b]Kooyman and Gentry (1986); [c]Warneke and Shaughnessy (1985); [d]Costa et al. (2004); [e]Gentry et al. (1986); [f]Kooyman and Trillmich (1986).

specific fur seals and sea lions. Australian fur seals are *benthic* foragers, whereas cape fur seals are *epipelagic* foragers; and California sea lions are *epipelagic* foragers, whereas Galapagos sea lions are *benthic* foragers. Hence, Australian fur seals and California sea lions appear to forage in modes not consistent with the trends observed in their respective phylogenetic groups.

The dive performance, measured as the ratio of mean dive duration to calculated aerobic dive limit (cADL), for individual Australian fur seals ($n = 9$) and California sea lions ($n = 6$) is given in Fig. 2. A ratio of 1 would indicate that animals are undertaking dive durations equivalent to their cADL. While mean dive depth did not differ significantly between the two species ($t_6 = 0.2$, $P > 0.1$), the ratio of individual mean dive depth to cADL was significantly greater in Australian fur seals (1.90 ± 0.03) than California sea lions (0.66 ± 0.01; $t_6 = 9.66$, $P < 0.001$). There are no comparable data for the cape fur seal or Galapagos sea lion but these results are consistent with data for the Australian sea lion, New Zealand sea lion, and Antarctic fur seal. This suggests that *benthic* foraging species regularly undertake dive durations exceeding their cADL, whereas the *epipelagic* foraging species rarely dive longer than their cADL.

The most common fish and cephalopod prey of *benthic* foraging Australian fur seals (50-5,000 g) are 10-60 times heavier than those consumed by *epipelagic* foraging, conspecific cape fur seals (4-85 g), but are similar to those consumed by *benthic* foraging sea lions (150-2,500 g) (Table 2). Conversely, the *epipelagic* foraging California sea lion consumes fish and cephalopod prey of similar size (17-150 g) to *epipelagic* foraging fur seals (2-195 g). Information on prey size in the Galapagos sea lion is limited to only a single fish species (anchovy, *Sardinops sagax*) of estimated mean mass 56 g, despite the diet of this species comprising numerous other fish and cephalopods species (Dellinger and Trillmich 1999). Con-

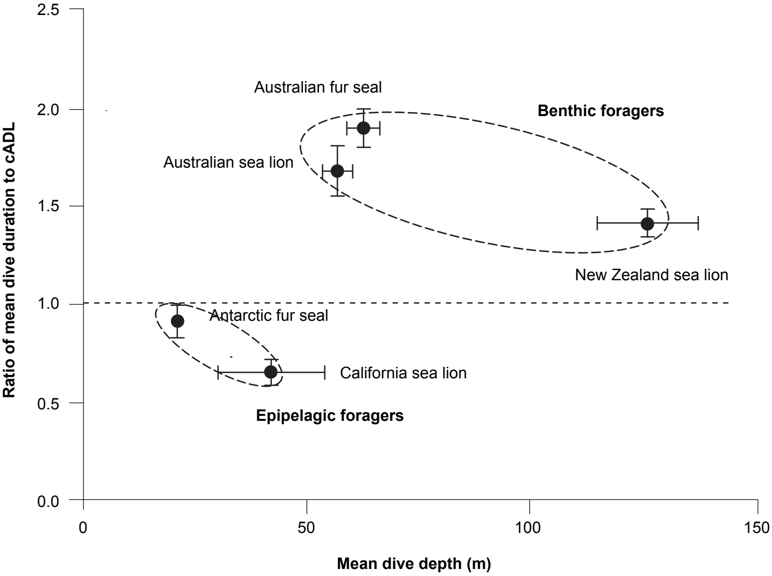


Figure 2. Ratio of mean dive duration to calculated aerobic dive limit (cADL) in adult females of five otariid seal species (3 sea lion, 2 fur seal) in relation to mean dive depth. Data presented as means ± SE. Adapted from Costa et al. (2004).

sequently, adequate comparisons of common prey size between this and other otariid species are not possible.

Foraging effort, measured as the amount of time at sea spent diving, is substantially higher in *benthic* foraging Australian fur seals (41%) than the conspecific cape fur seals (8%) and other *epipelagic* foraging fur seals (15-24%; Fig. 3). Conversely, the time at sea spent diving by *epipelagic* foraging California sea lions (32%) is substantially less than by conspecific Galapagos sea lions (64%) and other benthic foraging sea lions (44-58%). Overall, the proportion of time at sea spent diving is significantly greater ($t_8 = 5.68$, $P < 0.001$) in *benthic* (51.7 ± 4.3%) than *epipelagic* (20.7 ± 3.4%) foragers. The results suggest that foraging effort is greater in *benthic* foraging otariid species irrespective of phylogenetic grouping or body size.

The reproductive rate of the *benthic* foraging Australian fur seal (55%) is substantially lower than in the conspecific cape fur seal (77-79%) and other *epipelagic* foraging fur seals (77-84%) but is similar to benthic foraging sea lions (Table 3). Conversely, the reproductive rate of the *epipelagic* foraging California sea lion (77%) is similar to *epipelagic* fur seals but greater than in *benthic* foraging sea lions (55-69%).

Table 2. Mass of most common prey items consumed by fur seals and sea lions in relation to foraging mode. Range of means given for the four most numerically abundant species recorded in diet analyses.

	Mean mass (g)			
Species	Fish	Cephalopods	Crustacea	Foraging mode
Australian fur seal[a,b,c]	50-2,000	580-5,000		Benthic
Australian sea lion[m]	?	?	750-1,500	Benthic
New Zealand sea lion[d]	400-2,500	150-1,500		Benthic
California sea lion[e,f]	17-150	23-47		Epipelagic
Cape fur seal[g,h,i]	4-60	14-85		Epipelagic
Antarctic fur seal[j,k]	7-20		<5	Epipelagic
New Zealand fur seal[l]	2-11	195		Epipelagic

[a]Gales et al. (1993); [b]Gales and Pemberton (1994); [c]Hume et al. (2004); [d]Lalas (1997); [e]Antonelis et al. (1984); [f]Weise (2000); [g]Punt et al. (1995; [h]de Bruyn et al. (2003); [i]W.H. Oosthuizen (Marine and Coastal Management, South Africa, unpubl. data); [j]Reid and Arnould (1996); [k]Goldsworthy et al. (1997); [l]Fea et al. (1999). [m]Because of the clearly demonstrated biases resulting from scat analysis in this species (Gales and Cheal 1992), there are no reliable estimates of fish or cephalopod prey size. Direct observations of prey consumption, however, indicate this species regularly consumes large crayfish (R. Campbell, Dept. of Fisheries, Western Australia, unpubl. data).

Discussion

It was originally suggested that the observed differences in foraging mode between sea lions (*benthic*) and fur seals (*epipelagic*) were due to differences in their integument (single- versus double-fur layer) and/or body size (Gentry et al. 1986, Costa 1991, Costa et al. 1998). The results of the present study indicate that within the narrow range where sea lion and fur seal body masses overlap there is a fur seal that adopts the *benthic* foraging mode typical of sea lions (Australian fur seal) and a sea lion that adopts the epipelagic mode typical of fur seals (California sea lion), while the conspecifics of these two species follow the normal trends for their respective phylogenetic groups. This suggests that integument characteristics do not account for the observed differences in foraging mode between sea lions and fur seals. Likewise, the fact that these species are of similar mass suggests body size may not be the sole factor determining foraging mode.

A potential influence on foraging mode in otariid seals may be local marine productivity and its effect on prey availability for these species. The *epipelagic* foraging cape fur seal is mostly distributed along the southwest coast of South Africa and feeds in the nutrient-rich waters of the Benguela Current, whereas the *benthic* foraging Australian fur seal

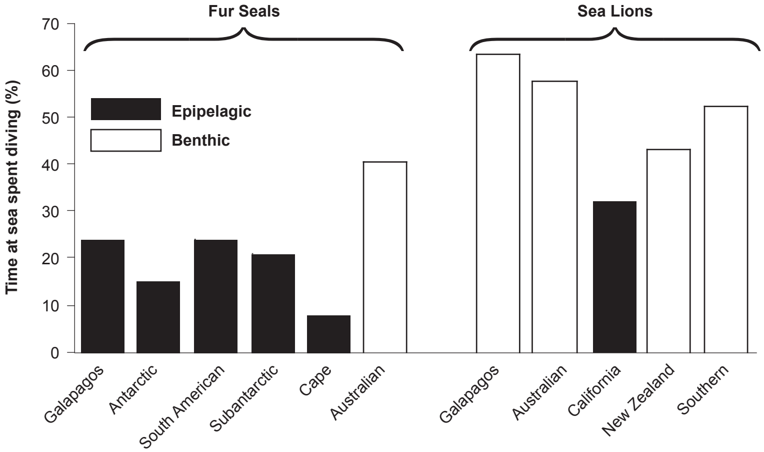


Figure 3. Proportion of time at sea spent diving by adult females in 11 otariid sea species (5 sea lion, 6 fur seal). References: Galapagos fur seal (Gentry et al. 1986); Antarctic fur seal (Costa et al. 2001); South American fur seal (Gentry et al. 1986); subantarctic fur seal (Georges et al. 2000b); cape fur seal (Kooyman and Gentry 1986); Australian fur seal (Arnould and Hindell 2001); Galapagos sea lion (Gentry et al. 1986); Australian sea lion (Costa and Gales 2003); California sea lion (Feldkamp et al. 1989); New Zealand sea lion (Costa and Gales 2000); Southern sea lion (Thompson et al. 1998).

feeds exclusively within Bass Strait between the Australian mainland and Tasmania, an area considered nutrient-poor with low marine productivity (Warneke and Shaughnessy 1985). Similarly, California sea lions on the California coast are *epipelagic* foragers in the cold productive waters of the California Current (Feldkamp et al. 1989, 1991), whereas the continental shelf habitat of the *benthic* foraging Galapagos sea lion is of generally lower productivity (Farina et al. 2003, Okey et al. 2004). It may be that, except in very productive regions, large size precludes foraging on a highly patchy but dense prey resource near the surface (zooplankton, small fish or squid) compared to a more evenly distributed but less dense prey resource on the benthos (larger fish, squid, octopus, and crayfish).

The high ratio of mean dive duration to cADL in the Australian fur seal and *benthic* foraging sea lions suggests this mode of foraging incurs a greater physiological cost than *epipelagic* feeding. Optimal foraging theory would predict, therefore, that *benthic* foraging species should consume larger or more rewarding prey than *epipelagic* foraging seals (Stephens and Krebs 1986, Bowen et al. 2002). The differences observed

Table 3. The reproductive rates of otariid seals in relation to their foraging mode.

Species	Birth rate (%)	Foraging mode
Australian fur seal[a]	55[i]	Benthic
New Zealand sea lion[b]	69	Benthic
Steller sea lion[c]	55-67[i]	Benthic
California sea lion[d]	77	Epipelagic
Cape fur seal[e,f]	77-79	Epipelagic
Antarctic fur seal[g]	77[i]	Epipelagic
South American fur seal[h]	82	Epipelagic
Subantarctic fur seal[g]	79-84	Epipelagic

[a]Arnould et al. (2003); [b]I.S. Wilkinson (Dept. of Conservation, Wellington, New Zealand, unpubl. data); [c]Pitcher et al. (1998); [d]Melin (2002); [e]Guinet et al. (1998); [f]Odendaal et al. (2002); [g]Wickens and York (1997); [h]Majluf (1992). [i]Late gestation pregnancy rate.

in the present study in the size of common prey items consumed by *benthic* and *epipelagic* foraging otariids of similar body size are consistent with this prediction. However, despite the apparent greater mass of prey items consumed by *benthic* foraging otariid species, they appear to spend a greater proportion of time at sea diving than *epipelagic* feeders (Fig. 3).

A potential consequence of this might be a reduced scope by *benthic* species for increasing foraging effort in times of nutritional stress in comparison to *epipelagic* species which, in turn, could impact reproductive output, offspring growth, or survival. A lower reproductive rate was observed in the Australian fur seal (and *benthic* feeding sea lions) than in the *epipelagic* conspecific cape fur seal and California sea lion, which suggests a relationship between foraging mode and life history in otariid seals. Indeed, the difference between the mean birth rate of all *benthic* (61.7 ± 4.0%) and *epipelagic* (79.1 ± 1.1%) foragers approached significance ($t_2 = 4.15$, $P = 0.053$). The low reproductive rate of Australian fur seals may explain their very slow recovery since the cessation of the commercial sealing era in comparison to the rapid recovery of the conspecific cape fur seal, which is now the most numerous otariid (Table 4). Similarly, the relatively high reproductive rate of the California sea lion is likely to have contributed to its population increase being rapid in comparison to that in *benthic* foraging sea lions.

Table 4. Population status and trends for benthic and epipelagic foraging otariid seal species.

Species	Foraging mode	Population size	Trend
Australian fur seal	Benthic	60,000	Very slow increase
Australian sea lion	Benthic	<11,700	Stable
New Zealand sea lion	Benthic	13,000	Stable
Southern sea lion	Benthic	275,000	Decreasing
Steller sea lion	Benthic	<75,000	Decreasing
California sea lion	Epipelagic	>237,000	Rapid increase
Antarctic fur seal	Epipelagic	1,600,000	Rapid increase
Cape fur seal	Epipelagic	1,700,000	Rapid increase
Subantarctic fur seal	Epipelagic	>310,000	Rapid increase

Adapted from Costa et al. (2006).

Acknowledgments

We thank I.S. Wilkinson, W.H. Oosthuizen, R. Campbell, D. Aurioles-Gamboa, M. Weise, and R. DeLong for providing access to their unpublished data. The assistance over the years of the many field workers involved in the data collection, upon which many of the ideas presented here were generated, is gratefully acknowledged. Financial support for this research was provided by the Australian Research Council, Sea World and Rescue Foundation Inc., National Geographic Society, Office of Naval Research, and the National Science Foundation.

References

Antonelis Jr., G.A., C.H. Fiscus, and R.L. DeLong. 1984. Spring and summer prey of California sea lions, *Zalophus californianus*, at San Miguel Island, California, 1978-79. Fish. Bull. U.S. 82:67-76.

Arnould, J.P.Y., and M.A. Hindell. 2001. Dive behaviour, foraging locations, and maternal-attendance patterns of Australian fur seals (*Arctocephalus pusillus doriferus*). Can. J. Zool. 79:35-48.

Arnould, J.P.Y., I.L. Boyd, and R.M. Warneke. 2003. Historical dynamics of the Australian fur seal population: Evidence of regulation by man? Can. J. Zool. 81:1428-1436.

Beauplet, G., L. Dubroca, C. Guinet, Y. Cherel, W. Dabin, C. Gagne, and M.A. Hindell. 2004. Foraging ecology of subantarctic fur seals *Arctocephalus tropicalis* breeding on Amsterdam Island: Seasonal changes in relation to maternal characteristics and pup growth. Mar. Ecol. Prog. Ser. 273:211-225.

Blanckenhorn, W.U. 2000. The evolution of body size: What keeps organisms small? Quart. Rev. Biol. 75:385-407.

Bowen, W.D., D. Tully, D.J. Boness, B.M. Bulheier, and G.J. Marshall. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. Mar. Ecol. Prog. Ser. 244:235-245.

Boyd, I.L. 2000. State-dependent fertility in pinnipeds: Contrasting capital and income breeders. Funct. Ecol. 14:623-630.

Boyd, I.L., N.J Lunn, and T. Barton. 1991. Time budgets and foraging characteristics of lactating Antarctic fur seals. J. Anim. Ecol. 60:577-592.

Boyd, I.L., J.P.Y. Arnould, T. Barton, and J.P. Croxall. 1994. Foraging behavior of Antarctic fur seals during periods of contrasting prey abundance. J. Anim. Ecol. 63:703-713.

Calder, W.A. 1984. Size, function and life history. Harvard University Press, Cambridge.

Costa, D.P. 1991. Reproductive and foraging energetics of pinnipeds: Implications for life history patterns. In: Behaviour of pinnipeds. Chapman and Hall, New York, pp. 300-344.

Costa, D.P., and N.J. Gales. 2000. Foraging energetics and diving behavior of lactating New Zealand sea lions, *Phocarctos hookeri*. J. Exp. Biol. 203:3655-3665.

Costa, D.P., and N.J. Gales. 2003. Energetics of a benthic diver: Seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. Ecol. Monogr. 73:27-43.

Costa, D.P., N.J. Gales, and D.E. Crocker. 1998. Blood volume and diving ability of the New Zealand sea lion, *Phocarctos hookeri*. Physiol. Zool. 71:208-213.

Costa, D.P., N.J Gales, and M.E. Goebel. 2001. Aerobic dive limit: How often does it occur in nature? Comp. Biochem. Phys. A 129:771-783.

Costa, D.P., M.J. Weise, and J.P.Y. Arnould. 2006. Worldwide pinniped population status and trends. In: Whales, whaling and ocean ecosystems. University of California Press, Berkeley.

Costa, D.P., C.E. Kuhn, M.J. Weise, S.A. Shaffer, and J.P.Y. Arnould. 2004. When does physiology limit the foraging behaviour of freely diving mammals? Internat. Congr. Ser. 1275:359-366.

de Bruyn, P.J.N., M.N. Bester, S. Mecenero, S.P. Kirkman, J.P. Roux, and N.T.W. Klages. 2003. Temporal variation of cephalopods in the diet of cape fur seals in Namibia. S. Afr. J. Wildl. Res. 33:85-96.

Dellinger, T., and F. Trillmich. 1999. Fish prey of the sympatric Galapagos fur seals and sea lions: Seasonal variation and niche separation. Can. J. Zool. 77:1204-1216.

Farina, J.M., S. Salazar, K.P. Wallem, J.D. Witman, and J.C. Ellis. 2003. Nutrient exchanges between marine and terrestrial ecosystems: The case of the Galapagos sea lion *Zalophus wollebaecki*. J. Anim. Ecol. 72:873-887.

Fea, N.I., R.G. Harcourt, and C. Lalas. 1999. Seasonal variation in the diet of the New Zealand fur seal (*Arctocephalus forsteri*) at Otago Peninsula, New Zealand. Wildl. Res. 26:147-160.

Feldkamp, S.D., R.L. DeLong, and G.A. Antonelis. 1989. Diving patterns of California sea lions, *Zalophus californianus*. Can. J. Zool. 67:872-883.

Feldkamp, S.D., R.L. DeLong, and G.A. Antonelis. 1991. Effects of El Niño 1983 on the foraging patterns of California sea lions (*Zalophus californianus*) near San Miguel Island, California. In: Pinnipeds and El Niño: Responses to environmental stress. Springer-Verlag, Berlin, pp. 146-155.

Francis, J., D. Boness, and H. Ochoa-Acuna. 1998. A protracted foraging and attendance cycle in female Juan Fernandez fur seals. Mar. Mamm. Sci. 14:552-574.

Gales, N.J., and A.J. Cheal. 1992. Estimating diet composition of the Australian sea lion (*Neophoca cinerea*) from scat analysis: An unreliable technique. Wildl. Res. 19:447-456.

Gales, N.J., and D.P. Costa. 1997. The Australian sea lion: A review of an unusual life history. In: Marine mammal research in the Southern Hemisphere. Vol. 1: Status, ecology and medicine. Surrey Beatty and Sons, Chipping Norton, pp. 78-87.

Gales, R., and D. Pemberton. 1994. Diet of the Australian fur seal in Tasmania. Aust. J. Mar. Freshw. Res. 45:653-664.

Gales, R., D. Pemberton, C.C. Lu, and M.R. Clarke. 1993. Cephalopod diet of the Australian fur seal: Variation due to location, season and sample type. Aust. J. Mar. Freshw. Res. 44:657-671.

Gentry, R.L., and G.L. Kooyman. 1986. Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton.

Gentry, R.L., D.P. Costa, J.P. Croxall, J.H.M. David, R.W. Davis, G.L. Kooyman, P. Majluf, T.S. McCann, and F. Trillmich. 1986. Synthesis and conclusions. In: Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton, pp. 220-264.

Georges, J.Y., F. Bonadonna, and C. Guinet. 2000a. Foraging habitat and diving activity of lactating subantarctic fur seals in relation to sea-surface temperatures at Amsterdam Island. Mar. Ecol. Prog. Ser. 196:291-304.

Georges, J.Y., Y. Tremblay, and C. Guinet. 2000b. Seasonal diving behaviour in lactating subantarctic fur seals an Amsterdam Island. Polar Biol. 23:59-69.

Goldsworthy, S.D., M.A. Hindell, and H.M. Crowley. 1997. Diet and diving behaviour of sympatric fur seals *Arctocephalus gazella* and *A. tropicalis* at Macquarie Island. In: Marine mammal research in the Southern Hemisphere. Vol. 1: Status, ecology and medicine. Surrey Beatty, Chipping Norton, pp. 151-163.

Guinet, C., J.P. Roux, M. Bonnet, and V. Mison. 1998. Effect of body size, body mass, and body condition on reproduction of female South African fur seals (*Arctocephalus pusillus*) in Namibia. Can. J. Zool. 76:1418-1424.

Harcourt, R.G., C.J.A. Bradshaw, and L.S. Davis. 2001. Summer foraging behaviour of a generalist predator, the New Zealand fur seal (*Arctocephalus forsteri*). Wildl. Res. 28:599-606.

Harcourt, R.G., C.J.A. Bradshaw, K. Dickson, and L.S. Davis. 2002. Foraging ecology of a generalist predator, the female New Zealand fur seal. Mar. Ecol. Prog. Ser. 227:11-24.

Harcourt, R.G., A.M. Schulman, L.S. Davis, and F. Trillmich. 1995. Summer foraging by lactating female New Zealand fur seals (*Arctocephalus forsteri*) off Otago Peninsula, New Zealand. Can. J. Zool. 73:678-690.

Heusner, A.A. 1991. Size and power in mammals. J. Exp. Biol. 160:25-54.

Hume, F., M.A. Hindell, D. Pemberton, and R. Gales. 2004. Spatial and temporal variation in the diet of a high trophic level predator, the Australian fur seal (*Arctocephalus pusillus doriferus*). Mar. Biol. 144:407-415.

Kooyman, G.L., and R.L. Gentry. 1986. Diving behavior of South African fur seals. In: Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton, pp. 142-152.

Kooyman, G.L., and F. Trillmich. 1986. Diving behavior of Galapagos sea lions. In: Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton, pp. 209-219.

Lalas, C. 1997. Prey of Hooker's sea lions *Phocarctos hookeri* based at Otago Peninsula New Zealand. In: Marine mammal research in the Southern Hemisphere. Vol. 1: Status, ecology and medicine. Surrey Beatty, Chipping Norton, pp. 130-136.

Lea, M.A., Y. Cherel, C. Guinet, and P.D. Nichols. 2002. Antarctic fur seals foraging in the Polar Frontal Zone: Inter-annual shifts in diet as shown from faecal and fatty acid analyses. Mar. Ecol. Prog. Ser. 245:281-297.

Majluf, P. 1992. Timing of births and juvenile mortality in the South American fur seal in Peru. J. Zool. (Lond.) 227:367-383.

Melin, S.R. 2002. The foraging ecology and reproduction of the California sea lion (*Zalophus californianus californianus*). Ph.D. thesis, University of Minnesota.

Odendaal, P.N., M.N. Bester, M. van der Merwe, and W.H. Oosthuizen. 2002. Seasonal changes in the ovarian structure of the cape fur seal, *Arctocephalus pusillus pusillus*. Aust. J. Zool. 50:491-506.

Okey, T.A., S. Banks, A.R. Born, R.H. Bustamante, M. Calvopina, G.J. Edgar, E. Espinoza, J.M. Farina, L.E. Garske, G.K. Reck, S. Salazar, S. Shepherd, V. Toral-Granda, and P. Wallem. 2004. A trophic model of a Galapagos subtidal rocky reef for evaluating fisheries and conservation strategies. Ecol. Model. 172:383-401.

Pitcher, K.W., D.G. Calkins, and G.W. Pendleton. 1998. Reproductive performance of female Steller sea lions: An energetics-based reproductive strategy? Can. J. Zool. 76:2075-2083.

Punt, A.E., J.H.M. David, and R.W. Leslie. 1995. The effects of future consumption by the cape fur seal on catches and catch rates of the cape hakes. 2. Feeding and diet of the cape fur seal *Arctocephalus pusillus pusillus*. S. Afr. J. Mar. Sci. 16:85-99.

Reid, K., and J.P.Y. Arnould. 1996. Diet of Antarctic fur seals during the summer breeding period at South Georgia. Polar Biol. 16:105-114.

Reijnders, P., S. Brasseur, J. Van der Toorn, O. Van der Wolf, I.L. Boyd, J. Harwood, D. Lavigne, and L. Lowry. 1993. Seals, fur seals, sea lions, and walrus. Status survey and conservation plan. IUCN/SSC Seal Specialist Group, Gland, Switzerland.

Stephens, D.W., and J.R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton.

Thompson, D., C.D. Duck, B.J. McConnell, and J. Garrett. 1998. Foraging behaviour and diet of lactating female southern sea lions (*Otaria flavescens*) in the Falkland Islands. J. Zool. (Lond.) 246:135-146.

Warneke, R.M., and P.D. Shaughnessy. 1985. *Arctocephalus pusillus*, the South African and Australian fur seal: Taxonomy, evolution, biogeography, and life history. In: Studies of sea mammals in south latitudes. South Australian Museum, Adelaide, pp. 153-177.

Weise, M.J. 2000. Abundance, food habits, and annual fish consumption of California sea lions (*Zalophus californianus*) and its impact on salmonid fisheries in Monterey Bay, California. M.S. thesis, San Jose State University, San Jose, California.

Wickens, P., and A.E. York. 1997. Comparative population dynamics of fur seals. Mar. Mamm. Sci. 13:241-292.

Trends in Abundance of Australian Sea Lions, *Neophoca cinerea*, at Seal Bay, Kangaroo Island, South Australia

Peter D. Shaughnessy
CSIRO Sustainable Ecosystems, Canberra, Australian Capital Territory, Australia

Rebecca R. McIntosh
La Trobe University, Zoology Department, Sea Mammal Ecology Group, Melbourne, Victoria, Australia

Simon D. Goldsworthy
South Australia Research and Development Institute (SARDI), Aquatic Sciences Centre, Adelaide, South Australia, Australia

Terry E. Dennis
Encounter Bay, South Australia, Australia

Mel Berris
Department for Environment and Heritage, Kingscote, South Australia, Australia

Abstract

Pups of the Australian sea lion have been counted at Seal Bay for 20 pupping seasons, 1973-74 to 2002-03. Temporal changes in counts of live pups over the course of each pupping season were fitted to Gaussian (normal) curves to determine objectively the date when pup numbers reached their peak. The mean interval between pupping seasons was 532 ± 31 days (i.e., 17.5 months). Maximum counts of live pups for 13 pupping seasons averaged 144 (s.d. 14) from 1985 (from when data quality was adequate) to 2002-03. The data show an annual decrease of 0.77% (exponential slope of regression was –0.0077, $r^2 = 0.216$), or –1.14% per breeding cycle (95% confidence limits –2.47% and +0.20%), but this exponential regression was not significant. Maximum pup numbers for each pupping season were correlated with duration of the interbreeding intervals, such that more pups were counted following shorter interbreeding intervals than following longer intervals. This relationship was not significant, but with one outlier removed it became highly significant, suggesting that pup numbers were influenced by the duration of interbreeding interval. A generalized linear model incorporating three predictor variables (year, interbreeding interval, and their interaction) produced a significant model that explained 51% of the variance in pup numbers, and both year and interbreeding interval had a significant negative effect on pup counts. A generalized additive model (GAM) using cubic spline smoothing functions produced a highly significant model with both terms (year and breeding interval) having negative coefficients. We conclude that year and duration of the interbreeding interval affect pup counts negatively, but that a significant component of the variance is accounted for by the interaction between year and breeding interval. Our best estimate for the rate of decline in the Seal Bay population is from the exponential regression analysis (i.e., 0.77% per year, 12.6% decline between 1985 and 2002-03). These analyses suggest that the reproductive output of Australian sea lions at Seal Bay has declined over the period 1985 to 2002-03. This decrease is contrary to recent increases of New Zealand fur seals, *Arctocephalus forsteri,* in Australia. The decrease of sea lion numbers at Seal Bay is a cause for concern and deserves further investigation.

Introduction

The Australian sea lion, *Neophoca cinerea,* breeds on the west and south coasts of Western Australia, and in South Australia. Seventy-three breeding colonies have been reported on islands and on the coast between Houtman Abrolhos Islands in Western Australia and The Pages Islands, near Kangaroo Island in South Australia (Gales et al. 1994, Dennis and Shaughnessy 1996, Shaughnessy et al. 2005, McKenzie et al. 2005). There are also recent records of a few vagrants on the New South Wales coast, in southern Tasmania and Victoria (reviewed by Shaughnessy 1999). The sea lion is an Australian endemic that is classed as a specially protected species by the Western Australian government, as rare by the South Australian government, and was listed as vulnerable by the Commonwealth government in 2005.

Surveys of the Australian sea lion conducted over several breeding seasons around 1990 throughout its range led to an estimate of pup production of 2,430 per breeding cycle. With the assistance of a population model, the population size was estimated to be between 9,300 and

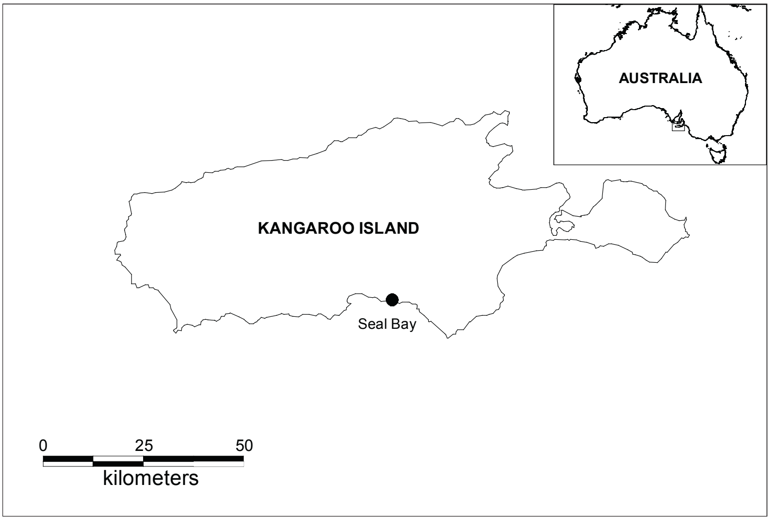


Figure 1a. Map showing the location of the Seal Bay colony of the Australian sea lion in South Australia.

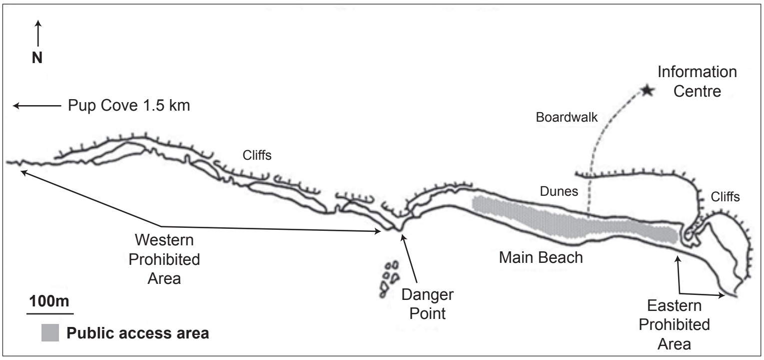


Figure 1b. Map of Seal Bay Conservation Park, South Australia.

11,700 (Gales et al. 1994). On the basis of another modeling exercise, the inclusion of recently discovered colonies in the Great Australian Bight and on Eyre Peninsula, and more recent estimates of abundance for several colonies, pup numbers were estimated at 2,861 and the population size at 11,200 (Goldsworthy et al. 2003).

In the surveys around 1990, the four largest colonies at the eastern end of the range accounted for 42% of the population (Gales et al. 1994). They were all east of Port Lincoln, South Australia. In order of size they were North Page Island, South Page Island, Dangerous Reef, and Seal Bay on Kangaroo Island (Fig. 1). Here we report on trends in abundance of pups in the fourth largest colony, Seal Bay, based on counts of pups for 20 pupping seasons from 1973-74 to 2002-03. The colony has been reported to produce up to 180 pups in a pupping season (Ling and Walker 1976, Gales et al. 1994).

The interval between pupping seasons of the Australian sea lion is about 17.6 months (Ling and Walker 1978, Higgins 1993). For breeding colonies on islands off the west coast of Western Australia, Gales et al. (1992) estimated the pupping interval at 17.5 months. For another 11 colonies throughout the range, Gales et al. (1994) noted that the pupping interval was 17-18 months. Thus, the breeding cycle is non-seasonal; furthermore its timing is asynchronous (Gales et al. 1994). The duration of the pupping season has been reported as 5 months at Seal Bay and at islands off the west coast of Western Australia (Higgins 1990, Gales et al. 1992), or even longer at Seal Bay (Ling and Walker 1976, Dennis 1999). Individual pupping seasons are referred to here by the single year or the split year in which they occurred.

Kangaroo Island has an area of 4,500 square kilometers and a human population of 4,200. Although its economy has been based on primary industries, in recent years tourism has developed into an important income generator (Twyford and Vickery 2001). A major attraction for visitors has been the controlled access program at Seal Bay that enables visitors to walk on the beach with interpretive officers to view Australian sea lions.

Our aim in this paper is to examine variation over several years in the interval between pupping seasons, and in the maximum counts of pups of the Australian sea lion colony at Seal Bay.

Materials and methods

Study colony

Seal Bay is on the south coast of Kangaroo Island in the Seal Bay Conservation Park. Its management by the South Australian Department for Environment and Heritage (DEH) has been reviewed by Robinson and Dennis (1988) and by Twyford and Vickery (2001). The colony extends along the coast for 7 km and comprises five areas: Pup Cove, the Western Prohibited Area, Main Beach, dunes and swales inland from Main Beach, and the Eastern Prohibited Area.

Most pups are born in the Western Prohibited Area and Pup Cove, with smaller numbers in the Eastern Prohibited Area (EPA) and on Main Beach. In the last two pupping seasons (2001-02 and 2002-03), the search for pups extended farther east beyond the Eastern Prohibited Area, as far east as Bales Bay. Because it is not clear if searches for pups were made east of the Eastern Prohibited Area before the 2001-02 pupping season, we have excluded data from those areas.

Pup counts

Sea lion pups and other age and sex classes at Seal Bay have been counted at monthly intervals by DEH rangers and interpretive officers based on Kangaroo Island. That project was initiated in February 1983 by one of us (TED). Before that, counts were made sporadically from 1962 by various people including researchers from the South Australian Museum (e.g., Ling and Walker 1979) and by DEH staff. Data to 1999 at Seal Bay have been collated by Dennis (1999) as part of a compilation of counts of sea lions at breeding colonies and haul-out sites in South Australia. In the 2002-03 pupping season, the intensity of counting at Seal Bay was considerably greater than previously because one of us (RRM) was involved in a population dynamics study of the sea lions there.

The usual method for estimating abundance of sea lions is for one or two observers to walk through a colony searching for and counting pups. Pup numbers are chosen as the index of abundance (Berkson and DeMaster 1985) because pups are easily recognizable, most stay ashore when people enter a colony, and they are manageable (if the estimating technique requires handling). In addition, most of the pups are in the colony at one time, unlike the other age classes in which a variable proportion is ashore at any one time. Because the pupping season lasts for several months, it is difficult to schedule any of the several counts made in a season to occur when pup numbers reach a maximum. In addition, some pups born early in the pupping season may leave with their mothers before the last pups have been born. For example, tagged pups from Seal Bay have been reported at other sea lion colonies on Kangaroo Island (Seal Slide and at Cape Bouguer) aged less than 6 months (Ling and Walker 1976, 1979). Consequently, each count of pups is likely to underestimate the number born in the breeding season and, unless several counts are made during the season, the pup production could be underestimated seriously.

Pups were recorded in four categories based on those used by Gales et al. (1994): *brown pups* = live pups in natal pelage or still molting it; *molted pups* = live pups that have completely molted their natal pelage, in most pups that occurs at about 5 months of age (T. Dennis and M. Berris, unpubl. obs.); *unclassed pups* = when the counter did not distinguish between live brown pups and live molted pups; and *dead pups*. In the analyses reported here, the first three categories were combined to form the category *live pups*.

Procedure for estimating pup abundance from counts

The number of dead pups was not recorded in some pupping seasons and was only recorded on a few occasions in other seasons. Many pups at Seal Bay are concealed under bushes or rock overhangs and in caves. This made some of the live pups difficult to find and made it even more difficult to locate dead pups. Furthermore, we suspect that efforts to record dead pups varied between seasons because personnel conducting the counts varied. Consequently, the search effort for live pups was more likely to have been uniform across seasons than that for dead pups. This belief was accentuated by the extremely high count of dead pups in the 2002-03 pupping season, when pups were searched for more frequently and more assiduously than in former seasons. Therefore, we decided to restrict our analyses of trends to counts of live pups. The maximum number of live pups was taken as the index of abundance for the pupping season; it was reached in most seasons on the visit to the colony in the fifth or sixth month of the pupping season.

Available count data and their analyses

Data for 18 pupping seasons at Seal Bay between 1973-74 and 1998-99 have been collated by Dennis (1999). In the 1978 pupping season, only a single count was made, of 87 pups. It was not used in the analyses because it was little more than half of the average pup numbers recorded in the colony and was presumably made well before numbers had peaked for that season. Counts were also available for the three pupping seasons from 2000 to 2002-03. Thus counts of live pups were available for a total of 20 seasons (Appendix 1) from 1973-74 to 2002-03. The beginning of each pupping season was indicated by the presence of the first brown pup in a monthly survey after their absence for several months. In a few seasons, the first brown pup recorded was dead.

For the analysis of trends, the complete set of live pup counts was first examined using the linear regression of log-transformed pup counts on year, which is based on an exponential regression of the form:

$$y = a \times e^{bx}$$

where y is the maximum count of live pups for each pupping season, x refers to the year calculated from 1 January 1973 which was set at 1, and a and b are constants. The constant b is the exponential rate of change of the population; it was expressed as a percentage rate of change using the formula

$$(e^{b} - 1) \times 100.$$

The statistical significance of regressions was examined using analysis of variance.

We limited most of our analyses to the data from the last 13 pupping seasons, from 1985 to 2002-03, when data seemed more reliable than previously. A counting protocol established by TED for Seal Bay was being used during this period and timing of pupping seasons had been established by 1985, which led to more focused data collection. Before 1985, data had been collected sporadically and the age-sex classes recognized had not been standardized.

Classifying some young Australian sea lions can be difficult because molted pups aged 5 to 7 months can be confused with small juveniles born in the previous pupping season, which are then aged between 18 and 36 months. Small juveniles can be recognized by their cranial development, particularly their slightly longer noses. Furthermore, when pups molt their natal coat (lanugo), they replace it with a silver gray and cream pelage. When juveniles that were born in the previous pupping season molt, their newly emerging silver gray coat shows through their aged, ginger colored outer hair, which gives them a different coloration from that of pups.

In some counts that we decided to omit, there was a high proportion of molted pups soon after the first of the brown pups would have completed their molt, which indicated that some juveniles had been included in the molted pup category. That problem was prevalent in counts from the 1970s and 1980s, and also occurred in other seasons several months after peak numbers were reached. In addition, in some of the early data sets, pups were simply categorized as “unclassed pups” in the monthly censuses, and no effort was made to distinguish between brown pups and molted pups. We suspect that such counts may also have included juveniles and caused an overestimation of the maximum pup count for the season. An example is the exceptionally high count for 1982-1983, almost six months after the beginning of the pupping season (Appendix 1). We have scrutinized these data carefully and omitted counts that we considered unsatisfactory.

Determining the peak of pupping seasons, their duration, and interbreeding intervals

Temporal changes in the counts of live pups over the course of each pupping season were fitted to Gaussian (normal) curves using the curve fitting function in the graphing software KaleidaGraph (V 3.09, Synergy Software), in order to determine objectively the date when pup numbers reached their peak.

Curves fitted to pup count data for each pupping season included at least one and preferably two counts after the maximum count. This approach standardized count data available for each season and enabled the calculation of a clearly defined peak in pup numbers for each pupping season and the interval (in days) between seasons.

Median pupping dates were calculated in two ways. First, by calculating the estimated date at which 50% of pups were born based on the equations for the Gaussian distribution for each pupping season. Median

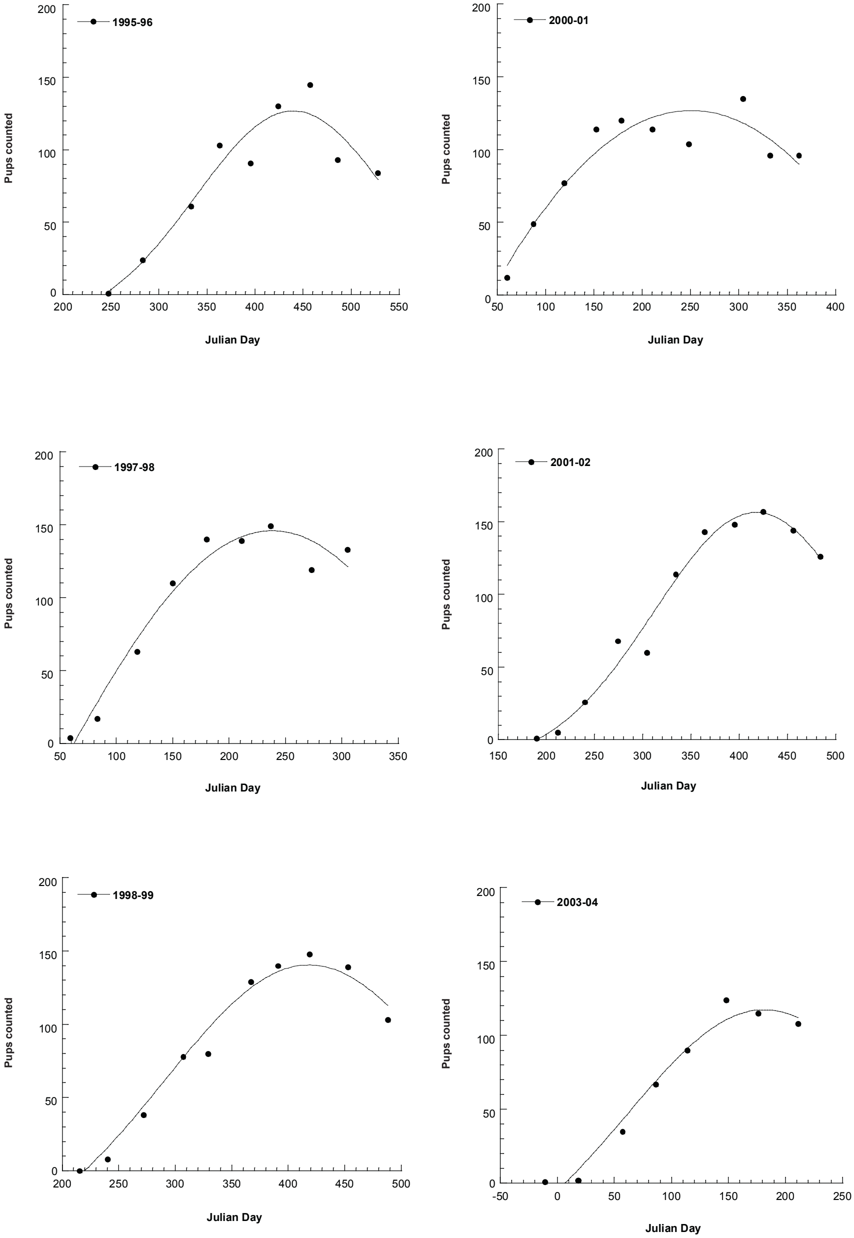


Figure 2. Examples of Gaussian curves fitted to counts of live pups of the Australian sea lion at Seal Bay, Kangaroo Island between 1995-96 and 2002-03 plotted against number of days from 1 January of each year.

Table 1. Estimates of the timing and duration of pupping seasons, and intervals between them based on fits of Gaussian curves to pup count data for Australian sea lions at Seal Bay, Kangaroo Island.

Timing and duration of pupping seasons							No. years			Interval between breeding seasons (d)			
Gaussian model		Probit analysis					Gaussian model		Probit	Gaussian model		Probit	
Peak	Median	Median	s.d. (d)	5% pups	95% pups	90% pups (d)	Peak	Median	Median	Peak	Median	Median	Max. pup counts
–	–	–	–	–	–	–	–	–	–	–	–	–	118
28-Aug-75	24-May-75	17-May-75	46.3	2-Mar-75	1-Aug-75	152	0.7	0.4	0.4	–	–	–	102
30-Dec-76	02-Oct-76	02-Oct-76	37.4	1-Aug-76	2-Dec-76	123	2.0	1.8	1.8	490	497	503	156
–	–	–	–	–	–	–	–	–	–	–	–	–	–
15-Jan-80	17-Sep-79	18-Sep-79	47.3	2-Jul-79	5-Dec-79	156	5.0	4.7	4.7	–	–	–	135
20-Jun-81	18-Apr-81	19-Apr-81	25.2	9-Mar-81	31-May-81	83	6.5	6.3	6.3	522	579	579	109
22-Nov-82	06-Sep-82	26-Aug-82	45.1	13-Jun-82	8-Nov-82	149	7.9	7.7	7.7	520	506	494	185
30-May-84	15-Feb-84	15-Feb-84	43.0	6-Dec-83	26-Apr-84	142	9.4	9.1	9.1	555	527	538	117
31-Oct-85	13-Aug-85	07-Aug-85	38.0	6-Jun-85	9-Oct-85	125	10.8	10.6	10.6	519	545	539	154
21-Apr-87	29-Jan-87	23-Jan-87	39.2	20-Nov-86	29-Mar-87	129	12.3	12.1	12.1	537	534	534	166
04-Nov-88	08-Jul-88	12-Jul-88	43.7	1-May-88	22-Sep-88	144	13.9	13.5	13.5	563	526	536	136
05-Mar-90	26-Dec-89	13-Dec-89	43.6	3-Oct-89	23-Feb-90	144	15.2	15.0	15.0	486	536	519	162
30-Oct-91	01-Jun-91	10-Jun-91	52.3	16-Mar-91	4-Sep-91	172	16.8	16.4	16.5	604	522	543	128
15-Mar-93	01-Dec-92	28-Nov-92	46.1	13-Sep-92	11-Feb-93	152	18.2	17.9	17.9	502	549	537	153
27-Sep-94	30-May-94	29-May-94	50.5	7-Mar-94	20-Aug-94	166	19.8	19.4	19.4	561	545	547	124
14-Mar-96	29-Nov-95	28-Nov-95	44.1	17-Sep-95	9-Feb-96	145	21.2	20.9	20.9	534	548	549	145
26-Aug-97	29-Apr-97	05-May-97	41.6	26-Feb-97	13-Jul-97	137	22.7	22.3	22.4	529	517	524	149
22-Feb-99	27-Oct-98	29-Oct-98	45.6	15-Aug-98	12-Jan-99	150	24.2	23.8	23.8	545	546	542	148
06-Sep-00	13-Apr-00	22-Apr-00	49.9	31-Jan-00	13-Jul-00	164	25.7	25.3	25.3	562	534	541	135
19-Feb-02	24-Oct-01	22-Oct-01	49.6	1-Aug-01	11-Jan-02	163	27.2	26.8	26.8	531	559	548	147
25-Jun-03	12-Mar-03	13-Mar-03	42.1	2-Jan-03	21-May-03	139	28.5	28.2	28.2	491	504	507	122
Mean			43.7			144				532	534	534	140
s.d.			6.1			20				31	21	20	21

The estimated date of the peak in counts of live pups and the date of median count (50%) based on a Gaussian model, and the date of median calculated from probit analysis of Gaussian curves are presented, as well as the inferred spread of pup counts based on probit analysis. The calculated timing of breeding seasons in years and the intervals between them based on Gaussian analyses are also presented, with the maximum counts of live pups for each pupping season. The year count began at 1 January 1975.

Data for the 1978 season were not used in analyses. Analyses were not done for the 1973-74 season because there were no pup counts after the maximum count.

pupping dates were also calculated using a modified probit analysis (Caughley 1980) based on the Gaussian curve data for each pupping season.

Linear regression analyses and generalized linear models (GLMs) were developed using SYSTAT (V10, SPSS), and generalized additive models (GAMs) were performed using SASS.

Results

Timing of pupping seasons and intervals between them

Examples of the Gaussian curves fitted to six of the breeding seasons of pup count data are illustrated in Fig. 2. The date on which peak numbers occurred, the estimated median pupping date, and the duration over which 90% of births occurred based on Gaussian curves and on probit analysis are presented in Table 1. The mean duration over which 90% of pups were counted, based on probit analysis of the Gaussian curves, was 144 days (s.d. = 20, *n* = 19), or approximately 4.7 months. The mean interval between pupping seasons based on dates for the peaks in pup numbers derived from the Gaussian curves was 532 days (s.d. = 31, range: 486-604 d, *n* = 17) or 17.5 months (range 16.0-19.9). Similar results were obtained from the interval between median pupping dates derived from the Gaussian model (534 days [17.6 months], s.d. = 21, range 497-579 [2.7

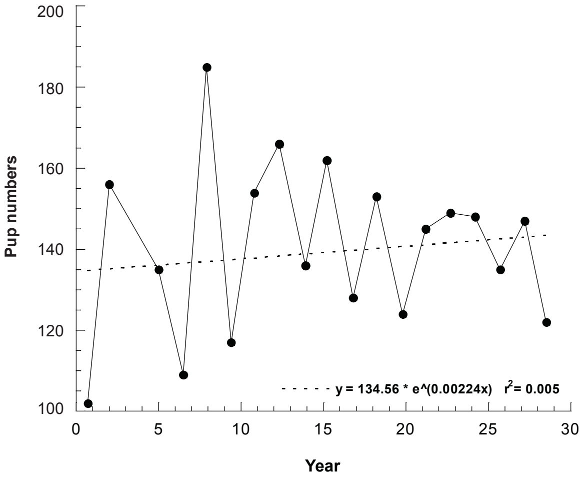


Figure 3. Maximum counts of live pups of the Australian sea lion at Seal Bay, Kangaroo Island between 1973-1974 and 2002-2003. "Year" refers to years since 1 January 1975.

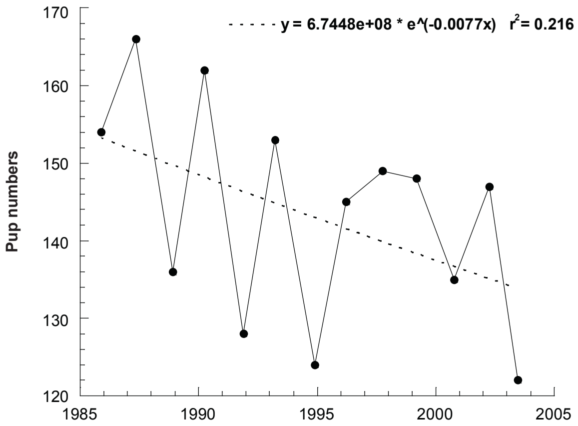


Figure 4. Maximum counts of live pups of the Australian sea lion at Seal Bay, Kangaroo Island, for pupping seasons between 1985 and 2002-2003 (*n* = 13).

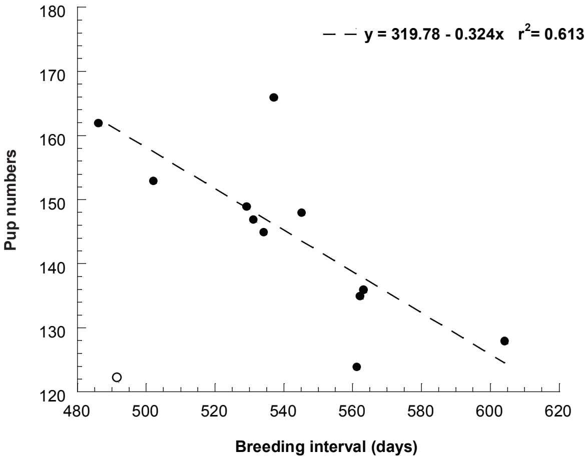


Figure 5. Relationship between interbreeding interval of Australian sea lions at Seal Bay and the maximum count of live pups between 1985 and 2002-2003. Linear regression of the relationship (with removal of the 1997 data point—open symbol) produced a significant regression.

months]), and from probit analysis (534 days [17.6 months], s.d. = 20, range 494-579 [2.8 months]). These estimates did not vary significantly with respect to method of calculation (paired *t*-tests: for Gaussian peak vs. Gaussian median, $t = 0.158$, $P = 0.877$; for Gaussian peak vs. probit median, $t = 0.247$, $P = 0.808$; and for Gaussian median vs. probit median, $t = 0.147$, $P = 0.885$).

Trends in live pup counts

Over 20 seasons (1973-74 to 2002-03), the peak number of live pups counted per pupping season averaged 140 (s.d. = 21) (Table 1). Although there was considerable variation in the number of pups born each season (range 102-185), no trends were apparent (exponential slope of regression was 0.0022, $r^2 = 0.005$; Fig. 3). Since the 1985 breeding season, pup numbers averaged 144 (s.d. = 14, range 122-166, $n = 13$) (Table 1, Fig. 4). This data set shows a general decline equivalent to an annual decrease of 0.77% (exponential slope of regression was –0.0077, $r^2 = 0.216$), or a decrease of 1.14% per breeding cycle (exponential slope of –0.0113), but this exponential regression was not significant.

From an examination of the trends in pup number across years (1985 to 2002-2003), we identified an apparent oscillation in pup numbers between high and low seasons (Fig. 4). This pattern is consistent, with the exception of one season, 1997. With the removal of this season, maximum pup numbers for each pupping season were correlated with the duration of the interbreeding intervals, such that more pups were counted following shorter interbreeding intervals than after longer ones (linear regression, $F_{1,11} = 14.23$, $P = 0.004$, $r^2 = 0.61$, Fig. 5). However, with the inclusion of the 1997 data, this relationship was not significant (linear regression, $F_{1,12} = 2.21$, $P = 0.17$, $r^2 = 0.18$). Visual examination of changes in pup numbers with time indicated that within the interbreeding season oscillation, there was a general decline in pup numbers with year, suggesting an interaction between duration of the interbreeding interval and year. This was examined further using generalized linear models (GLMs).

A GLM was developed incorporating backward stepwise inclusion of three predictor variables (year, interbreeding interval, and their interaction). It used the interbreeding interval between seasons based on dates for peaks in pup numbers derived from the Gaussian curves, and P set at 0.15 to enter or remove a predictor. A significant model (Table 2) included all predictor variables ($F_{3,9} = 5.14$, $P = 0.024$, adjusted $r^2 = 0.51$) and explained 51% of the variance in pup numbers. An additional model that excluded the interaction term produced a marginally significant model ($F_{2,10} = 4.08$, $P = 0.051$, adjusted $r^2 = 0.34$) that explained less variance, indicating that the inclusion of the interaction significantly improved the fit of the model. These results indicate that year, interbreeding interval, and the interaction between year and interval, all contribute significantly to explaining variance in the numbers of pups counted at Seal Bay over

Table 2. A generalized linear model (GLM) investigating the influence of year and interbreeding interval (and their interaction) on counts of Australian sea lion pups at Seal Bay for 13 pupping seasons between 1985 and 2002-03.

Effect	Coefficient	Standard error	Standard coefficient	Tolerance	*t*-value	*P*
Constant	664.977	189.167	0	–	3.515	0.007
Year	–21.819	9.774	–9.048	0.002	–2.232	0.052
Interval	–0.940	0.358	–2.205	0.058	–2.628	0.027
Interval × year	0.039	0.019	8.581	0.002	2.111	0.064

Table 3. Summary of the generalized additive model (GAM) with identity link, cubic spline smoothing function, and 4 degrees of freedom examining nonlinear relationships between counts of Australian sea lion pups, with year and interbreeding interval as factors for 13 pupping seasons between 1985 and 2002-03.

Parameter	Parameter estimate	Standard error	*t*-value	*P*
Intercept	305.856	39.285	7.790	0.002
Year	–1.297	0.040	–3.240	0.032
Interval	–0.252	0.070	–3.590	0.023

13 consecutive breeding seasons between 1985 and 2002-2003. Furthermore, coefficients of the terms indicate that both year and interbreeding interval have a significant negative effect on numbers of pups counted. Due to high co-linearity between predictor variables, as indicated by the very low tolerance values in the GLM (Table 2), predictor variables were re-scaled by centering (subtracting the mean from each observation), and the model rechecked (following Quinn and Keough 2002).

Although the above GLMs were significant, one of the data points had large leverage. When this was removed, subsequent fits to the model also produced outliers; subsequent removal of these led eventually to the removal of all data points. This result suggested that the relationships between pup numbers and year and breeding interval were nonlinear. To address the potential nonlinearity in the two covariates, a generalized additive model (GAM) was tested, because these apply nonparametric smoothing functions to predictor variables (Quinn and Keough 2002). The GAM model we developed used a normal (Gaussian) probability

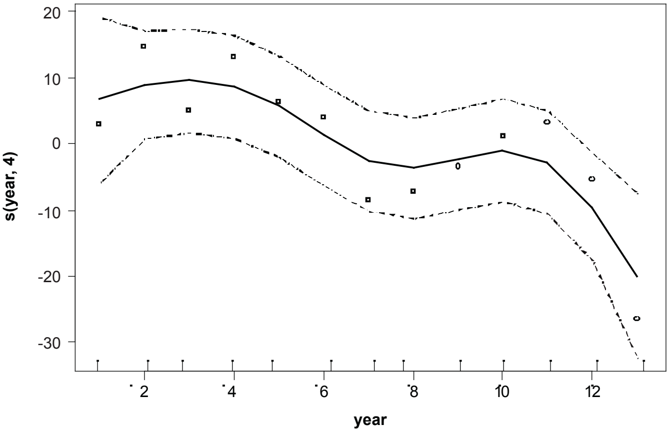


Figure 6. A generalized additive model of maximum pup count data of Australian sea lions at Seal Bay for pupping seasons between 1985 and 2002-2003 (*n* = 13) fitted to "year" data, with years beginning at 1 January 1975. The model was developed with a Gaussian probability distribution using a cubic spline smoothing function and 4 degrees of freedom, which is expressed as "s(year, 4)" on the y-axis. On the x-axis, "year" refers to pupping seasons from 1985 to 2002-2003. The dashed lines represent the 95% confidence limits.

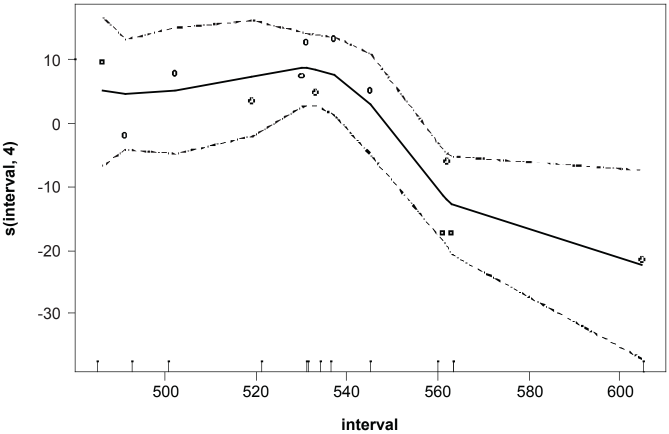


Figure 7. A generalized additive model of maximum pup count data of Australian sea lions at Seal Bay for pupping seasons between 1985 and 2002-2003 (*n* = 13) fitted to interbreeding interval data. The model was developed with a Gaussian probability distribution using a cubic spline smoothing function and 4 degrees of freedom, which is expressed as "s(interval, 4)" on the y-axis. On the x-axis, the duration of the interbreeding "interval" is expressed in days. The dashed lines represent the 95% confidence limits.

distribution with a cubic spline smoothing and identity link function. We applied this GAM to the data with a range of degrees of freedom from 1 to 5. The best fit to the data was derived using a cubic spline smoothing function with 4 degrees of freedom (Figs. 6 and 7). All of the terms had significant nonparametric components, suggesting a nonlinear model was appropriate for year and interbreeding interval. Both terms had negative coefficients (as found in the GLM), indicating that each had a negative effect on maximum pup numbers in each pupping season (Table 3). The fit of this GAM to pup counts indicated that the model accounted for approximately 89% of the variance in pup numbers ($R = 0.949$, $F_{1,12} = 99.8$, $P < 0.0001$, adjusted $r^2 = 0.89$, Fig. 8).

We conclude from these analyses that both year and interbreeding interval significantly affect maximum counts of live pups in each season, but that a significant component of the variance explained by each of these factors is accounted for by their interaction. Consequently, it is difficult to isolate a year effect and breeding interval effect without taking account of their interaction. Therefore, our best estimate of the rate of decline in pup counts at Seal Bay comes from the exponential regression analysis, which indicates a decline of 0.77% per year, which equates to a

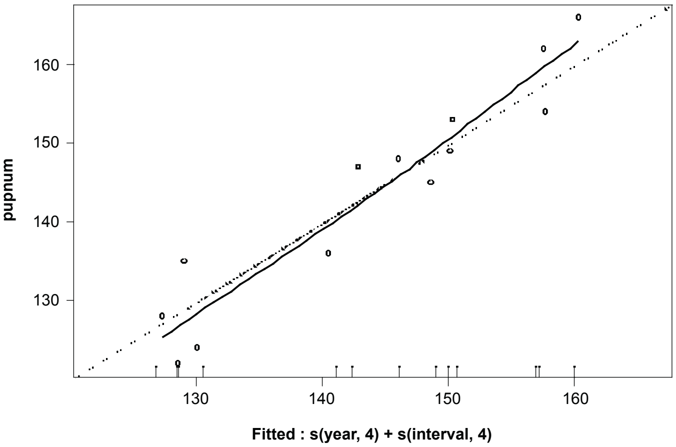


Figure 8. Fit of the generalized additive model (identity link, cubic spline smoothing function) to maximum pup count data of Australian sea lions at Seal Bay for pupping seasons between 1985 and 2002-2003 (open circles, *n* = 13), indicating a significant correlation of the modeled data to actual data (adjusted $r^2 = 0.89$). The solid line represents the regression and the dotted line has a slope of one and illustrates the deviance of the predicted vs. actual pups counts with parity.

1.14% decline per pupping season (95% confidence limits of –2.47% and +0.20%, based on the slope of the exponential regression of –0.0113, with s.e. 0.00678, $n = 13$). Between 1985 and 2002-2003 there was a 12.6% decline (i.e., over 13 breeding seasons covering 17.7 years).

We noted that breeding seasons following long interbreeding intervals were of longer duration than those following short interbreeding intervals. This was indicated by a positive relationship between the interbreeding interval and the standard deviation of the duration of the following breeding season, both of which were calculated from the Gaussian curves (slope = 2.95, $F_{1,11} = 5.64$, $P = 0.037$, $r^2 = 0.34$).

We performed the same type of GLM analysis as above with duration of the interbreeding interval replaced by the standard deviation (s.d.) of the duration of the following breeding season. That model removed "year" as a factor as well as interactions between "year" and "s.d." The only significant factor remaining was "s.d." That model explained less variance in pup numbers than the original model ($F_{1,11} = 4.89$, $P = 0.049$, adjusted $r^2 = 0.245$). Thus more of the variance was explained by the original model (51%, using duration of the interbreeding interval as a factor) compared with this model (24.5%, using s.d. as a factor). Because the second model explains less variation than the original model, and because the interbreeding interval precedes the subsequent pupping season, it is more logical to use duration of the interbreeding interval as an independent variable in the model.

Discussion

Biases and reliability of counts

Several characteristics of the Australian sea lion make estimation of pup abundance difficult. The most important is that pups are born over an extended period of up to 7 months. This leads to the problem of availability bias (Seber 1982, p. 132), which arises because some of the pups have not been born at the time of counting or, near the end of the pupping season, some may have moved to other colonies or be in the sea nearby. Similar problems arise in estimating abundance of other pinniped species, such as hooded seals, *Cystophora cristata* (Bowen et al. 1987).

A further problem in determining the abundance of Australian sea lion pups by direct counting is sightability bias. Live pups not attended by an adult female were not always easy to see, especially if they were solitary and sleeping in a rock hole or under a bush. For instance, mark-recapture estimates of pup numbers in most of the Seal Bay colony in June 2003 averaged 187% of the counts in the same area (McIntosh et al. 2006). Therefore the index of abundance of pup numbers for Seal Bay used in this study most likely underestimates pup production for each pupping season.

Interval between breeding seasons

Although previous studies have identified the unusual non-annual breeding pattern in Australian sea lions, with intervals between pupping seasons of 17-18 months (Ling and Walker 1978, Gales et al. 1992, Higgins 1993), none has identified such a range in interbreeding intervals as this study. Higgins (1993) calculated median pupping dates for four successive breeding seasons at Seal Bay, enabling her to calculate three interbreeding intervals (1986-87 to 1988 of 526 days; 1988 to 1989-90 of 533 days; 1989-90 to 1991 of 543 days), with a mean of 534 ± 8.5 days (i.e., 17.6 ± 0.3 months). Using a different method that calculated breeding intervals based on the dates of maximum pup counts, this study determined a similar mean inter-birth interval with a larger sample size (17.5 ± 1.0 months, *n* = 17). Whereas the range of Higgins's (1993) inter-birth intervals was only 17 days (i.e., 0.6 months), we identified a range of 118 days (i.e., 3.9 months). It is possible that our method has a tendency to both overestimate and underestimate intervals compared with that of Higgins (1993) based on mean pupping date, in the sense that for the three intervals that have been calculated by both methods, the differences were +37, –47, and +61 days, respectively. Variation in these results might be caused by differences in the duration of pupping seasons across years. However, if the distribution of births throughout a pupping season approximates a normal distribution, as data in Higgins (1993, Fig. 1) suggests, then duration of pupping season alone should not affect estimates of interbreeding interval, as long as the estimating method is the same across years. Higgins (1993) also recorded 33 inter-birth intervals for 22 individual females; these ranged from 512 to 576 days (i.e., 16.8 to 18.9 months, a range of 2 months) with a combined mean of 542.5 days (i.e., 17.8 months).

Given that the period of embryonic diapause (delayed implantation) in Australian sea lions appears to be fixed and similar in duration to that of other otariid species (4-5 months, Gales and Costa 1997), the considerable variation in pupping season interval may be caused by variation in the period of placental gestation. If our estimates of interbreeding intervals are correct, this would lead to variation in the duration of placental (active) gestation of about 6 months. Such plasticity in gestation duration in Australian sea lions is unique among pinnipeds, and among mammalian species in general, and deserves further investigation. In addition, as fewer pups are counted following longer breeding intervals, extended intervals may reduce the fecundity rates of breeding females. If reductions in fecundity are asymmetrical across age-groups (greater effects on younger females), and younger females tend to breed earlier within each breeding season, then an apparent extension of breeding interval could be accounted for by asymmetrical reductions in fecundity.

The ultimate cause for variability in interbreeding season interval of Australian sea lions is unknown. However, the fact that fewer pups appear to be counted, subsequent to long interbreeding intervals, suggests that variations in fecundity in response to resource availability may be a contributing factor.

Trends in abundance

It is uncertain how live pup counts relate to pup production and pup mortality rates across seasons. The most parsimonious conclusion is that live pup counts are positively affected by pup production and negatively affected by mortality rates. Given this, live pup counts are likely to be a realistic measure of relative pup numbers available for recruitment to juvenile age classes from each pupping season.

Our analyses of peak pup counts at Seal Bay over 13 breeding seasons from 1985 to 2002-03 suggest that much of the inter-seasonal variance in pup numbers is driven by a seasonal oscillation in the duration of interbreeding interval, but that within these oscillations there is a significant decline in pup numbers with year.

These analyses indicate that the reproductive output of Australian sea lions at Seal Bay has declined over the period 1985 to 2002-03. No significant trends in abundance were noted by Ling (1992). King and Marlow (1979, p. 14) reported a possible decrease in population size, particularly on the west coast of Western Australia, but no supporting data were provided. Gales et al. (2000) also indicated that numbers of sea lions were decreasing in Western Australia.

The decrease in numbers of sea lion pups at Seal Bay is contrary to increases in numbers of pups of the New Zealand fur seal, *Arctocephalus forsteri,* at nearby colonies on Kangaroo Island, at the North Neptune Islands in South Australia and at islands on the south coast of Western Australia (Shaughnessy et al. 1995, Shaughnessy and McKeown 2002, Gales et al. 2000). Numbers of Australian fur seals, *A. pusillus doriferus*, have also increased at the major colonies in Bass Strait (Shaughnessy et al. 2002, Kirkwood et al. 2005). The increase in fur seal numbers is attributed to a recovery from overharvesting since Europeans arrived in South Australia. Because the Australian sea lion was also harvested in the same area (Ling 1999) and its numbers and range are considered to be depleted (Gales et al. 1994), the sea lion population is also expected to recover, unless some other factor or factors are restraining it.

That sea lion pup numbers at Seal Bay have decreased is a cause for concern, and the extent and possible causes of this decline deserve further investigation. Contributing factors include the high levels of pup mortality (e.g., Marlow 1975) and the possibility of competition between the sea lions and fur seals for prey and/or for space ashore. The latter seems unlikely because the two species occupy different areas ashore, especially for breeding. The former (competition for similar prey) deserves further attention, although it has been reported that Australian sea lions are benthic feeders on the continental shelf (Costa and Gales 2003), in contrast to New Zealand fur seals, which are predominantly epipelagic (mid-water) feeders, although some foraging also occurs on the benthos (Mattlin et al. 1998, Page et al. 2005).

Another factor that may have contributed to the decrease in sea lion numbers at Seal Bay is interaction with commercial fisheries, especially the inshore bottom-set gillnet fishery for sharks (Robinson and Dennis 1988, Shaughnessy 1999, Gibbs 2002, Shaughnessy et al. 2003, Page et al. 2004). An example of a sea lion almost drowning in a commercial shark net comes from Baird Bay, western Eyre Peninsula, South Australia. A net set in shallow water adjacent to the sea lion colony at Jones Island on 3 November 2001 caught a juvenile sea lion by the next day. The sea lion had sufficient strength to reach the surface to breathe and was subsequently cut out of the net alive (A. Payne, Baird Bay Charters, pers. comm.). Ling and Walker (1979) have also recorded sea lions being caught in nets of commercial shark fishers. The 150 mm monofilament netting used in that industry is the most frequently encountered entanglement material recorded on sea lions at colonies in South Australia (Dennis 1999). Page et al. (2004) reported that monofilament netting was the most frequently encountered entangling material (55%) recovered from 35 Australian sea lions between 1988 and 2002 at Seal Bay on Kangaroo Island.

In addition, sea lions interact with the rock lobster fishery, in which baits are placed in traps set on the seafloor. Sea lions drown in rock lobster pots (Gales et al. 1994) and take baits from pots and damage them, which causes retaliation by fishers (Robinson and Dennis 1988, Southern Fisheries 1996). The feeding regime of the Australian sea lion (benthic feeding on the continental shelf) is likely to place them at greater risk of mortality with these forms of fishery interaction than is the New Zealand fur seal, which breeds in the same area but feeds farther offshore. Based on the reported interactions between sea lions and the shark and rock lobster industries, we recommend that the setting of gillnets and rock lobster pots near breeding colonies of the Australian sea lion should be reviewed.

Because of the variability in estimates of abundance in Australian sea lions between pupping seasons, it is essential that high quality, long-term data are collected systematically from widely spaced colonies across the species' range to determine trends in abundance accurately. This will require an improved level of monitoring compared with that achieved to date. Furthermore, because of the high incidence of pup mortality during pupping seasons, it is essential that several visits are made to a colony during each season so that dead pups can be marked and counted, in order to obtain meaningful estimates of their abundance, and that further investigations are directed at causes of pup mortality.

Acknowledgments

For assistance in conducting surveys at Seal Bay, we thank staff of the Department for Environment and Heritage SA from Kangaroo Island. For data from early surveys, we thank John Ling, Pin Needham, and Greg Walker. For assistance with data analyses we thank Yongshun Xiao of the South Australian Aquatic Sciences Centre. Permission to conduct the project and to work in the sea lion colonies within Seal Bay Conservation Park, including its Prohibited Areas, was granted by the Department for Environment and Heritage SA. For commenting on a draft of the manuscript we thank Cath Kemper, Graeme Moss, Jeff Laake, and Grey Pendleton.

References

Berkson, J.M., and D.P. DeMaster. 1985. Use of pup counts in indexing population changes in pinnipeds. Can. J. Fish. Aquat. Sci. 42:873-879.

Bowen, W.D., R.A. Myers, and K. Hay. 1987. Abundance estimation of a dispersed, dynamic population: Hooded seals (*Cystophora cristata*) in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 44:282-295.

Caughley, G. 1980. Analysis of vertebrate populations. Wiley, London.

Costa, D.P., and N.J. Gales. 2003. Energetics of a benthic diver: Seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. Ecol. Monogr. 73:27-43.

Dennis, T. 1999. Australian sea lion survey (and historical) records for South Australia. Report to the Wildlife Conservation Fund, Department for Environment, Heritage and Aboriginal Affairs, South Australia.

Dennis, T.E., and P.D. Shaughnessy. 1996. Status of the Australian sea lion, *Neophoca cinerea,* in the Great Australian Bight. Wildl. Res. 23:741-754.

Gales, N.J., and D.P. Costa. 1997. The Australian sea lion: A review of an unusual life history. In: M. Hindell and C. Kemper (eds.), Marine mammal research in the Southern Hemisphere. Surrey Beatty and Sons, Chipping Norton, Sydney, pp. 78-87.

Gales, N.J., A.J. Cheal, G.J. Pobar, and P. Williamson. 1992. Breeding biology and movements of Australian sea-lions, *Neophoca cinerea*, off the west coast of Western Australia. Wildl. Res. 19:405-416.

Gales, N.J., B. Haberley, and P. Collins. 2000. Changes in the abundance of New Zealand fur seals, *Arctocephalus forsteri*, in Western Australia. Wildl. Res. 27:165-168.

Gales, N.J., P.D. Shaughnessy, and T.E. Dennis. 1994. Distribution, abundance and breeding cycle of the Australian sea lion *Neophoca cinerea* (Mammalia: Pinnipedia). J. Zool. Lond. 234:353-370.

Gibbs, S.E. 2002. Perceptions in the South Australian commercial fishing industry with regard to seals. Master of environmental studies thesis, University of Adelaide, Adelaide. 114 pp.

Goldsworthy, S.D., C. Bulman, X. He, J. Larcombe, and C. Littnan. 2003. Trophic interactions between marine mammals and Australian fisheries: An ecosystem approach. In: N. Gales, M. Hindell, and R. Kirkwood (eds.), Marine mammals: Fisheries, tourism and management issues. CSIRO Publishing, Melbourne, pp. 62-99.

Higgins, L.V. 1990. Reproductive behavior and maternal investment of Australian sea lions. Ph.D. thesis, University of California, Santa Cruz. 126 pp.

Higgins, L.V. 1993. The nonannual, nonseasonal breeding cycle of the Australian sea lion, *Neophoca cinerea*. J. Mammal. 74:270-274.

King, J.E., and B.J. Marlow. 1979. Australian sea lion. In: Mammals in the seas. FAO Fisheries Series 5(II):13-15.

Kirkwood, R., R. Gales, A. Terauds, J.P.Y. Arnould, D. Pemberton, P.D. Shaughnessy, A.T. Mitchell, and J. Gibbens. 2005. Pup production and population trends of the Australian fur seal (*Arctocephalus pusillus doriferus*). Mar. Mamm. Sci. 21:260-282.

Ling, J.K. 1992. *Neophoca cinerea*. Mamm. Species 392:1-7.

Ling, J.K. 1999. Exploitation of fur seals and sea lions from Australian, New Zealand and adjacent subantarctic islands during the eighteenth, nineteenth and twentieth centuries. Aust. Zool. 31:323-350.

Ling, J.K., and G.E. Walker. 1976. Seal studies in South Australia: Progress report for the year 1975. S. Aust. Nat. 50:59-68, 72.

Ling, J.K., and G.E. Walker. 1978. An 18-month breeding cycle in the Australian sea lion? Search 9:464-465.

Ling, J.K., and G.E. Walker. 1979. Seal studies in South Australia: Progress report for the period April 1977 to July 1979. S. Aust. Nat. 54:68-78.

Marlow, B.J. 1975. The comparative behaviour of the Australasian sea lions *Neophoca cinerea* and *Phocarctos hookeri* (Pinnipedia: Otariidae). Mammalia 39:159-230.

Mattlin, R.H., N.J. Gales, and D.P. Costa. 1998. Seasonal dive behaviour of lactating New Zealand fur seals (*Arctocephalus forsteri*). Can. J. Zool. 76:350-360.

McIntosh, R.R., P.D. Shaughnessy, and S.D. Goldsworthy. 2006. Mark-recapture estimates of pup production for the Australian sea lion, *Neophoca cinerea* at Seal Bay Conservation Park, South Australia. In: A. Trites, S. Atkinson, D. DeMaster, L. Fritz, T. Gelatt, L. Rea, and K. Wynne (eds.), Sea lions of the world. Alaska Sea Grant College Program, University of Alaska Fairbanks.

McKenzie, J., S.D. Goldsworthy, P.D. Shaughnessy, and R. McIntosh. 2005. Understanding the impediments to the growth of Australian sea lion populations. Final report to Department of the Environment and Hertitage, Migratory and Marine Species Section. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication RD4/0171. 107 pp.

Page, B., J. McKenzie, and S.D. Goldsworthy. 2005. Inter-sexual differences in New Zealand fur seal diving behaviour. Mar. Ecol. Prog. Ser. 304:249-264.

Page B., J. McKenzie, R. McIntosh, A. Baylis, A. Morrissey, N. Calvert, T. Haase, M. Berris, D. Dowie, P.D. Shaughnessy, and S.D. Goldsworthy. 2004. Entanglement of Australia sea lions and New Zealand fur seals in lost fishing gear and other marine debris before and after government and industry attempts to reduce the problem. Mar. Pollut. Bull. 49:33-42.

Quinn, G.P., and M.J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, U.K.

Robinson, A.C., and T.E. Dennis. 1988. The status and management of seal populations in South Australia. In: M.L. Augee (ed.), Marine mammals of Australasia: Field biology and captive management. Royal Zoological Society of NSW, Sydney, Australia, pp. 87-110.

Seber, G.A.F. 1982. The estimation of animal abundance and related parameters. MacMillan, New York.

Shaughnessy, P.D. 1999. The action plan for Australian seals. Environment Australia, Canberra. 116 pp.

Shaughnessy, P.D., and A. McKeown. 2002. Trends in abundance of New Zealand fur seals, *Arctocephalus forsteri,* at the Neptune Islands, South Australia. Wildl. Res. 29:363-370.

Shaughnessy, P.D., T.E. Dennis, and P.G. Seager. 2005. Status of Australian sea lions, *Neophoca cinerea*, and New Zealand fur seals, *Arctocephalus forsteri*, on Eyre Peninsula and the far west coast of South Australia. Wildl. Res. 32:85-101.

Shaughnessy, P.D., S.D. Goldsworthy, and J.A. Libke. 1995. Changes in the abundance of New Zealand fur seals, *Arctocephalus forsteri,* on Kangaroo Island, South Australia. Wildl. Res. 22:201-215.

Shaughnessy, P.D., R.J. Kirkwood, and R.M. Warneke. 2002. Australian fur seals, *Arctocephalus pusillus doriferus*: Pup numbers at Lady Julia Percy Island, Victoria, and a synthesis of the species' population status. Wild. Res. 29:185-192.

Shaughnessy, P., R. Kirkwood, M. Cawthorn, C. Kemper, and D. Pemberton. 2003. Pinnipeds, cetaceans and fisheries in Australia: A review of operational interactions. In: N. Gales, M. Hindell, and R. Kirkwood (eds.), Marine mammals: Fisheries, tourism and management issues. CSIRO Publishing, Melbourne, pp. 136-152.

Southern Fisheries. 1996. "Seal friendly" lobster potting. Southern Fisheries 4(3):2.

Twyford, K., and F. Vickery. 2001. User-pays fees and regional development on Kangaroo Island. In: G. Worboys, M. Lockwood, and T. De Lacy (eds.), Protected area management principles and practices. Oxford University Press, South Melbourne, p. 175.

Appendix 1. Counts of live Australian sea lion pups at Seal Bay colony, Kangaroo Island, at each visit for pupping seasons between 1973-74 and 2002-03. The maximum count for each pupping season is shown in bold.

Date	Live pups
1973-74	
19 Jul 73	1
23 Aug 73	15
11 Sep 73	31
12 Nov 73	65
4 Feb 74	**118**
1975	
14 Jan 75	0[b]
19 Feb 75	3
21 Feb 75	7
24 Mar 75	19
21 Apr 75	13
24 Apr 75	25
30 Apr 75	53
24 Jun 75	77
2 Aug 75	**102**
15 Sep 75	99
5 Oct 75	99
5 Oct 75	95
6 Feb 76	88
1976-77	
28 Jul 76	12
17 Aug 76	16
28 Sep 76	83
6 Oct 76	96
27 Oct 76	142
– Nov 76	150
6 Feb 77	**156**
29 Apr 77	54
1978[a]	
20 Apr 78	**87**
1979-80	
20 Jun 79	3
4 Jul 79	8
8 Aug 79	20
1 Sep 79	76
26 Nov 79	**135**
15 May 80	76
1981	
– Apr 81	60
1 May 81	**109**
14 Aug 81	88
1982-83	
5 Jun 82	3
9 Jul 82	25
1 Sep 82	73
9 Oct 82	126
31 Oct 82	129
27 Nov 82	154
29 Nov 82	**185**
3 Jan 83	107
5 Feb 83	90
5 Mar 83	70
5 Apr 83	44
6 May 83	41
3 Jun 83	43
30 Jul 83	27
31 Aug 83	5
27 Sep 83	2
22 Oct 83	2

[a] The single count in 1978 pupping season was not used in the analyses (see text).

[b] Beginning of the pupping season was indicated by the observation of a dead brown pup.

Date	Live pups
1983-84	
17 Nov 83	2
9 Dec 83	7
31 Jan 84	15
23 Feb 84	67
28 Mar 84	102
19 May 84	86
12 Jun 84	**117**
12 Jul 84	72
22 Aug 84	80
6 Oct 84	77
30 Nov 84	78
27 Dec 84	63
30 Jan 85	85
27 Feb 85	48
1985	
26 Mar 85	1
30 Apr 85	0
31 May 85	10
28 Jun 85	19
23 Jul 85	54
30 Aug 85	92
29 Sep 85	142
31 Oct 85	**154**
30 Nov 85	126
31 Dec 86	108
25 Jan 86	101
28 Feb 86	84
26 Mar 86	81
30 Apr 86	55
30 May 86	58
30 Jun 86	33
30 Jul 86	45
29 Aug 86	35
1986-87	
30 Sep 86	0[b]
30 Oct 86	2
27 Nov 86	9
24 Dec 86	25
26 Jan 87	86
28 Feb 87	83
31 Mar 87	135
29 Apr 87	**166**
27 May 87	86
30 Jun 87	100
31 July 87	91
30-Aug-87	77
30-Sep-87	75
2-Nov-87	103
2-Dec-87	78
4-Jan-88	90
30-Jan-88	57
29-Feb-88	40
31 Mar 88	40
1988	
30 Apr 88	2
30 May 88	17
30 Jun 88	68
3 Aug 88	92
31 Aug 88	101
30 Sep 88	127
30 Oct 88	**136**
5 Dec 88	122
5 Jan 89	114
31 Jan 89	123
28 Feb 89	97
30 Mar 89	96
30 Apr 89	44
31 May 89	50

[b] Beginning of the pupping season was indicated by the observation of a dead brown pup.

Date	Live pups
1988 (cont.)	
29 Jun 89	37
1 Aug 89	58
1989-90	
2 Sep 89	14
2 Oct 89	13
31 Oct 89	12
30 Nov 89	51
31 Dec 89	81
31 Jan 90	135
23 Feb 90	**162**
28 Feb 90	141
30 Mar 90	144
30 Apr 90	97
5 Jun- 0	100
3 Jul 90	101
3 Aug 90	69
1 Sep 90	75
30 Sep 90	75
11 Nov 90	69
3 Dec 90	53
2 Jan 91	64
31 Jan 91	46
4 Mar 91	46
1991	
2 Apr 91	4
30 Apr 91	16
3 Jun 91	72
3 Jul 91	91
30 Jul 91	108
30 Aug 91	119
30 Sep 91	123
31 Oct 91	89
30 Nov 91	112
31 Dec 91	**128**

Date	Live pups
1991 (cont.)	
30 Jan 92	88
28 Feb 92	94
30 Mar 92	81
1992-93	
30 Aug 92	1
30 Sep 92	22
30 Oct 92	47
30 Nov 92	61
31 Dec 92	100
31 Jan 93	134
11 Mar 93	132
14 Apr 93	**153**
14 May 93	88
7 Jun 93	108
30 Jun 93	85
9 Aug 93	88
31 Aug 93	74
30 Sep 93	76
31 Oct 93	72
30 Nov 93	90
31 Dec 93	63
31 Jan 94	84
1994	
28 Feb 94	3
31 Mar 94	26
31 May 94	41
1 Jun 94	73
1 Aug 94	111
1 Sep 94	**124**
22 Oct 94	101
29 Nov 94	111
1 Dec 94	118
26 Jan 95	94
26 Feb 95	103

Date	Live pups
1994 (cont.)	
23 Mar 95	99
5 May 95	41
12 May 95	117
14 Jun 95	71
22 Jul 95	38
1995-96	
4 Sep 95	1
10 Oct 95	24
29 Nov 95	61
29 Dec 95	103
30 Jan 96	91
28 Feb 96	130
1 Apr 96	**145**
30 Apr 96	93
11 Jun 96	84
28 Jun 96	68
29-Jul-96	80
– Aug 96	79
26 Sep 96	84
27 Oct 96	76
28 Nov 96	67
29 Dec 96	63
24 Jan 97	55
1997	
28 Feb 97	4
24 Mar 97	17
28 Apr 97	63
30 May 97	110
29 Jun 97	140
30 Jul 97	139
25 Aug 97	**149**
30 Sep 97	119
1 Nov 97	133
26 Nov 97	107
1997 (cont.)	
29 Dec 97	100
23 Jan 98	102
23 Feb 98	106
30 Mar 98	94
2 May 98	77
27 May 98	48
30 Jun 98	42
1998-99	
3 Aug 98	0[b]
28 Aug 98	8
29 Sep 98	38
3 Nov 98	78
25 Nov 98	80
2 Jan 99	129
26 Jan 99	140
23 Feb 99	**148**
29 Mar 99	139
3 May 99	103
27 May 99	101
29 Jun 99	98
2 Aug 99	87
24 Aug 99	84
21 Sep 99	75
3 Nov 99	66
30 Nov 99	59
6 Jan 00	60
1 Feb 00	39
2000	
29 Feb 00	12
27 Mar 00	49
28 Apr 00	77
31 May 00	114
26 Jun 00	120
28 Jul 00	114

Date	Live pups
2000 (cont.)	
4 Sep 00	104
30 Oct 00	**135**
27 Nov 00	96
27 Dec 00	96
23 Jan 01	61
2 Mar 01	76
30 Mar 01	90
1 May 01	46
2 June 01	32
1 Jul 01	22
2001-02	
9 Jul 01	1
31 Jul 01	5
28 Aug 01	26
1 Oct 01	68
31 Oct 01	60
30 Nov 01	114
30 Dec 01	143
30 Jan 02	144
1 Mar 02	**147**
1 Apr 02	131
29 Apr 02	126
26 May 02	113
2 Jul 02	96
31 Jul 02	105
1 Sep 02	94
1 Oct 02	70
29 Oct 02	69
2002-03	
28 Nov 02	0[b]
20 Dec 02	1
18 Jan 03	2
26 Feb 03	35
27 Mar 03	67
2002-03 (cont.)	
24 Apr 03	90
28 May 03	**122**
25 Jun 03	114
30 Jul 03	102
28 Aug 03	106
28 Sep 03	103
31 Oct 03	85
26 Nov 03	74
31 Dec 03	67
30 Jan 04	63
26 Feb 04	76
29 Mar 04	64
29 Apr 04	42

[b] Beginning of the pupping season was indicated by the observation of a dead brown pup.

Mark-Recapture Estimates of Pup Production for the Australian Sea Lion (*Neophoca cinerea*) at Seal Bay Conservation Park, South Australia

Rebecca R. McIntosh
La Trobe University, Zoology Department, Sea Mammal Ecology Group, Melbourne, Victoria, Australia

Peter D. Shaughnessy
CSIRO Sustainable Ecosystems, Canberra, Australian Capital Territory, Australia

Simon D. Goldsworthy
South Australian Research and Development Institute (SARDI), Aquatic Sciences Centre, Adelaide, South Australia, Australia

Abstract

Australian sea lion *(Neophoca cinerea)* pup counts have been conducted at monthly intervals at Seal Bay Conservation Park, South Australia, since 1983. The protracted breeding season of the Australian sea lion causes difficulties for estimating pup production as simple counts of pups are likely to underestimate pup abundance. Here we describe the use of a mark-recapture technique, the modified Petersen estimate, to estimate the total number of sea lion pups produced at Seal Bay by the end of the breeding season in late June 2003. Our aims were to compare the estimate of pup numbers from direct counting with that from mark-recapture, and evaluate methods used to estimate pup abundance at the end of the pupping season. Pups ($n = 74$) were marked over a four month period by clipping the hair on the rump. Pups were also given individually identifying microchips (23 mm TIRIS™ RFID) that were inserted subcutaneously. These identifying microchips were used to test for unequal catchability and estimate the number of marked pups in the population at the time of the mark-recapture ($n = 74$). The mark-recapture was conducted after peak pup production in the seventh month of the breeding season. The best estimate of the number of sea lion pups in the Seal Bay colony was 230 (95% CI 203-257). These incorporate the mark-recapture estimates. In their absence, the estimate from direct counting of pups in the whole colony was 163 (95% CI 147-179). Thus the mark-recapture estimate was 187% of the direct count (95% CI 173-201), highlighting that pup counts underestimate pup production at Seal Bay Conservation Park.

Introduction

Seal Bay on the south coast of Kangaroo Island, South Australia, is one of the largest breeding colonies of the Australian sea lion, *Neophoca cinerea*. During 1990, a survey through the species' range ranked Seal Bay the fourth largest colony with an estimated 180 pups (Gales et al. 1994). Sea lions at Seal Bay are the major attraction for visitors to Kangaroo Island, where tourism has become an important income generator for the island (Twyford and Vickery 2001).

During the breeding season, pups have been counted at monthly intervals since 1983. The usual method for determining abundance of Australian sea lions is for two or three observers to walk through a colony searching for and counting pups and, in some instances, animals of other age and sex classes. Observers travel in a survey line, tallying pups as they move through the colony, resulting in a single count of pups for each monthly survey. The number of pups is the preferred index of abundance because pups are easily recognizable and most of the pups are ashore at one time. Long-term pup counts are a valuable tool for wildlife management and research as they are considered to be reliable indicators of population change when used in conjunction with life history information (Berkson and DeMaster 1985).

Simple counts of pups are likely to underestimate pup abundance because some pups ashore will be in places such as rock holes or under bushes where they are likely to be overlooked (Shaughnessy et al. 1995, Shaughnessy and Dennis 1999). Australian sea lion populations are notoriously difficult to census because of their unusual reproductive strategy that includes an aseasonal (average of 17.6 month) breeding cycle and a protracted (five to seven month) breeding season (Ling and Walker 1976, 1978; Higgins 1993). The extended breeding season of the Australian sea lion further increases the likelihood of underestimating pup production, as pups born earlier in the breeding season may be up to seven months old, molted and actively mobile, while newborn pups are still being produced in the colony.

By using a mark-recapture approach to estimate abundance of pups, problems with overlooking pups that are ashore can be addressed, reducing sightability bias in the estimate. Additionally, the mark-recapture method enables the variance or error around the mean number of pups to be estimated, which cannot be obtained from a single count. Observation error and variance can be calculated from direct counts if counts are made by several observers or if replicate counts are made. But such counts do not address sightability biases as effectively as a mark-recapture model that compares proportions of marked and unmarked individuals.

Mark-recapture methods have been applied successfully to estimate population parameters (e.g., Cormack 1964, Jolly 1965, Lebreton et al. 1992, Nichols 1992, Cameron and Siniff 2004), and as an effective method of estimating pup production in seal populations (e.g., Chapman and Johnson 1968, York and Kozloff 1987, Ries et al. 1998). In mark-recapture studies of Australian otariid species, surveys generally estimate the number of live pups found in the colony at the time of the mark recapture using the Petersen formula or its modification (Shaughnessy et al. 1995, Shaughnessy et al. 2000), adding the number or percentage of dead pups identified at the time of the survey to this estimate when such data are available (Pemberton and Kirkwood 1994, Shaughnessy and Dennis 1999, Shaughnessy et al. 2002, Shaughnessy and McKeown 2002).

There are four basic assumptions for Petersen mark-recapture estimates: (i) every animal, marked and unmarked, must have the same probability of capture and recapture; (ii) every animal must have the same probability of mortality or of leaving the sampling area for the duration of the experiment; (iii) marks must not be lost and must be correctly reported; and (iv) no animal is born or immigrates to the study area between marking and recapturing (Caughley 1977, Seber 1982). These assumptions are often difficult to reconcile for mark-recapture experiments in wild populations (Caughley 1977).

Movement of pups out of the colony is not a problem for mark-recapture estimates provided the rate of movement is equal for marked and unmarked individuals (Caughley 1977). Repeated counts and simple mark-recapture models provide an estimate of the number of pups that are in a colony at the time of the recaptures, but do not account for the number of pups that may have moved out of the colony between marking and recapture periods (Caughley 1977). There can therefore be an availability bias in mark-recapture estimates, where not all the marked pups are available at the time of the estimate and total pup production cannot be calculated.

Applying an individual identification, such as numbered tags, to marked pups is not necessary for a simple mark-recapture model. However, in order to test the assumptions of a mark-recapture study, and to evaluate the level of availability bias in marked pups, such information is necessary (Leslie and Chitty 1951, Orians and Leslie 1958). In this study, pups were physically marked by clipping the fur of the rump and also by implanting subcutaneous microchips (TIRIS™ RFID 23 mm passive transponders). These microchips provide an individual number for each marked pup and allow frequency of recapture to be analyzed to test for unequal catchability (zero-truncated Poisson model [Darroch 1958, Orians and Leslie 1958, Caughley 1977]) and the number of marked pups in the population at the time of the mark-recapture to be estimated (modified Petersen estimate).

Recent surveys of pup production at Seal Bay suggest that visual counts underestimate pup production, because of the propensity of animals that are obscured or absent from the colony on the day of the survey. In November 2001, during one of the monthly counts of animals in the colony only 23 of the 53 live pups (43%) that had been marked with fore-flipper tags were located (D. Dowie, Department for the Environment and Heritage, South Australia, 2001, pers. comm.). Furthermore, in July 1999 a mark-recapture trial undertaken on the population of Australian sea lions at Dangerous Reef (Shaughnessy and Dennis 1999) showed that pup production estimates based on the mark-recapture estimation procedure were 19% larger than those derived from direct counting.

Here we describe the use of a mark-recapture technique to estimate the number of Australian sea lion pups produced at Seal Bay at the end of the breeding season in late June 2003. Our aims were to compare the estimate of pup numbers from direct counting with that from mark-recapture, and evaluate methods used to estimate pup abundance at the end of the pupping season.

Methods

Seal Bay colony

Seal Bay Conservation Park (35º41'S, 136º53'E) is situated on the southern coast of Kangaroo Island in South Australia (Fig. 1). The sea lion colony at Seal Bay comprises five areas (Fig. 2) that are referred to as Pup Cove (2 km from the visitor center), the Western Prohibited Area (WPA), Main Beach, sand dunes and swales inland from Main Beach, and the Eastern Prohibited Area (EPA). The sand dune area inland from Main Beach and the EPA beach is vegetated with grey saltbush (*Atriplex cinerea)* while the swales and inland area behind the saltbush are vegetated with the low-lying Bower spinach (*Tetragonia implexicoma*) and coast velvet bush (*Laisiopetalum discolor*). Limestone promontories separate the WPA and EPA from Main Beach. The colony extends along the coast for 7 km. Most pups are born at Pup Cove and in the WPA; smaller numbers of pups are born to the east of Main Beach in the EPA, at the western end of Main Beach and inland from the WPA and Main Beach.

Mark-recapture procedure

Pups from the 2002/03 breeding season were born over a six month period commencing in late November 2002 and were marked over a four month period by clipping a strip of hair across their rump almost

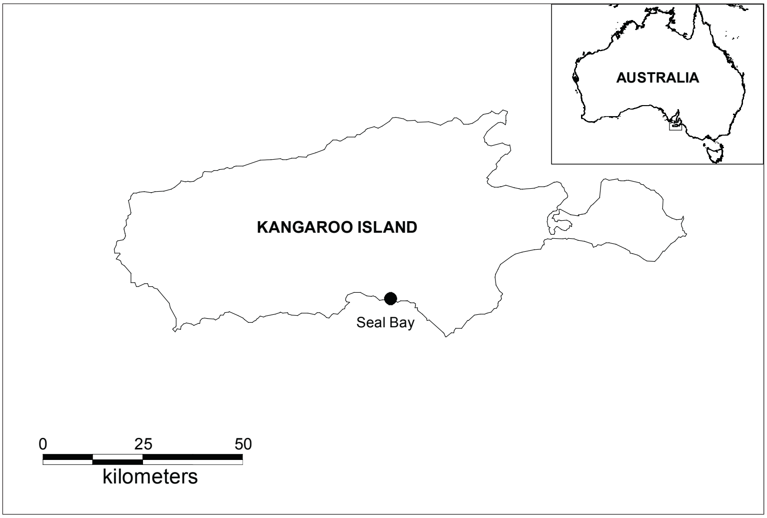


Figure 1. Map of Kangaroo Island, South Australia, showing the location of Seal Bay Conservation Park.

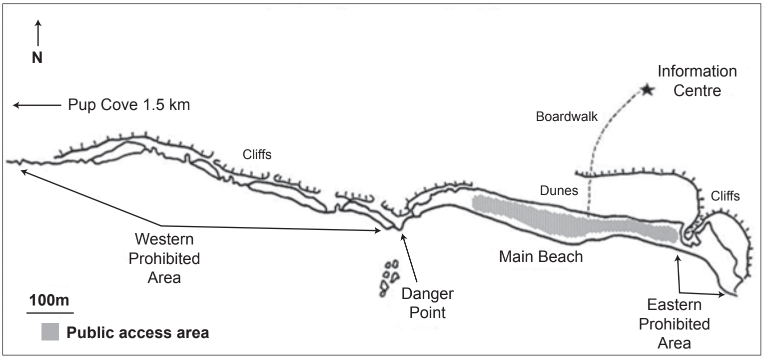


Figure 2. Map of Seal Bay Conservation Park showing the main features of the breeding colony.

down to skin level. A microchip was inserted subcutaneously in the pup's rump, which provided it with an individual identification number. To successfully identify a pup, an RFID reader was held at a distance of up to 10 cm from the site where the microchip was inserted. No handling of the pups was required after initial marking. Criteria for choosing pups to be marked were that they were a minimum of two months old, were not accompanied by an adult female, and that little disturbance would result from their initial capture. By 24 June 2003, when the mark-recapture study commenced, seventy-four pups had been marked in this manner. Pups were marked in the WPA, on Main Beach, and in the nearby dunes. Due to steep limestone cliffs that made access difficult, pups were not marked in Pup Cove. Marked pups were not seen in Pup Cove at any time during the breeding season. Permit limitations prevented the marking of pups in the EPA. Pups that ventured from the EPA to Main Beach were marked, and marked pups were seen frequently in the EPA.

The three recapture sessions were conducted on 25, 26, and 27 June 2003, in the WPA, on Main Beach, and inland from these areas (where pups had been marked). Each recapture session required a full day due to the large area to be covered. In addition, recapture sessions extended into the EPA because pups and their mothers are known to move eastward in the Seal Bay colony during the pupping season (Higgins and Gass 1993). All areas of the colony except Pup Cove made up the mark-recapture area. Numbers of pups in Pup Cove were estimated by direct counting from the cliff-tops on three occasions.

Recaptures (essentially “re-sights”) were conducted visually, without handling the pups, by one to three people working separately in allocated areas of the colony. At least 35 marked pups required recapturing to provide an unbiased estimate with a standard error of 10% or lower of the Petersen estimate (Caughley 1977) assuming a total pup population of 180 pups (Gales et al. 1994). All marked pups that were located were scanned with a microchip reader so that their identity could be established. That information was used to estimate the number of marked pups present in the study population.

Classification of pups

Four groups of pups were recognized, as follows.

1. *Marked pups*: identified by a clipped strip of hair across the rump as noted above. Very few pups were fully molted at the time of the mark-recapture study. A few pups had completed their molt. If they had been marked, the clipped area would no longer have been visible. Therefore all molted pups were scanned and identified as “marked” if a microchip was recorded.

2. *Dead pups*: counted as they were found, and a cumulative record of the number of dead pups was maintained during the pupping season. Dead pups were either removed from the colony for further analysis, or marked with quick-drying paint when they were found to avoid recounting.

3. *Unclassed pups*: un-molted and molted pups that were seen but the

presence or absence of a mark could not be confirmed due to their swimming in shallows near the shore. Unclassed pups were not included in the estimate for pup production.

4. *Pups outside the mark-recapture area*: pups within Pup Cove that were not marked due to its inaccessibility.

Mark-recapture methodology

The modified Petersen formula (Seber 1982) as outlined in Shaughnessy et al. (1995) was used as the basis for the mark-recapture design. The pupping season of the Australian sea lion is of 5-7 months duration and pups were marked over four months leading up to the mark-recapture survey. Therefore some pups may have dispersed with their mothers before the mark-recapture project was conducted. In order to satisfy this assumption, the number of marked pups within the mark-recapture area available for recapture was estimated.

Pups were marked in equal proportions throughout the colony, except for the EPA due to permit limitations. It is most important that marks are not lost. Identification of the clipped mark was reliable until well after the

Table 1. Estimates of the number of Australian sea lion pups at Seal Bay, Kangaroo Island, in June 2003 from three mark-recapture sessions.

	Mark-recapture session		
	1	2	3
Date of recapture session	25 June	26 June	27 June
M (number of marked pups in the study population)	74	74	74
n_1 (number of live pups seen)	69	81	81
m_1 (number of marked pups seen)	39	41	38
N (pup population estimate for the mark-recapture study population)	130.2	145.4	156.7
Standard deviation	9.2	10.3	12.5
Dead pups	70	70	70
Unclassed pups	2	7	0
Pup Cove (direct count)	15	19	15
Best estimate for whole colony, including the mark-recapture estimate	215.2	234.4	241.7
Direct count for whole colony	154	170	166

mark-recapture study was completed. These marks were visible even in pups that were molting. The microchip implanted under the skin enabled all marked pups to be individually identified in order to estimate the number of marked pups in the colony at the time of the mark-recapture. Molted pups were identified as marked by the presence of a microchip; if no microchip was present they were identified as unmarked. There were few molted pups in the population, and the only unclassed pups were those swimming in the shallows (Table 1).

Unequal probability of recapture was tested for by analyzing the recapture frequency of microchipped, known-identity pups. A truncated Poisson distribution was first fitted to the observed frequencies of identified individuals over the three sampling days and then the model was tested for goodness of fit using the χ^2 distribution (Darroch 1958, Orians and Leslie 1958, Caughley 1977), given that each individual identified over the three days of the sampling period had the opportunity to be identified 1, 2, or 3 times. A significant result of this test was interpreted as unequal catchability; a nonsignificant result indicated that unequal catchability could not be demonstrated (Roff 1973).

The modified Petersen estimate was used as the basis of the mark-recapture design. The total number of pups in the mark-recapture study population (N) was estimated by

$$N = \left\{\left[(M+1)(n_1+1)\right]/(m_1+1)\right\} - 1. \tag{1}$$

Where

M = number of marked pups in the population

n_1 = number of live pups seen, including marked pups

m_1 = number of marked pups seen.

The variance of this estimate was calculated from

$$\frac{(M+1)(n_1+1)(M-m_1)(n_1-m_1)}{(m_1+1)^2(m_1+2)} \tag{2}$$

The variance of the mean ($\hat{N}$) of several recapture estimates of the colony ($\hat{N}_j$) was calculated from

$$\text{Var }\hat{N} = \frac{1}{q^2}\sum_{j=1}^{q}\text{Var }(\hat{N}_j) \tag{3}$$

where q was the number of recapture sessions. The standard deviation of the mean was calculated from

$$\left[\text{Var }(N)\right]^{1/2} \tag{4}$$

As some pups may have dispersed from the colony or died, the number of marked pups remaining in the study population at the time of survey (M) was estimated by M_1 by examining a sub-sample of microchipped pups over two consecutive days (day 1 and day 2).

The number of marked pups in the study population was calculated from

$$M_1 = \{[(M_2 + 1)(n_2 + 1)] / (m_2 + 1)\} - 1 \qquad (5)$$

where

M_2 = number of individual marked pups identified on day 1, the day before a recapture session

n_2 = number of marked pups identified at a recapture session (day 2)

m_2 = number of individual marked pups re-identified at a recapture session (i.e., identified on day 1 and again on day 2).

The best estimate of pup production is obtained from the following summation:

$$\text{Best estimate} = N + \text{Dead pup count} + \text{Pup count for Pup Cove.} \qquad (6)$$

An estimate of pup numbers based on direct counting using the same data set is obtained from:

$$\begin{aligned}\text{Direct count} = n_1 &+ \text{Unclassed pup count} + \text{Dead pup count}\\ &+ \text{Pup count for Pup Cove.}\end{aligned} \qquad (7)$$

The 95% confidence interval (CI) of the estimated pup numbers were calculated with the estimate ± (1.96 × s.d.).

Results

Equal catchability

Unequal catchability could not be demonstrated for marked pups ($\chi^2 = 2.21$, d.f. = 1, $P > 0.10$) (Table 2). This indicated that the marked pups identified over the three days of the census were randomly recaptured, allowing the assumption of equal catchability to be accepted.

Number of marked pups in the study population

Marked pups were found in all parts of the Seal Bay colony that had been designated as the mark-recapture study area, namely the WPA, Main Beach, nearby dunes, and the EPA. The number of marked pups in the study population was estimated, using data from the marked pups on three consecutive days (Table 3) that gave estimates of 57 (s.d. = 12.9) and 73 (s.d. = 12.2) marked pups. The variation between the estimates may have two explanations: observer bias on 25 June, or fewer pups

Table 2. Observed and expected frequencies of resights of microchipped Australian sea lion pups over three consecutive days based on uniform catchability of pups and a truncated Poisson distribution.

Number of times captured i	Number of individuals f	Expected frequencies $E(f)$	$\frac{[f-E(f)]^2}{E(f)}$
1	27	30.653	0.435
2	18	13.426	1.558
3	3	3.920	0.216
	$\sum f = 48$		$\chi^2 = 2.210$
			d.f. = 1
			$P > 0.10$

available for identification on 25 June. A greater number of microchipped pups was identified on the second and third day of the survey (Table 3). As pups not identified on the first day, but identified on the second and third day must have been alive on the first day of the survey, the estimate of 73 pups was considered a more likely result. It was therefore concluded that all 74 marked pups were available in the colony at the time of the mark-recapture.

No marked pups were found dead in the colony by 27 June (date of third census). After two months of age, pups are better able to defend themselves and as a consequence suffer lower mortality rates compared to younger pups (Higgins and Tedman 1990). Given that pups in this study were marked after two months of age, it has been assumed that mortality of marked and unmarked pups from 2 to 7 months of age was equal and therefore unequal mortality would not violate the assumptions of mark-recapture. It was also assumed that no pups died over the three days of the surveys.

Number of pups in the study population

For the mark-recapture estimation procedure, it was assumed that all of the marked pups were available for recapturing (as discussed above), and M was set at 74. Data are available for three recapture sessions (Table 1). Estimates of the number of pups in the study area (N) ranged from 130 to 157, with mean 144.1 and standard deviation 6.2 (95 % CI 132-156). No births were observed during the recapture sessions.

Table 3. Estimate of the number of marked Australian sea lion pups in the mark-recapture study population at Seal Bay, Kangaroo Island, in June 2003 from three consecutive days of resights involving only marked microchipped pups.

	Date	
	25 and 26 June	26 and 27 June
Number of observers identifying microchips	1	2
M_2, number of marked pups identified on day 1	14	26
n_2, number of marked pups identified on day 2	26	32
m_2, number of individual marked pups identified on day 1 and day 2	6	11
M_1, number of marked pups in the study population	57	73
Standard deviation	12.9	12.2

Estimate of pup numbers at Seal Bay in June 2003

The best estimates of the number of sea lion pups in the Seal Bay colony in late June 2003 ranged from 215 to 242 (Table 1), with mean 230 and standard deviation 13.7 (95% CI 203-257). In contrast, the estimates based on direct counting of pups in the whole colony ranged from 154 to 170, with mean 163 and standard deviation 8.3 (95% CI 147-179). On average, the estimates based on the mark-recapture (N) were 1.87 times that of those based on direct counting methods (n_1) (s.d. = 7.2, 95% CI 173-201).

Discussion

Satisfying mark-recapture assumptions

Several assumptions are made in estimating population size by the mark-recapture technique (Seber 1982). Pertinent ones are reviewed here for estimates of abundance of Australian sea lion pups at Seal Bay.

Migration

Marks were applied over a period of four months prior to the mark-recapture survey. A potential problem is that some pups may have left the colony prior to the recapture sessions. This seems unlikely because we estimated that all marked pups were still in the colony at the time of the mark-recapture estimate. These results indicate that little or no emigration of pups had taken place prior to the mark-recapture estimates, seven months after the commencement of the breeding season.

Reliability of marks

No problems were experienced in recognizing the marks on pups that were ashore, even on pups that were molting and few fully molted pups were observed. Several pups were swimming and it was not possible to determine whether or not they were marked; they were categorized as "Unclassed." Fortunately there were few of them and they would have little effect on the comparison between the estimates from direct counting and from mark-recapture.

Probability of recapture

The probability of marking and recapturing pups should be identical in a mark-recapture. The test of unequal catchability demonstrated that it was fair to assume equal catchability throughout the survey area. Pups were marked in the WPA, on Main Beach, and in the dunes behind these areas. Recapture sessions were conducted in these areas and in the EPA. Several marked pups were recorded in the EPA; that and previous evidence that adult females and their pups generally move eastwards within the colony and that some of them move into the EPA (Higgins and Gass 1993) gave us confidence that marked and unmarked pups had mixed sufficiently within the mark-recapture study area. It is recognized that adequate mixing of marked and un-marked pups does not suffice to accept the assumption that pups are marked evenly throughout the mark-recapture area (Caughley 1977). In order to accept this assumption, the permit limitations at this study site must be addressed for future mark-recapture experiments in order include marking pups in the EPA.

Timing of mark-recapture estimation

The mark-recapture estimates reported here were made in June 2003, seven months after pupping began, when approximately half of the pups in the mark-recapture study area were marked. Based on direct counts of pups in the colony, maximum numbers of pups were observed in late May and it would have been preferable to have made the mark-recapture estimation then. An aim in future seasons should be to mark half of the pups by the fifth month of the season and then perform the mark-recapture estimate.

Comparison of estimates by direct counting and mark-recapture

If the number of live pups in the mark-recapture study area had been estimated by direct counting on the three days from 25 to 27 June, the estimates would have been 69, 81, and 81, respectively, which are the values for n_1 in Table 1. Thus the mark-recapture estimates were 189%, 179%, and 193% of the direct counts for these days, with an average of 187% and standard deviation 7.2 (95% CI 173-201). This is much greater than the difference obtained for this species at Dangerous Reef colony in 1999, where the mark-recapture estimate was 119% of the direct count (Shaughnessy and Dennis 1999). Such a difference is not unexpected because the terrain at Dangerous Reef is more open (with no bushes) than at Seal Bay, and hence fewer pups are likely to be overlooked by direct counting at Dangerous Reef.

The results of this study indicate that estimates of abundance of Australian sea lion pups are biased downward to varying extents. We suspect that the underestimate for small colonies of the Australian sea lion, especially those on rocky islands, are much smaller than indicated here for Seal Bay, where pups are easier to locate.

Conclusion

This is the first mark-recapture study to estimate pup production numbers of Australian sea lions at Seal Bay Conservation Park. The resulting best estimate of 230 pups represents the sum of the estimated number of pups alive in the colony at the end of the breeding season and the cumulative number of dead pups. This estimate is 187% of the mean pup count, suggesting that historic pup count data at this site are biased downward to a large extent, primarily due to the difficulty of finding pups in direct counts. This estimate is also greater than the previous estimate of pup production at Seal Bay (Gales et al. 1994) of 180 pups.

Due to the inability to access Pup Cove and the inability to mark pups in the EPA, the pup production mark-recapture estimate in this study is also likely to be biased downward. Even so, the pup production estimate in this study is a better estimate of total pup production than those derived from simple pup counts, as it was established that there was no emigration of marked pups from the survey site. The counting of newborn pups may provide a good way of estimating pup production in a breeding colony where 230 pups may be born. This method is not ideal as it is very laborious over the lengthy sea lion breeding season and is not currently possible due to restrictions on access to the EPA and Pup Cove. With further investigation, application of a mark-recapture method that best suits this population will be developed to monitor pup production more accurately.

Acknowledgments

We thank Mel Berris and the staff of Seal Bay Conservation Park and Kangaroo Island Department for the Environment and Heritage (DEH) for logistic and field support and all the research volunteers for their assistance, particularly Clarence Kennedy, Jason Nicholls, Kiera Perrott, and Georgie Schotter. This research was supported by Sea World Research and Rescue Foundation Incorporated, the South Australian DEH, PADI Asia Pacific, Kangaroo Island Sealink, Kangaroo Island Central Hostel, and Ms. R. Gray. We thank the Australian Marine Science Association for awarding R. McIntosh the International Student Prize and the Alaska Sea Grant College Program for conference support. R. McIntosh received the La Trobe University Postgraduate Award to conduct this project. All work was conducted under DEH permit number Z24347, ethics approval number AEC00/42(L).

References

Berkson, J.M., and D.P. DeMaster. 1985. Use of pup counts in indexing population changes in pinnipeds. Can. J. Fish. Aquat. Sci. 42:873-879.

Cameron, M.F., and D.B. Siniff. 2004. Age-specific survival, abundance, and immigration rates of a Weddell seal (*Leptonychotes weddellii*) population in McMurdo Sound, Antarctica. Can. J. Zool. 82:601-615.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, Chichester.

Chapman, D.G., and A.M. Johnson. 1968. Estimation of fur seal pup populations by randomized sampling. Trans. Am. Fish. Soc. 97:264-270.

Cormack, R.M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51:429-438.

Darroch, J.N. 1958. The multiple recapture census. I. Estimation of a closed population. Biometrika 45:343-359.

Gales, N.J., P.D. Shaughnessy, and T.E. Dennis. 1994. Distribution, abundance and breeding cycle of the Australian sea lion *Neophoca cinerea* (Mammalia: Pinnipedia). J. Zool. Lond. 234:353-370.

Higgins, L.V. 1993. The nonannual, nonseasonal breeding cycle of the Australian sea lion, *Neophoca cinerea*. J. Mammal. 74:270-274.

Higgins, L.V., and L. Gass. 1993. Birth to weaning: Parturition, duration of lactation, and attendance cycles of Australian sea lions (*Neophoca cinerea*). Can. J. Zool. 71:2047-2055.

Higgins, L.V., and R.A. Tedman. 1990. Effect of attacks by male Australian sea lions, *Neophoca cinerea*, on mortality of pups. J. Mammal. 71:617-619.

Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225-247.

Lebreton, J.D., K.P. Burnham, J. Clobert, and D.R. Anderson. 1992. Modelling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecol. Monogr. 62:67-118.

Leslie, P.H., and D. Chitty. 1951. The estimation of population parameters from data obtained by means of the capture-recapture method. I. The maximum-likelihood equations for estimating death-rate. Biometrika 38:269-292.

Ling, J.K., and G.E. Walker. 1976. Seal studies in South Australia: Progress report for the year 1975. S. Aust. Nat. 50:59-68, 72.

Ling, J.K., and G.E. Walker. 1978. An 18-month breeding cycle in the Australian sea lion? Search 9:464-465.

Nichols, J.D. 1992. Capture-recapture models: Using marked animals to study population dynamics. BioScience 42:94-102.

Orians, G.H., and P.H. Leslie. 1958. A capture-recapture analysis of a shearwater population. J. Anim. Ecol. 27:71-86.

Pemberton, D., and R.J. Kirkwood. 1994. Pup production and distribution of the Australian fur seal, *Arctocephalus pusillus doriferus*, in Tasmania. Wildl. Res. 21:341-352.

Ries, E.H., L.R. Hiby, and P.J.H. Reijnders. 1998. Maximum likelihood population size estimation of harbour seals in the Dutch Wadden Sea based on a mark-recapture experiment. J. Appl. Ecol. 35:332-339.

Roff, D.A. 1973. An examination of some statistical tests used in the analysis of mark-recapture data. Oecologia 12:35-54.

Seber, G.A.F. 1982. The estimation of animal abundance and related parameters. MacMillan, New York.

Shaughnessy, P.D., and T. Dennis. 1999. Seal research in South Australia, 1998/1999: Abundance of New Zealand fur seal pups on Kangaroo Island and Australian sea lion pups at Dangerous Reef. Report to South Australian National Parks and Wildlife, Department of Environment, Heritage and Aboriginal Affairs. 39 pp.

Shaughnessy, P.D., and A. McKeown. 2002. Trends in abundance of New Zealand fur seals, *Arctocephalus forsteri*, at the Neptune Islands, South Australia. Wildl. Res. 29:363-370.

Shaughnessy, P.D., S.D. Goldsworthy, and J.A. Libke. 1995. Changes in abundance of New Zealand fur seals, *Arctocephalus forsteri*, on Kangaroo Island, South Australia. Wildl. Res. 22:201-215.

Shaughnessy, P.D., R.J. Kirkwood, and R.M. Warneke. 2002. Australian fur seals, *Arctocephalus pusillus doriferus*: Pup numbers at Lady Julia Percy Island, Victoria, and a synthesis of the species' population status. Wildl. Res. 29:185-192.

Shaughnessy, P.D., S.K. Troy, R. Kirkwood, and A.O. Nicholls. 2000. Australian fur seals at Seal Rocks, Victoria: Pup abundance by mark-recapture estimation shows continued increase. Wildl. Res. 27:629-633.

Twyford, K., and F. Vickery. 2001. User-pays fees and regional development on Kangaroo Island. In: G. Worboys, M. Lockwood, and T. De Lacy (eds.), Protected area management principles and practices. Oxford University Press, South Melbourne, p. 175.

York, A., and P. Kozloff. 1987. On the estimation of numbers of northern fur seal, *Callorhinus ursinus*, pups born at St. Paul Island, 1980-86. Fish. Bull. U.S. 85:367-375.

Population Status and Trends of the California Sea Lion (*Zalophus californianus californianus*) in the Gulf of California, Mexico

Diana Szteren and David Aurioles
Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, La Paz, B.C.S., México

Leah R. Gerber
Department of Biology, Arizona State University, Tempe, Arizona

Abstract

California sea lions breed along the Pacific Coast of the United States, south to Baja California, Mexico, and throughout the Gulf of California. Although the population in the United States has been increasing over the last 15 years, the status of the population in the Gulf of California is unknown. The last published census in 1994 yielded an estimate of 31,393 animals, but some rookeries have subsequently declined in abundance. The aim of this study is to provide a new estimate of population size for California sea lions in the Gulf of California and to examine the relative risk of extinction among thirteen sites using census data from 1970-2004. Our initial population estimate for 2004 is 17,484 including 4,299 pups, and the total number of sea lions when correction factors were applied was between 24,062 and 31,159. Four of the thirteen rookeries exhibited increasing trends: the two northernmost islands (Consag and San Jorge), the southernmost island (Los Islotes), and San Esteban in the Central Gulf. The remaining rookeries were either stable or declining in abundance. In our analysis of total population and pup production trends, we identified a group of sea lion rookeries that are growing in total numbers and pup production, and exhibit low probability of extinction. Another group shows total abundances decreasing, pup production declining, negative population growth, and a high probability of extinction. Finally, a third group of rookeries exhibit high fluctuations in abundance and no clear population trend. Rookeries with maximum probability of extinction and declining trends are situated at or near Angel de la Guarda Island (Central Gulf). We discuss several possible causes of these declines, including the influence of sardine in the diet of sea lions.

Introduction

By virtue of their large size, morphology, and physiology, marine mammals have been targeted in both commercial and subsistence exploitation. California sea lions (*Zalophus californianus californianus*) have been exploited for centuries in the Gulf of California (Zavala and Mellink 2000), and small-scale poaching still occurs to this day. The extent to which sea lions have recovered from past exploitation, and the demographic consequences of this exploitation, are not well understood. Nonetheless, California sea lions are the most abundant pinniped, and have the broadest distribution of any pinniped, in Mexico.

California sea lions range throughout temperate and subtropical waters off the western coast of North America, from southern Canada to the south of Mexico, including the Gulf of California (Lowry et al. 1992). Breeding areas are located in three geographic regions which are considered different stocks: (1) the U.S. stock that extends from Canada to the U.S.-Mexico border, (2) the western Baja California stock, from the U.S.-Mexico border to the southern tip of the Baja California Peninsula, and (3) the Gulf of California stock (Carretta et al. 2003). In 1983 the global population included 145,000 animals (Le Boeuf et al. 1983), but in 2002 only the U.S. population was estimated at 237,000 to 244,000 animals, representing a recent growth of 5.4% to 6.1% per year (Carretta et al. 2003). The Gulf of California population of California sea lions comprises thirteen rookeries and sixteen haul-out sites (Aurioles-Gamboa and Zavala-González 1994; Fig. 1). In 1983, approximately 16% of Mexico's 90,000 animals were estimated to occur in the Gulf of California (Le Boeuf et al. 1983). The population was estimated to include 25,354 animals in 1988 (Aurioles Gamboa 1988) and 31,393 animals by 1993 (Aurioles-Gamboa and Zavala-González 1994). Adult females were the dominant age class (40.7%) in this latter estimate.

Maldonado et al. (1995) reported genetic differences between the U.S. stock and the Gulf of California stock. Animals from the central Gulf of California had a unique control region in their mitochondrial DNA, which was not found in individuals of the Pacific Coast. By means of a molecular variance analysis (AMOVA), Schramm (2002) found that the sea lion population was structured in four well-defined groups: (1) Pacific group (which includes the rookeries at Coronados Island, Benitos Islands, Cedros Island, Asunción, and Santa Margarita); (2) Southern Gulf (Los Islotes), (3) Central Gulf (which comprises the rookeries of San Esteban, Los Cantiles, Isla Granito, and Isla Lobos); and (4) Northern Gulf (which

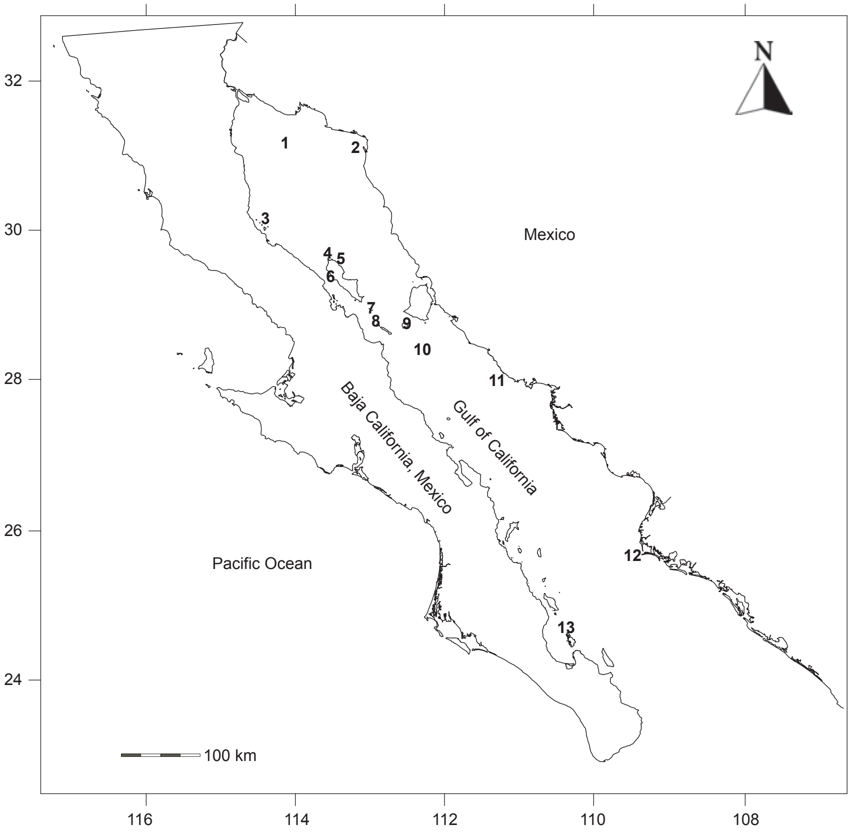


Figure 1. Location of sea lion rookeries on the Gulf of California, Mexico. Rookeries: 1. R. Consag, 2. San Jorge, 3. Isla Lobos, 4. Isla Granito, 5. Los Cantiles, 6. Los Machos, 7. El Partido, 8. Rasito, 9. San Esteban, 10. San Pedro Mártir, 11. San Pedro Nolasco, 12. Farallón de San Ignacio, 13. Los Islotes.

includes San Jorge island). Genetic diversity was highest in the Northern Gulf, and lowest in the Pacific, with an intermediate level of diversity in the Central Gulf. Based on these results, Schramm (2002) suggests that these four groups be considered as separate management units in conservation plans.

In light of these factors, an evaluation of the status of California sea lions in the Gulf of California is urgently needed. Quantitative analyses of population trends may also be applied to conservation decisions (Gerber and Van Blaricom 2001). The main goal of this paper was to describe and analyze the population trend of the breeding rookeries of the Gulf of California using census databases to evaluate population status, and pup production of each rookery, as a measure of reproductive success. We summarize 25 years of abundance data for sea lions in the Gulf of California and provide an assessment of population status. We also analyze sea lion population viability for the thirteen sea lion rookeries throughout the Gulf of California and discuss implications for conservation and management. Finally, we discuss the likely fate of this population in face of increasing anthropogenic impacts.

Methods

Historical census data of *Z. californianus californianus* in the Gulf of California were compiled for sea lion rookeries throughout the gulf from 1976 to 2004 (Table 1). Censuses were done during the breeding season (within the first 2 weeks of July). In this period most of the population is found ashore, and almost all pups have already being born (Garcia-Aguilar and Aurioles-Gamboa 2003), while pup mortality has not caused significant decrease in pup numbers (Aurioles and Sinsel 1988). Due to geographical constraints, only one census was performed at each site. Counts were conducted using binoculars and from a boat circumnavigating each island at a distance of 40 meters (Le Boeuf et al. 1983, Aurioles-Gamboa and Zavala-González 1994). We calculated the total population size in the Gulf of California as the sum of the most recent count data for each site (Table 1). These data were compared with the last published census year by Aurioles-Gamboa and Zavala-González (1994) for each rookery.

We applied correction factors for both pups and adults to empirical census data. Le Boeuf et al. (1983) found that the number of pups counted on rocky and pebble beaches was 50% higher in abundance than the counts made from a boat; because all the rookeries in the gulf have a large proportion of this type of terrain, we did not calculate specific pup estimates relative the extension of rocky beach at each rookery. Thus, we augmented our boat-based counts by 50% to account for the number of pups that cannot be seen from a boat at all the sites (Le Boeuf et al. 1983). Also the number of adult females was corrected to account for the number of females that are feeding at sea when the censuses are made. Bonnell and Ford (1987) suggested two correction factors: 23% and 54%, the first one for the first weeks of the breeding season, and the second for the last weeks. These values were estimated in California (USA). Because the pupping season is different in the Gulf of California (García-Aguilar and Aurioles-Gamboa 2003), we used both numbers to incorporate the full range of uncertainty in these correction factors.

We also calculated the fecundity for the last year of data at each rookery. This variable assesses the percentage of females that have a pup, and was calculated as the number of pups divided by the total number of females. We calculated values for both non-corrected fecundity (using

Table 1. Number of pups and total population counted at each sea lion rookery of the Gulf of California in the last census year, and percentage of increase or decline of each rookery since the Aurioles-Gamboa and Zavala-González (1994) report.

Rookery, year last census	Pups	Total	% increase or decline (year)	NCfec	Afec 23%	Afec 54%
R. Consag 2002	140	600	42.5 (1981)	55.3	85.2	50.9
San Jorge 2004	968	3,833	12.3 (1985)	55.5	85.4	51.0
Isla Lobos 2004	195	1,950	–37.4 (1984)	15.5	23.9	14.3
Isla Granito 2004	246	848	–49.0 (1991)	70.9	100[a]	65.2
Los Cantiles 2004	144	634	–51.6 (1991)	48.5	74.7	44.6
Los Machos 2004	102	580	–61.5 (1990)	31.3	48.2	28.8
El Partido 2004	82	449	–50.8 (1991)	35.5	54.7	32.7
El Rasito 2004	55	375	–12.8 (1991)	25.3	39.0	23.3
San Esteban 2004	1,748	5,666	8.2 (1990)	75.8	100[a]	69.8
S.P. Mártir 2004	247	1171	–36.5 (1991)	40.8	62.9	37.6
S.P. Nolasco 1997	171	659	–44.8 (1991)	52.0	80.0	47.8
F. de San Ignacio 2004	58	280	–47.6 (1985)	51.8	79.7	47.6
Los Islotes 2004	143	439	50.6 (1993)	79.4	100[a]	73.1
Total	4,299	17,484	20.1	52.4		
Corrected	8,598[b]	24,062[b,c] -31,159[b,d]			80.7[b,c]	48.2[b,c]

[a] These values were higher than 100% because the adjusted number of females was lower than the adjusted pups number. We adjusted them to 100% on the basis that there should be at least an equal number of pups and females.
[b] 50% added to number of pups.
[c] 23% added to number of females.
[d] 54% added to number of females (see text).

NCfec = non-corrected fecundity, Afec = adjusted fecundity.

census data) and adjusted fecundity (using the mentioned corrections for female and pup numbers).

There are several quantitative approaches for evaluating population status. Our approach focuses on two critical aspects of a population: population size and trends in population size that comprise both average tendencies to increase or decrease and variability about these tendencies due to variability in population growth rates. To characterize patterns of population growth we used the population trend data described above and performed linear regression analysis for each rookery to examine population trends over time. To incorporate variability in growth rates we extracted a maximum likelihood estimator of growth rate and confidence interval about that growth rate (Dennis et al. 1991). Using this approach, λ was approximated as $\mu + (\sigma^2/2)$, where μ is a rate that determines how quickly the mean population size changes, and σ^2 determines how quickly the variance increases over time (Morris et al. 1999). The probability of extinction (PE) requires defining a critical population threshold, or a population size at which population would be effectively extinct (Ne). A review of available data for otariids indicates that numerous otariid populations have been reduced to very low densities and have recovered to levels where they are no longer at risk of extinction (Gerber and Hilborn 1999). For example, several very small populations of pinnipeds, such as northern elephant seals and Guadalupe fur seals, reached populations below 100 individuals and escaped from extinction (Hoelzel et al. 2002, Weber et al. 2004). Thus, reductions in population growth at low densities may not be of great importance for otariids, and the concept herein should be used as a measurement of which populations are more vulnerable.

As such, we calculated the probability that the population has fallen below a threshold of 1 individual by a specified time in the future. The mean time to extinction is calculated as the difference between the natural logarithm of the initial population size and the extinction threshold, divided by the absolute value of μ (Morris et al. 1999).

We calculated the probability of extinction and the mean time to extinction for each rookery. These calculations assume no movement between breeding colonies; therefore these estimates should be used only to compare relative risk among populations, since movement between sites is largely unknown. We also calculated the growth rate for the entire gulf (as the median λ of all individual rookeries), and the probability of extinction (multiplying the PE of all individual rookeries). Conversely, the parameters for the entire gulf assume the greatest movement between rookeries.

Results

Our estimated total abundance of sea lions in the Gulf of California in 2004 was 17,484 animals with a pup production of 4,299 (Table 1). When correction factors were applied, the estimated total number of sea lions was between 24,062 and 31,159 and the pup production 8,598. The most abundant colonies were San Esteban, San Jorge, and Isla Lobos, and the least abundant were F. de San Ignacio, Partido, and Rasito (Table 1).

Population trends for sea lions in the Gulf of California have changed dramatically since the last published estimate. Compared with the last published estimates of California sea lion populations in the Gulf of

California (Aurioles-Gamboa and Zavala-González 1994), Los Islotes was the rookery that increased most (50.6%), followed by Consag (42.5%), San Jorge 12.3%, and San Esteban 8.2%. All additional rookeries decreased to varying degrees and the whole population decreased 20.05% (Table 1).

Trends for each sea lion rookery in time are shown in Fig. 2, and the regression results between sea lion totals versus years and pup numbers are in Table 2. Consag, San Jorge, and Los Islotes populations increased significantly; San Esteban exhibited a marginally significant increase, whereas Granito, Los Cantiles, Los Machos, Partido, and F. de San Ignacio decreased significantly. Isla Lobos, and S. Pedro Nolasco rookeries showed a marginally significant decrease, while Rasito and S.P. Mártir showed non-significant decrease (Table 2, Fig. 2).

Our estimated rate of increase was highest for Rasito, F. de San Ignacio, and Los Islotes, and lowest for Cantiles and Machos (Table 3). However, the examination of relative extinction risk analysis suggested that Isla Lobos, Los Cantiles, Granito, Los Machos, Partido, S. Pedro Nolasco, and F. de San Ignacio are most vulnerable, while Consag, San Jorge, San Esteban, and Los Islotes are comparably viable (Table 3). The population growth for the whole gulf indicates that it is stable (1.037), and the probability of extinction was very low (2.24×10^{-27}).

When comparing the periods of time in which each rookery increased or decreased, we observed some common patterns. First, the three rookeries of the Northern Gulf (Consag, San Jorge, and Isla Lobos) increased from the late 1960s to 1984. The first two continued growing until 2004. Granito and Rasito increased until 1986 and then declined. Rookeries of Angel de la Guarda (Los Cantiles, Los Machos, and Partido) grew until 1989-1990 and declined. At S.P. Mártir and San Esteban an important drop occurred in 1992 followed by recuperation.

Pup production decreased significantly at Los Cantiles, Los Machos, and F. de San Ignacio, while Granito, Rasito, and S.P. Mártir showed non-significant decreases. Remaining rookeries increased significantly (Los Islotes, Partido, and S. Pedro Nolasco since 1992), or non-significantly (Consag, San Jorge, Isla Lobos, and San Esteban) (Table 2). Los Islotes and San Esteban showed the greatest non-corrected fecundity (more than 75%) while Isla Lobos and Rasito had the minimum proportion of pups (less than 26%) (Table 1). The fecundities in 2004 show that a bit more than half of the females in the gulf produced a pup. For the corrected fecundity values we found the same trends; when using the 23% correction factor for females fecundity values were higher; and when the 54% correction factor was applied the fecundity values were lower. The overall fecundity value was 48.2% as a minimum and 80.7% as a maximum.

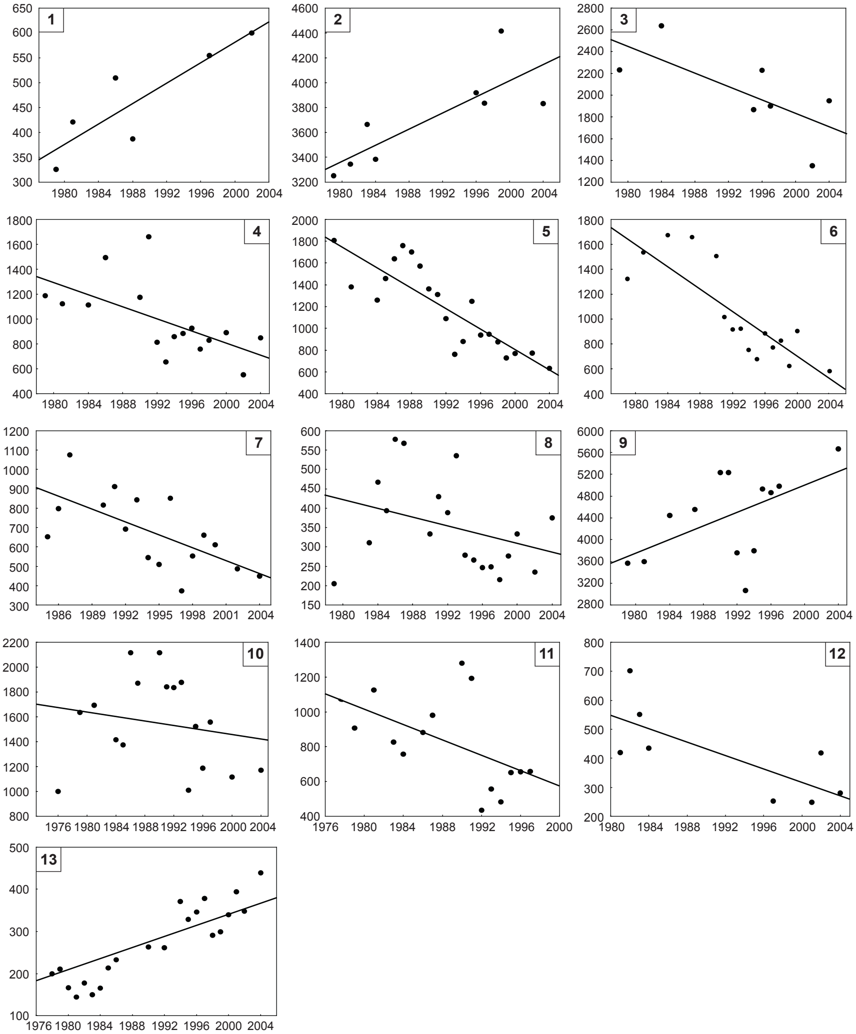


Figure 2. Regression trend for total population in time, for each sea lion rookery at the Gulf of California. Rookeries: 1. R. Consag, 2. San Jorge, 3. Isla Lobos, 4. Isla Granito, 5. Los Cantiles, 6. Los Machos, 7. El Partido, 8. Rasito, 9. San Esteban, 10. San Pedro Mártir, 11. San Pedro Nolasco, 12. Farallón de San Ignacio, 13. Los Islotes.

Table 2. Regressions for abundance (total and pup) versus year at each sea lion rookery in the Gulf of California.

Rookery	Yt	Total abundance vs. years	Yp	Pup abundance vs. years
R. Consag	6	$R = 0.87$, $P = 0.023$[a]	4	$R = 0.86$, $P = 0.135$
San Jorge	8	$R = 0.81$, $P = 0.015$[a]	8	$R = 0.32$, $P = 0.479$
Isla Lobos	7	$R = -0.71$, $P = 0.077$	6	$R = 0.79$, $P = 0.112$
Isla Granito	16	$R = -0.60$, $P = 0.014$[a]	16	$R = -0.41$, $P = 0.116$
Los Cantiles	21	$R = -0.85$, $P < 0.001$[a]	21	$R = -0.71$, $P < 0.001$[a]
Los Machos	16	$R = -0.83$, $P < 0.001$[a]	16	$R = -0.69$, $P < 0.003$[a]
El Partido	16	$R = -0.65$, $P = 0.007$[a]	16	$R = 0.58$, $P = 0.019$[a]
Rasito	20	$R = -0.33$, $P = 0.161$ 1976-1986 ($R = 0.95$, $P = 0.003$) 1987-2004 ($R = -0.57$, $P = 0.032$[a])	19	$R = -0.10$, $P = 0.697$
San Esteban	13	$R = 0.53$, $P = 0.059$ 1979-1991 ($R = 0.98$, $P < 0.001$[a]) 1992-1997 ($R = 0.83$, $P = 0.022$[a])	13	$R = 0.543$, $P = 0.055$ 1979-1991 ($R = 0.78$, $P = 0.068$) 1992-1997 ($R = 0.73$, $P = 0.063$)
S.P. Mártir	17	$R = -0.19$, $P = 0.476$ 1976-1990 ($R = 0.75$, $P = 0.031$[a]) 1990-2004 ($R = -0.73$, $P = 0.017$[a])	16	$R = -0.05$, $P = 0.856$ 1979-1990 ($R = 0.82$, $P = 0.023$) 1990-1994 ($R = -0.95$, $P = 0.014$[a])
S.P. Nolasco	15	$R = -0.48$, $P = 0.079$ 1984-1991 ($R = 0.96$, $P = 0.008$[a]) 1992-1997 ($R = 0.87$, $P = 0.026$[a])	15	$R = -0.08$, $P = 0.777$ 1992 to 1997 ($R = 0.90$, $P = 0.015$[a])
F. de San Ignacio	8	$R = -0.74$, $P = 0.037$[a]	8	$R = -0.72$, $P = 0.043$[a]
Los Islotes	21	$R = 0.91$, $P < 0.001$[a]	21	$R = 0.94$, $P < 0.001$[a]

[a]Significant value at $P < 0.05$

Yt = number of years of available total census data.

Yp = number of years of available pup census data.

Discussion

Our results indicate that the sea lion population in the Gulf of California has declined 20.1% since the last published report (Aurioles-Gamboa and Zavala-Gonzalez 1994). While the total U.S. population of *Z. californianus californianus* is growing, the rookeries in the Gulf of California are decreasing as a whole. Only four colonies are significantly increasing, while the remaining populations are either stable or declining in abundance. According to these trends, we discuss three patterns of population trends for sea lions in the Gulf of California.

1. Rookeries that are growing in total numbers and pup productions include Consag, San Jorge, Los Islotes; and since 1992 include San Esteban and S.P. Nolasco. Except for the latter, they all have low probabilities of extinction.

2. Rookeries whose abundance is declining, and have a maximum probability of extinction include Granito, Los Cantiles, Los Machos, Partido, and F. de San Ignacio.

3. Rookeries that are fluctuating widely or did not show any clear trend in their regressions were Isla Lobos, Rasito, and S.P. Mártir.

The first group of rookeries may be considered viable breeding units, particularly San Esteban and Los Islotes which exhibited high pup production. The rookeries in the second group may be of considerable conservation concern as they all declined more than 45% since the last published estimate (Aurioles-Gamboa and Zavala-González 1994). Partido's pup production is increasing significantly so it may be in the process of recovery. Only Los Cantiles and Los Machos had a growth rate slightly lower than one, and seem to be the most vulnerable (Table 3). The rookeries of the third group may have different fates in the future, some may recover while others may continue to decline. Isla Lobos may have a better opportunity of recovering due to its relative high abundance. Rasito is a small population and exhibited a significant increase in abundance between 1976 and 1986, followed by a significant decline between 1987 and 2002; therefore the status of this population is difficult to assess.

Fecundity varied according to the estimation method (i.e., without corrections, with 23% or 54% correction to females, and 50% to pup numbers). This suggests the importance of estimating a site-specific correction factor for pup production for rookeries in the Gulf of California. Nevertheless, San Esteban and Los Islotes showed the greatest fecundities, which is concordant with their increasing trends. The lowest fecundities were at Isla Lobos and Rasito, which are in the third group, implying that in the future they may continue to decline.

It should be noted that the time period length of the census data for these rookeries is limited. Morris et al. (1999) recommended using at

Table 3. Results of the PVA analysis for each sea lion rookery in the Gulf of California.

Rookery	μ	σ^2	λ (0.1% confidence limits)	Relative PE (Ne = 1)	Relative MTE
R. Consag	0.0265	0.0190	1.037 (0.987-1.089)	3.21×10^{-10}	241.2
San Jorge	0.0066	0.0043	1.009 (0.983-1.035)	1.40×10^{-13}	1250.21
Isla Lobos	–0.0054	0.0327	1.011 (0.950-1.076)	1.0	581.43
Isla Granito	–0.013	0.076	1.025 (0.934-1.126)	1.0	518.68
Los Cantiles	–0.0419	0.0271	0.972 (0.920-1.026)	1.0	153.62
Los Machos	–0.033	0.0407	0.987 (0.923-1.056)	1.0	192.82
El Partido	–0.0197	0.1173	1.040 (0.909-1.189)	1.0	101.42
Rasito	0.0654	0.0981	1.121 (1.014-1.240)	0.0002	63.72
San Esteban	0.0185	0.0257	1.032 (0.978-1.089)	1.27×10^{-6}	458.15
S.P. Mártir	0.0056	0.0695	1.041 (0.957-1.133)	0.297	1261.72
S.P. Nolasco	–0.0177	0.1096	1.038 (0.908-1.186)	1.0	367.04
F. de San Ignacio	–0.0176	0.1245	1.046 (0.914-1.196)	1.0	319.61
Los Islotes	0.0302	0.0236	1.043 (0.990-1.098)	7.72×10^{-8}	201.32
Total gulf			1.037	8.06×10^{-27}	

μ = mean population, σ^2 = variance, λ = population growth rate, PE = probability of extinction for a population threshold (Ne) of 1 individual, and MTE = mean time to extinction. Both PE and MTE assume no movement between breeding colonies. PE for entire gulf was calculated by multiplying PE of all individual rookeries, and λ as the median of all individual rookeries.

least ten years of census data for the diffusion approximation approach. In relation to the accuracy of our PVA analysis, Consag, San Jorge, and Isla Lobos had less than ten years of count data, so we suggest that the conclusions for those sites should be considered with caution. Nonetheless, our results may offer some provisional guidance to assess the relative measures of the health of the sea lion populations in the Gulf of California.

Many factors are potentially important in determining population trends for sea lions in the Gulf of California. These include (1) contamination, (2) diseases, (3) human disturbance, including tourism, (4) illegal killing and incidental catch, and (5) decrease in prey availability. High content of contaminants such as DDT and PCBs have been reported in *Zalophus californianus* from California (e.g., Kannan et al. 2004) and linked to physiological impairments (Debier et al. 2005) and cancer associated mortality (Ylitalo et al. 2005). However, data on these kinds of contaminants are not available for the Gulf of California. Due to the relatively low industrialization and little freshwater discharges, we suspect this may not be a significant problem in the gulf. Unpublished data of metal content in bone of California sea lions from 10 rookeries suggest that the highest level of the most dangerous metals (As, Hg, and Pb) concentrates around Angel de la Guarda Island (decreasing populations) and at Los Islotes (increasing population) (Szteren and Aurioles unpubl.). However, the relationship between high levels of these metals, health condition, and mortality are unclear.

Little information exists regarding diseases and their effects on population dynamics. Some studies indicate the presence of *Leptospira* (Godínez et al. 1999, Acevedo-Whitehouse et al. 2003), but no mass mortality events have been recorded in the Gulf. Osteoarthritis and osteomyelitis in skull bones have a decreasing trend in frequency from north to the south Gulf of California (Aurioles et al., accepted for publication by *Journal of Wildlife Diseases*), with no apparent relationship with the decreasing sea lion population pattern focused in the Central Gulf.

Most of the islands where sea lions have rookeries are protected as the "Islas del Golfo de California Natural Reserve"; thus anthropogenic impacts are relatively low. Sea lion–fisheries interactions exist along the Gulf of California, with some artisanal fishing gear affecting species such as the vaquita (*Phocoena sinus*) (D'Agrosa et al. 2000). The incidence of sea lion entanglement measured as the percentage of sea lions with net scars or with net debris varies between 0 and 2.5% in populations of the Central Gulf (Zavala and Mellink 1997). However, the rookery with the highest entanglement index (7-9%) is Los Islotes (Harcourt et al. 1994, Aurioles et al. 2003), and receives the maximum tourism visitors and a high incidence of disturbance (Labrada et al. 2005). Nevertheless, it is one of the rookeries exhibiting a higher population increase.

No data on illegal killing are available for the gulf; however, we suspect that poaching by artisanal fishermen occurs, but is limited as the islands and rookeries are surveyed and viewed by government representatives, tourists, and researchers.

Finally, prey availability is another possible factor that may affect the local or regional abundance of pinnipeds (Trillmich and Ono 1991). Many pinniped populations exhibit seasonal fluctuations according to the availability of their main prey (e.g., Ainley et al. 1982, Trites and Donnelly 2003). With the exception of F. de San Ignacio, breeding areas that were most vulnerable are situated on or near Angel de la Guarda Island. This area has great concentrations of Pacific sardine (*Sardinops caeruleus*) year-round (Lluch-Cota and Lluch-Belda 2000). Moreover, dietary studies have correlated the distribution pattern of the Pacific sardine with the importance of this prey in the sea lion diet (García-Rodríguez and Aurioles-Gamboa 2004). There is some evidence for a possible relationship between the decline of sea lion colonies in the Central Gulf and sardine abundance. First, the surroundings of Angel de la Guarda Island is a very variable ecosystem, where the sardine is one of the most important components, influencing many other trophic groups in the system. Sardine catches have been highly variable, being one of the major pelagic fish in the Gulf of California (Nevárez 2000). Second, the Pacific sardine was the dominant prey at the Los Machos rookery (García-Rodríguez and Aurioles-Gamboa 2004), and this rookery is declining dramatically. This may also be occurring at Los Cantiles, Granito, and Rasito given their close proximity to Los Machos. Third, from 1989 to 1992 a sharp decrease on sardine fisheries occurred, in which landings dropped from 292,000 tons in 1988-1989 to less than 7,500 tons in 1991-1993 (Cisneros-Mata et al. 1995). This coincided with the time in which most rookeries in the Gulf of California showed decreasing trends, again, reinforcing the idea that sea lion abundance fluctuates with sardine landings.

Another consideration that may contribute to population trends is the diversity of the sea lion diet. For example, Merrick et al. (1997) found the greatest rates of decline in areas with low diet diversity of Steller sea lions of the Gulf of Alaska and the Aleutian Islands. In the Gulf of California, García-Rodríguez and Aurioles-Gamboa (2004) found that S.P. Mártir, Rasito, and San Esteban rookeries support high prey diversity, while Los Machos, Los Cantiles, and Granito depend on a smaller diversity of prey. Populations at the latter sites may be more susceptible to the influence of changes in the abundance or availability of preferred prey.

Sea lions in the Gulf of California may be particularly vulnerable because of their small population size and potentially significant population subdivision. While the Gulf of California has many small sea lion rookeries, the U.S. stock includes four large colonies with 237,000-244,000 animals (Carretta et al. 2003). According to Schramm (2002) the movement of animals between different areas is very low. The magnitude of the divergence between groups suggested that females do not migrate between regions. The causes that could inhibit these migrations might be ethological factors such as female philopatry or ecological factors such as patchy distribution of prey (Maldonado et al. 1995). At least one of the three groups of rookeries defined by Schramm (2002) (the central region) has many rookeries that are decreasing markedly and should be considered vulnerable in conservation strategies. The situation in the northern and southern gulf may be more optimistic, but many of these colonies were not included in Schramm's genetic study. Moreover, the level of interchange of animals between different areas is largely unknown. Future research should address these uncertainties, but precautionary management in the face of these unknowns may be warranted.

Acknowledgments

Thanks to CONACyT projects (400302-5-3371-N and 26430-N), SEMARNAT-CONACyT (2002-C01-1230), and DEPI-IPN (968013) during different aspects of the study. Many thanks to SEMARNAT (Instituto Nacional de Ecología; Dirección General de Vida Silvestre) for the respective research permits: No. 240996-213-03 (1996), DOO 750.-4172/97 (1997), DOO 750.-4443/98 (1998), DOO.02.-327O (1999), DOO.02.-3345 (2000), SGPA/DGVS.-0579 (2002), SGPA/DGVS-03473 (2003), and SGPA/DGVS-04160 (2004). The U.S. National Science Foundation (Animal Behavior, Biological Oceanography, and International Programs) provided partial support for this work (award no. 0347960 to Leah Gerber).

References

Acevedo-Whitehouse, K., H. de la Cueva, F.M.D. Gulland, D. Aurioles-Gamboa, F. Arellano-Carbajal, and F.J. Suárez-Guemes. 2003. Evidence of *Leptospira interrogans* infection of California sea lion pups from the Gulf of California. J. Wildl. Dis. 39(1):145-151.

Ainley, DG., H.R. Huber, and K.M. Bailey. 1982. Population fluctuations of California sea lions and the Pacific whiting fishery off central California. Fish. Bull. U.S. 80:253-258.

Aurioles-Gamboa, D. 1988. Behavioral ecology of California sea lions in the Gulf of California. Ph.D. thesis, University of California, Santa Cruz. 186 pp.

Aurioles G.D., and F. Sinsel. 1988. Mortality of California sea lion pups at Los Islotes, Baja California Sur, México. J. Mammal. 69:180-183.

Aurioles-Gamboa, D., and A. Zavala-González. 1994. Algunos factores ecológicos que determinan la distribución y abundancia del lobo marino *Zalophus californianus*, en el Golfo de California. Cienc. Mar. 20(4):535-553.

Aurioles, G.D., F. García-Rodríguez, M. Ramírez-Rodríguez, and C. Hernández-Camacho. 2003. Interaction between the California sea lions and the artisanal fishery in the Bay of La Paz, Gulf of California, Mexico. Cienc. Mar. 29(3):357-370.

Bonnell, M.L., and R.G. Ford. 1987. California sea lion distribution: A statistical analysis of aerial transect data. J. Wildl. Manag. 51(1):13-20.

Carretta, J.V., K.A. Forney, M.M. Muto, J. Barlow, J. Baker, and M. Lowry. 2003. Draft U.S. Pacific marine mammal stock assessments: 2003. NOAA-TM-NMFS-SWSC Tech. Memo. 307 pp.

Cisneros-Mata, M.A., M.O. Nevárez-Martínez, and G. Hammann. 1995. The rise and fall of the Pacific sardine, *Sardinops sagax caeruleus* Girard, in the Gulf of California, Mexico. CalCOFI Rep. 36:136-143.

D'Agrosa, C., C.E. Lennert-Cody, and O. Vidal. 2000. Vaquita bycatch in México's artisanal gillnet fisheries: Driving a small population to extinction. Conserv. Biol. 14:1110-1119.

Debier, C., G.M. Ylitalo, M. Weise, F. Gulland, D.P. Costa, B.J. Le Boeuf, T. de Tillesse, and Y. Larondelle. 2005. PCBs and DDT in the serum of juvenile California sea lions: Associations with vitamins A and E and thyroid hormones. Environ. Pollut. 134:323-332.

Dennis, B., P.L. Munholland, and J.M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. Ecol. Monogr. 61:115-143.

García-Aguilar, M.C., and D. Aurioles-Gamboa. 2003. Breeding season of the California sea lion (*Zalophus californianus*) in the Gulf of California, México. Aquat. Mamm. 29(1):67-76.

García-Rodríguez, F.J., and D. Aurioles-Gamboa. 2004. Spatial and temporal variation in the diet of the California sea lion (*Zalophus californianus*) in the Gulf of California, Mexico. Fish. Bull. U.S. 102:47-62.

Gerber, L.R., and R. Hilborn. 1999. Catastrophic events and recovery from low densities in populations of otariids: Implications for risk of extinction. Mamm. Rev. 31(2):131-150.

Gerber, L.R., and G. VanBlaricom. 2001. Implications of three viability models for the conservation status of the western population of Steller sea lions (*Eumetopias jubatus*). Biol. Conserv. 102:261-269.

Godínez, C., B. Zelaya, D. Aurioles, A. Verdugo, E. Reyes and A. de la Peña. 1999. Antibodies against *Leptospira interrogans* in California sea lion pups from the Gulf of California. J. Wildl. Dis. 35(1):106-111.

Harcourt, R., D.G. Aurioles, and J. Sánchez. 1994. Entanglement of California sea lions at Los Islotes, Baja California Sur, México. Mar. Mamm. Sci. 10(1):122-125.

Hoelzel, A.R., R.C. Fleischer, C. Campagna, B.J. Le Boeuf, and G. Alvord. 2002. Impact of a population bottleneck on symmetry and genetic diversity in the northern elephant seal. J. Evol. Biol. 15:567-575.

Kannan, K., N. Kajiwara, B.J. Le Boeuf, and S. Tanabe. 2004. Organochlorine pesticides and polychlorinated biphenyls in California sea lions. Environ. Pollut. 131:425-434.

Labrada-Martagón V., D. Aurioles-Gamboa, and S.F. Martínez-Díaz. 2005. Natural and human disturbance in a rookery of California sea lion (*Zalophus californianus californianus*) in the Gulf of California, Mexico. Latin American J. Aquat. Mamm. 4(2)

Le Boeuf, B., D. Aurioles, R. Condit, C. Fox, R. Gisiner, R. Romero, and F. Sinsel. 1983. Size and distribution of the California sea lion population in Mexico. Proc. Cal. Acad. Sci. 43(7):77-85.

Lluch-Cota, S.E., and D. Lluch Belda. 2000. Caso de estudio sobre el uso de bases de datos ambientales de baja resolución espacial, como una alternativa para inferir habitat de desove. Oceánides 15(1):63-65. (In Spanish.)

Lowry, M.S., P. Boveng, R.J. DeLong, C.W. Oliver, B.S., Stewart, H. DeAnda, and J. Barlow. 1992. Status of the California sea lion (*Zalophus californianus californianus*) population in 1992. NOAA NMFS SWFSC Admin. Rep. LJ-92-32. La Jolla, California.

Maldonado, E.J., F. Orta-Davila, B.S. Stewart, E. Greffen, and R.K. Wayne. 1995. Intraspecific genetic differentiation in California sea lions (*Zalophus californianus*) from southern California and the Gulf of California. Mar. Mamm. Sci. 11(1):46-58.

Merrick, R.L., M.K. Chumbley, and G.V. Byrd. 1997. Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: A potential relationship. Can. J. Fish. Aquat. Sci. 54:1342-1348.

Morris, W., D. Doak, M. Groom, P. Kareiva, J. Fieberg, L. Gerber, P. Murphy, and D. Thompson. 1999. A practical handbook for population viability analysis. The Nature Conservancy. 79 pp.

Nevárez, M.O. 2000. Variabilidad de la población de sardina (*Sardinops caeruleus*) en el Golfo de California, México. Ph.D. thesis, CICIMAR-IPN, La Paz. 103 pp. (In Spanish.)

Schramm, Y. 2002. Estuctura genética y filogeografía de *Zalophus californianus californianus* en aguas adyacentes a la península de Baja California, México. Ph.D. thesis, Univ. Autónoma de Baja California, Ensenada, Baja California, México. 146 pp. (In Spanish.)

Trillmich, F., and K.A. Ono. 1991. Pinnipeds and El Niño: Responses to environmental stress. Springer-Verlag, Berlin. 293 pp.

Trites, A.W., and C.P. Donnelly. 2003. The decline of Steller sea lions *Eumetopias jubatus* in Alaska: A review of the nutritional stress hypothesis. Mamm. Rev. 33:3-28.

Weber, D.S., B.S. Stewart, and N. Lehman 2004. Genetic consequences of a severe population bottleneck in the Guadalupe fur seal (*Arctocephalus townsendi*). J. Hered. 95(2):144-153.

Ylitalo, G.M., J.E. Stein, T. Hom, L.L. Johnson, K.L. Tilbury, A.J. Hall, T. Rowles, D. Greig, L.J. Lowenstine, and F.M.D. Gulland. 2005. The role of organochlorines in cancer-associated mortality in California sea lions (*Zalophus californianus*). Mar. Pollut. Bull. 50:30-39.

Zavala, G.A., and E. Mellink. 1997. Entanglement of California sea lions, *Zalophus californianus californianus*, in fishing gear in the central-northern part of the Gulf of California. Fish. Bull. U.S. 95:180-184.

Zavala-Gonzalez, A., and E. Mellink. 2000. Historical exploitation of the California sea lion, *Zalophus californianus*, in Mexico. Mar. Fish. Rev. 62(1):35-40

Klebsiella pneumoniae Epidemics: Possible Impact on New Zealand Sea Lion Recruitment

Ian S. Wilkinson
Department of Conservation, Science and Research Unit, Wellington, New Zealand.

Pádraig J. Duignan, Aurelie Castinel, and Alex Grinberg
Massey University, New Zealand Wildlife Health Centre, Institute of Veterinary, Animal and Biomedical Sciences, Palmerston North, New Zealand

B. Louise Chilvers
Department of Conservation, Science and Research Unit, Wellington, New Zealand

Bruce C. Robertson
School of Biological Sciences, Canterbury University, Christchurch, New Zealand

Abstract

Epidemics among New Zealand sea lion pups in the 2001/02 and 2002/03 breeding seasons highlight the importance of examining the role of disease in the population dynamics of this threatened species. The pathogen implicated in both events was the gram negative bacterium *Klebsiella pneumoniae.* Isolates from both seasons were genetically indistinguishable, suggesting that the events were caused by a single introduction of an epidemic strain of the pathogen. The events were characterized by a sharp rise in pup mortality approximately three weeks after the start of the pupping season. On post mortem examination, affected pups had one or more of the following lesions: acute suppurative arthritis or polyarthritis, cellulitis, peritonitis, pleuritis, or meningitis. Adults were not apparently affected. Prior to the appearance of *Klebsiella,* mortality to mid January (~six weeks of age) among pups was 6.2%, with mortality by mid

February (~10 weeks) 16.7%. Mean values for the years in which *Klebsiella* affected pup mortality were estimated at 18.5% (6 weeks) and 26.8% (10 weeks). The increase in mortality attributable to *Klebsiella* was 12.3% at 6 weeks and 10.1% at 10 weeks and the latter value was used in calculations to assess impacts on recruitment of females. Observed levels and temporal patterns of pup mortality in 2003/04 were consistent with those of pre-*Klebsiella* seasons. Using survival data from tagged fully mature cohorts, the reduction in the number of females recruiting to the adult population from epidemic years (2001/02 and 2002/03) was estimated. Between 42 and 72 fewer females from the 2001/02 cohort would reach age five, while between 47 and 80 fewer females from the 2002/03 cohort would reach age five. By 2007/08, when both the 2001/02 and 2002/03 cohorts would contribute significantly to the mature female population, between 93 and 144 fewer females would be present in the population. These missing females potentially represent between 2.3% and 4.6% of the adult female population.

Introduction

Epidemics affecting marine mammal populations may be stochastic events, but they are not unusual, with many examples in recent years from around the world. Indeed, they may be so common as to be a significant factor in population dynamics and genetics, particularly for already threatened species in diminishing populations (May 1988, Harwood and Hall 1990, Young 1994, Gulland 1995). For pinnipeds, with spatial and temporal constraints on foraging and reproduction, even relatively modest elevations in morbidity and mortality during the energetically demanding breeding season could have important implications for population survival.

The behavior and ecology of pinnipeds would tend to predispose them to the transmission of infectious agents even for species that occur at low population density (Harwood and Hall 1990, Thompson and Hall 1993). The earliest records of what was probably an infectious disease epidemic among pinnipeds occurred in harbor seals (*Phoca vitulina*) in Scottish waters during the eighteenth and nineteenth centuries (Harwood and Hall 1990). The descriptions of these events bear a remarkable resemblance to more recent viral epidemics caused by influenza A and phocine distemper virus, PDV (Geraci et al. 1982, Callan et al. 1995, Duignan 1998). The impact of the first PDV epidemic on the North Sea harbor seal population was documented (Heide-Jorgensen et al. 1992). Since that first event in 1988 an even larger epidemic recurred among the same population in 2002 (Jensen et al. 2002). Where phocid populations are larger and diseases may become endemic, mortality events are less common and generally limited to the naive animals in the population (Duignan et al. 1995, 1997).

Although other viral infections have been identified in pinnipeds, their role in causing epidemics is more equivocal. Phocid herpes viruses for example, have been implicated as the cause of elevated levels of mortality among neonatal harbor seals in rehabilitation facilities in North America and Europe (Osterhaus et al. 1985, Borst et al. 1986, Gulland et al. 1997). However, even though herpes viruses occur in free-living pinnipeds worldwide, their role in mass mortality has not been established (Osterhaus 1988, Kennedy et al. 1989, Harder et al. 1991, Stenvers et al. 1992, Munro et al. 1992, Zarnke et. al. 1997). Similarly, caliciviruses are ubiquitous in North Pacific pinnipeds and for individual animals infection may result in premature parturition, neonatal death, encephalitis, or pneumonia (Smith 1981, Smith et al. 1998). Nevertheless, their role in population dynamics has not been properly investigated.

Bacterial diseases have been infrequently implicated as the primary etiology in pinniped epidemics. The best example is the recurrent outbreaks of leptospirosis among California sea lions, *Zalophus californianus,* and northern fur seals, *Callorhinus ursinus* (Vedros et al. 1971, Smith et al. 1977, Gulland et al. 1996, Gulland 1999). *Campylobacter* sp. was suggested as a possible cause of an epidemic among New Zealand (Hooker's) sea lions, *Phocarctos hookeri*, in 1998 but the limited investigation of this event precludes a more definitive conclusion (Duignan 1999, Stratton et al. 2001). This bacterium has not been associated with epidemics among marine mammals elsewhere and the histopathological lesions seen in New Zealand sea lions and fur seals have not been reported in any other species of marine mammal. However, *Campylobacter* sp. have been isolated from several seabird species and from Antarctic fur seals (*Arctocephalus gazella*) sampled on Bird Island, South Georgia, so clinical disease may yet be discovered in other species (Broman et al. 2000). Indeed there are remarkable similarities in clinical presentation and gross lesions between the disease of New Zealand pinnipeds, and a mass mortality among crabeater seals, *Lobodon carcinophagus*, in Antarctica in the mid 1950s (Laws and Taylor 1957), perhaps suggesting a similar cause.

The New Zealand sea lion is one of the world's rarest and most highly localized pinnipeds. They are classified as "vulnerable" by the IUCN (Reijnders et al. 1993) and "threatened" under the New Zealand Marine Mammals Protection Act, 1978 (Molloy and Davis 1994). New Zealand sea lions breed on New Zealand's subantarctic Islands between latitudes 48ºS and 53ºS (Gales and Mattlin 1997). Their population size is estimated at between 12,000 and 15,000 animals, comprising approximately 7,000 mature age animals (Gales and Fletcher 1999, Wilkinson et al. 2003). This is one of the smallest population sizes reported for an otariid and available data suggest that this population has remained static for at least the last 27 and possibly 40 years (Taylor 1971, Wilkinson et al. 2003). Ninety percent of all breeding is highly localized, occurring on Dundas and Enderby islands within the Auckland Island group.

Over the past decade, there has been considerable concern about the interaction between New Zealand sea lions and the arrow squid, *Nototodarus sloanii*, trawl fishery, which operates on the Auckland Island shelf between February and May each year (Gales 1995). The presence of the squid, which makes up a consistent, but variable proportion of the sea lions diet (Childerhouse et al. 2001) around the Auckland Island, coincides with the early part of lactation of the New Zealand sea lion (Gales 1995). With both sea lions and trawlers targeting the same prey, accidental captures of sea lions in squid trawl nets are inevitable, and between 17 to 140 sea lion deaths are reported to occur each season (Baird 1996, Wilkinson et al. 2003). The impact of fisheries on the sea lion population is as yet unknown but several models suggest that this level of take may limit the capacity for New Zealand sea lions to increase in numbers and under some scenarios result in population decline (Doonan and Cawthorn 1984, Woodley and Lavigne 1993). This uncertainty about anthropogenic impacts on the population is heightened when considering other natural regulators, such as disease, on population growth. During the past seven years three epidemics have occurred among New Zealand sea lions on the Auckland Islands (Duignan 1999, Wilkinson et al. 2003). The January 1998 event resulted in the deaths of 53% of the 1997/98 season's pup production as well as an unknown number of adult animals (Baker 1999, Wilkinson et al. 2003). This epidemic was the first evidence for the role of disease as a factor in the demography of the New Zealand sea lion. Here we describe two further epidemics that occurred during the 2001/02 and 2002/03 breeding seasons and their implications for subsequent recruitment to the adult population. This paper will describe the 2001/02 and 2002/03 epidemics and examine (i) pup mortality levels prior to the epidemic years; (ii) the observed levels of mortality seen in the 2003/04 breeding season; and (iii) the effect of any elevated pup mortality on the numbers of recruiting adults.

Methods

During the past decade detailed daily counts were undertaken at the Sandy Bay rookery on Enderby Island, Auckland Islands (50º30'S, 166º17'E), of live and dead pups, and accurate pup production estimates using direct counts and mark-recapture techniques (see Gales and Fletcher 1999, Wilkinson et al. 2003) made for the rookeries at South East Point (Enderby Island), Dundas Island, and Figure of Eight Island. Following the January 1998 epidemic a surveillance programme was established to monitor in detail all mortality in the population at Sandy Bay. Since the 1998/99 breeding season all pups that died at this location have been necropsied in the field to determine cause of death. A standard necropsy procedure was conducted and samples collected for histopathology, serology, parasitology, bacteriology, virology, genetics, and life history studies. Histopathology samples from all internal organs were fixed in 10% buffered formalin, while samples for serology, bacteriology, and virology were frozen in liquid nitrogen for later analysis. Cause of death was categorized as follows: stillbirth, trauma, malnutrition, hookworm infection, and bacterial infection. Diagnoses were not mutually exclusive and any pup may have had more than one diagnosis ranked in order of significance as the cause of death.

All estimates of mortality were taken from the Sandy Bay rookery as this was the most intensively studied site, and the only one for which such detailed data were available. In this paper these estimates were used as a proxy for the entire population. Levels of pup mortality were calculated for Sandy Bay between the years of 1992/93 and 2003/04, as a proportion of the estimated pup production. Pup production was estimated by combining the cumulative total of dead pups with the numbers of live pups calculated using mark-recapture techniques on January 16 each year (see Gales and Fletcher 1999, Wilkinson et al. 2003). Data were available for the mid January benchmark (~6 weeks from start of season at which time pup production estimates were made) in each of the years, and for mid February (~10 weeks, which marked the end of the field season) in the years 1997/98 to 2003/04. Cumulative pup mortality as a proportion of pup production was calculated for the years prior to the epidemics, then a further "epidemic" mean calculated. The increase in mean during the epidemic seasons was applied to first year mortality as the cost of elevated pup mortality due to the epidemic. The lower of the two values for epidemic related mortality was used in calculations.

Daily cumulative mortality totals at Sandy Bay between December and mid February for the years 2000/01 to 2003/04 were compared to examine possible differences between "epidemic" and "non-epidemic" years.

To assess the impacts of increased mortality on the number of recruiting adult females, it was necessary to examine mortality patterns among cohorts. Empirical estimates of pup survival to age one and then to maturity were available only from marked cohorts that had reached full maturity. Data were available for cohorts single flipper tagged as pups in 1986/87, and 1989/90-1992/93. Although the use of single flipper tags for marking of these cohorts prevented the analyses of tag loss, another study at the same site where adult females were double flipper tagged in the late 1990s indicated that tag loss was negligible three years after application (I. Wilkinson unpubl. data). It was therefore assumed for the purpose of this study that tag loss was zero. While pups were also marked from 1997/98 onward, maturity of these cohorts was incomplete, and so any survival values produced would be underestimated as all females were not necessarily available for resighting prior to the age at which they are first seen on breeding sites. Recapture histories of females tagged in 1986/87 and 1989/90-1992/3 were examined using a Cormack-Jolly-Seber (CJS) live recapture model in the software program MARK (White and Burnham 1999), to produce survival and recapture probabilities. While it was not possible to distinguish permanent emigration from mortality in the study, New Zealand sea lion females do show strong fidelity to breeding sites (unpublished data) suggesting permanent absence can be considered as mortality. In all years the most parsimonious models were those that gave a constant survival and age-specific recapture probability. The highest and lowest of these annual survival estimates were then applied to the numbers of female pups, derived from total pup production estimates assuming a 1:1 male:female ratio of pups (unpublished data), to estimate the numbers reaching five years of age. While four is the earliest age at which marked females have been observed to breed in the last decade, significant numbers only commence breeding from age five (I. Wilkinson unpubl. data). These figures were then modified by reducing first year survival in the 2001/02 and 2002/03 cohorts by the epidemic-related mortality, to account for the impact of disease on survival of this age class, while leaving survival rates of two, three, and four year olds unchanged.

To calculate the combined impact of the *Klebsiella* epidemics on the adult female population from both 2001/02 and 2002/03, the numbers of females estimated to be alive in 2007/08 was determined. This would be the first year that significant breeding would occur among both cohorts. The reduction in recruitment in the 2001/02 cohort at age six was combined with the reduction in the numbers of the 2002/03 cohort at age five.

Results

Pup production and mortality rates

Estimates of pup production were calculated at each of the four breeding sites in the Auckland Islands. Mark recapture estimates were made for Sandy Bay and Dundas Island, the two principal rookeries. In 2001/02 there was the marked reduction in numbers of pups born at the Auckland Islands. The estimate of 403 at Sandy Bay was the lowest ever recorded at this site, and was almost 30% lower than in 2000/01. The Dundas count was 20% lower than 2000/01 and the figure of 27 for South East Point was the lowest since 1992/93. Comparisons of the number of females ashore and daily pup:cow ratios at Sandy Bay in 2001/02 with the previous three seasons indicated that the lowered pup production was a result of lowered fecundity rather than a reduction in the number of breeding females ashore. By contrast, the estimate of pup numbers in 2002/03 was approximately 10% higher than that seen in 2001/02, but still 12% below the figures for the previous three seasons. In this season, comparisons of the number of females ashore, and daily pup:cow ashore ratios, with the previous four seasons indicated that the increased pup production was

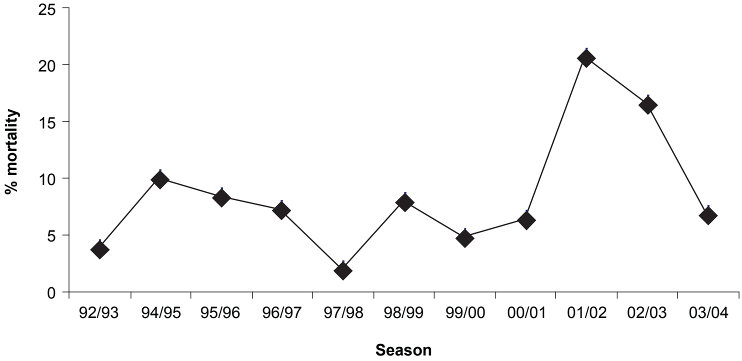


Figure 1. Mortality rates of pups at Sandy Bay, Enderby Island estimated on 16 January for years 1992/93-2003/04.

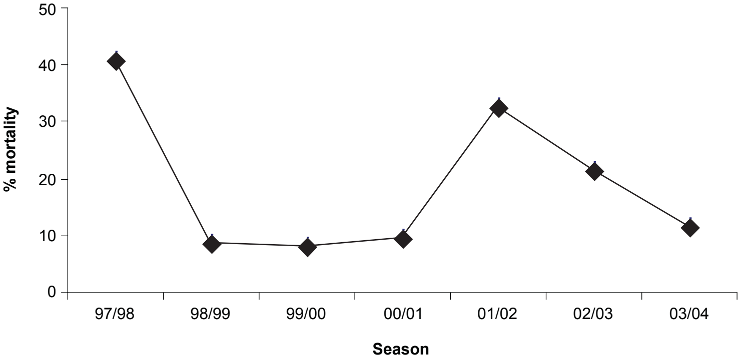


Figure 2. Mortality rates of pups at Sandy Bay, Enderby Island estimated in mid February for years 1997/98-2003/04.

likely to be the result of increased fecundity in 2002/03 over 2001/02 rather than a change in the number of breeding females ashore.

In addition to the low pup production in 2001/02, mortality of pups during the first two months post partum was markedly elevated. At Sandy Bay, pup mortality by mid January was almost three times the mean, and by the end of February 33% of the pups had died. This pattern was repeated in 2002/03 with the level of mortality in mid January almost twice the mean, and by the end of February 21.2% of the pups had died representing twice the normal level of mortality for that time of year (Figs. 1 and 2).

Pup mortality as a percentage of pup production at Sandy Bay calculated in mid January for the years 1992/93-2003/04 is shown in Fig. 1. Data on pup mortality for the period up to mid February for the years 1997/98-2003/04 and the mortality rates are shown in Fig. 2.

Pathology and bacteriology

Ante-and post-mortem examination of pups found moribund and dead at Sandy Bay in January and February 2002 (2001/02 season) revealed a suite of lesions not observed during the previous three seasons (Duignan et. al. unpubl. data). Moribund pups presented with fluctuant swelling affecting one or more limbs, progressive lameness, lethargy, and terminal convulsions. Some pups died from progression of this clinical course while others died as a result of trauma due to their loss of mobility. Necropsies were conducted respectively on 126 and 117 pups during the 2001/02 and 2002/03 seasons. At necropsy the most common findings in pups with this novel disease were acute suppurative and necrotizing arthritis, tenosynovitis, and cellulitis of the carpus and tarsus often progressing to more proximal limb joints. Suppurative arthritis of the atlanto-occipital joint was common as was meningitis, peritonitis, and pleuritis. In 2001/02 but not in 2002/03 or 2003/04, necrotic dermatitis of the face and head was observed.

Samples were collected for aerobic culture where there was gross evidence of suppurative bacterial infection. In 2001/02, 33 of 40 (83%) of pups diagnosed as having bacterial infection had *Klebsiella pneumoniae* in pure culture from multiple organs. For 2002/03, 31 of 40 (76%) had this bacterium in pure culture. *Klebsiella pneumoniae* was not isolated from pups that died during the 1999/2000 (n = 15) and 2000/01 (n = 4) seasons and has not been isolated previously from New Zealand sea lions either from the 1997/98 epidemic, bycatch, or animals found dead at other sites. In October 2003 an adult male sea lion was found dead on the South Island of New Zealand at Cannibal Bay on the Catlins Coast with an extensive pharyngeal abscess from which *K. pneumoniae* was also isolated in pure culture. Isolates from both 2001/02 and 2002/03 epidemics have been compared using full pheno-identification (with API 20E kits) and Pulsed Field Gel Electrophoresis (PFGE) and determined to be monoclonal in origin (Castinel et al. unpubl. data).

Elevation in pup mortality attributable to Klebsiella pneumoniae

The mean (±SE) level of mortality to 16 January each season between 1992/93 and 2000/01 was 6.2 ± 0.9%. The level increased to 18.5 ± 2.1% for the two following seasons due to the *K. pneumoniae* epidemics, and fell to 6.7% in 2003/04. The increase in mortality attributable to *K. pneumoniae* at six weeks was 18.5%-6.2%, or 12.3%. The mean (±SE) level of

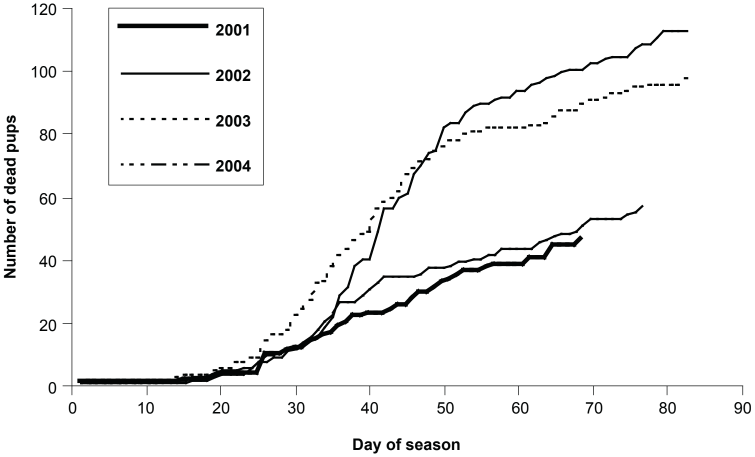


Figure 3. Cumulative totals of dead New Zealand sea lion pups at Sandy Bay, Enderby Island for years 2000/01-2003/04.

mortality to mid February each season between 1997/98 and 2000/01 was 16.7 ± 8.0%. The value for the two epidemic seasons was 26.8 ± 5.5%. The mortality level for 2003/04 was only 11.2%. The increase in mortality attributable to *K. pneumoniae* in mid February was 26.8%-16.7%, or 10.1%.

If the 1997/98 data point was excluded from the non-epidemic data, on the basis that while not a *K. pneumoniae* epidemic, there was an observed epidemic in that year and mortality was elevated, the figure for mortality to mid February was 8.6 ± 0.4%. This figure would produce an increase in mortality attributable to *K. pneumoniae* in mid February of 26.8%-8.6%, or 18.2%.

The increased mortality attributable to *K. pneumoniae* determined in mid February, incorporating the 1997/98 data point, was used in all calculations. While similar to that figure determined for mid January it provides more information from later in the season, encompassing the entire epidemic during the 2001/02 and 2002/03 seasons.

Trends in mortality within season are shown in Fig. 3. In both 2001/02 and 2002/03 numbers of pup mortalities were greater than the other two years, and there is a clear increase in the rate of mortality between days 30 and 50 (30 December to 19 January), which is not as evident in 2000/01 and 2003/04. Annual survival rates for cohorts of females derived from CJS models in program MARK ranged from 0.778 to 0.890 (see Table 1).

Table 1. Estimates of annual survival probabilities from five cohorts of females New Zealand sea lions.

Cohort	Estimate of survival rate ϕ	Standard error of estimate
1992/93	0.874	0.010
1991/92	0.890	0.009
1990/91	0.873	0.011
1989/90	0.841	0.014
1986/87	0.778	0.031

Table 2. Reduction in numbers of females alive at age 5 of the *Klebsiella* affected 2001/02 and 2002/03 cohorts, using highest and lowest survival estimates and an increase in mortality attributable to *Klebsiella* of 10.1%

Survival rate	Cohort	Number alive at age 5 (N5)	N5 with increased mortality rate in year 1	Reduction in number of females potentially recruiting
0.778	2001/02	325	283	42
	2002/03	359	312	47
0.89	2001/02	637	565	72
	2002/03	703	623	80

Table 3. Combined estimated reduction in numbers of females alive in 2007/08 of the *Klebsiella* affected 2001/02 and 2002/03 cohorts, using highest and lowest survival estimates and an increase in mortality attributable to *Klebsiella* of 10.1%

Survival rate	Cohort	Number alive at age 5 (N5)	Number alive at age 6 (N6)	N5 with increased mortality rate in year 1	N6 with increased mortality rate in year 1	Reduction in number of females in 2007/08
0.778	2001/02		253		220	33
	2002/03	359		312		60
0.89	2001/02		567		503	64
	2002/03	703		623		80

Table 4. Combined estimated reduction in numbers of females alive in 2007/08 of the *Klebsiella* affected 2001/02 and 2002/03 cohorts, using highest and lowest survival estimates and an increase in mortality attributable to *Klebsiella* of 18.2%.

Survival rate	Cohort	Number alive at age 5 (N5)	Number alive at age 6 (N6)	N5 with increased mortality rate in year 1	N6 with increased mortality rate in year 1	Reduction in number of females in 2007/08
0.778	2001/02		253		194	59
	2002/03	359		275		84
0.89	2001/02		567		451	126
	2002/03	703		559		144

Figures 4a-4d show the numbers of females surviving from the 2000/01, 2001/02, and 2002/03 cohorts after 1, 2, 3, 4, and 5 years. Figures 4a and 4b show the numbers alive at age assuming a 0.778 survival rate and a 0.89 survival rate through to age 5. Figs 4c and 4d show numbers alive with an additional 10.1% mortality in year 1 due to *K. pneumoniae.* This increase has been applied only to the 2001/02 and 2002/03 cohorts affected by the disease.

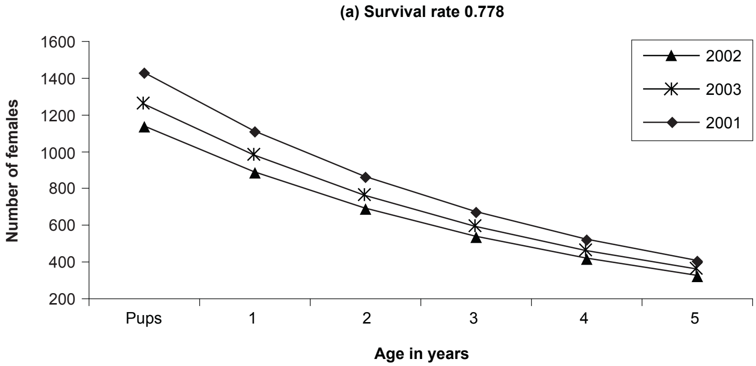
The reduction in numbers of females reaching 5 years of age due to increased first year mortality is shown in Table 2. Estimates for the 2001/02 cohort range from 42 to 72 depending on the survival rate used, while for the 2002/03 cohort the numbers range from 47 to 80.

Estimates of the combined loss of females from both the 2001/02 and 2002/03 cohorts when both are potentially mature will occur in 2007/08. Table 3 shows the possible reduction in number of females alive in 2007/08 (2001/02 cohort age 6, and 2002/03 cohort age 5) using the survival rates of 0.778 and 0.89, and the increase in mortality of 10.1% attributable to *K. pneumoniae*. At the lower survival rate the reduction was estimated at 93 females while at 0.89 the reduction was 144 females.

Table 4 shows the possible reduction in number of females alive in 2007/08 (2001/02 cohort age 6, and 2002/03 cohort age 5) using the survival rates of 0.778 and 0.89, and the increase in mortality of 18.2% attributable to *K. pneumoniae*. At the lower survival rate the reduction was estimated at 143 females while at 0.89 the reduction was 270 females

Discussion

Although *K. pneumoniae* has previously been recorded as a sporadic cause of septicaemia in marine mammals (Dunn et al. 2001), this is the



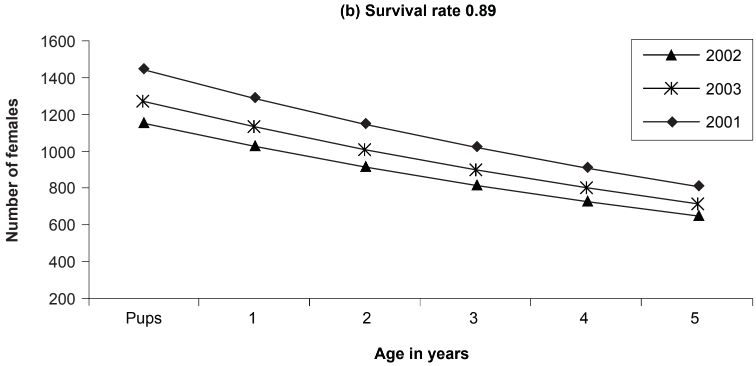
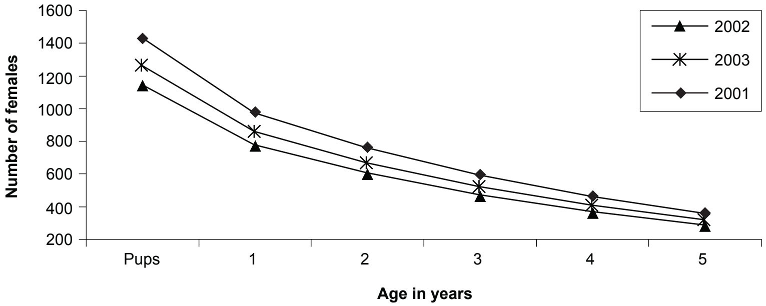


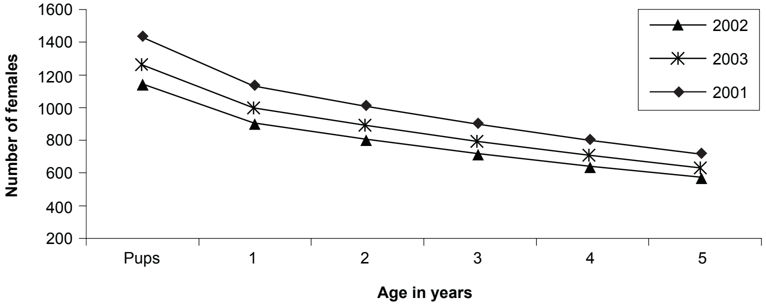
Figure 4. Numbers of female New Zealand sea lions of 2000/01, 2001/02, and 2002/03 cohorts surviving to ages 1-5 assuming an annual survival rate of (a) 0.778; (b) 0.89; (c) 0.778 with first year survival reduced by the additional mortality associated with a *Klebsiella* outbreak (10.1%) during the breeding seasons of 2001/02 and 2002/03; and (d) 0.89 with the additional first year mortality of 10.1% associated with a *Klebsiella* outbreak in 2001/02 and 2002/03.

first report of this pathogen causing epidemics. The sudden increase in neonatal mortality on approximately day 25 of two successive seasons suggest the highly infectious nature of this pathogen in the rookery. The fact that mortality and morbidity was limited to pups of the year further suggests that most adults may be resistant to, or even carriers of, this pathogen as occurs with *Salmonella* serotypes in this host (Leyland et al. 2003). Detailed disease investigation of this population prior to 2001/02

(c) Survival rate 0.778 with 10.1% increase in 1st year mortality



(d) Survival rate 0.89 with 10.1% increase in 1st year mortality



confirmed that the lesions characteristically found during the epidemics were not seen previously nor was this organism isolated from samples collected in those seasons. This evidence, combined with genetic typing of isolates from pups that died in 2001/02 and 2002/3, strongly suggests the introduction of a novel pathogen into a naive population and most likely from a single source. The death of an adult male sea lion from *Klebsiella* septicaemia on the South Island of New Zealand in October 2002 raises the possibility that infection may have originated on the mainland and been carried to the islands by an adult returning to breeding rookeries. Alternatively, animals dispersing away from the Aucklands after the breeding season could carry infection to the mainland or to other subantarctic islands (Robertson et al. 2006). Because bacterial infections are rarely the primary cause of epidemics among marine mammals (Higgins 2000, Dunn et al. 2001) investigations have focused on all possible aetiologies. However, there is no evidence for involvement of viruses, toxins, or other potential causes of immune dysfunction or disease.

Lesions consistent with *K. pneumoniae* infection were only found in 5 of 62 (8%) of pups that died during the 2003/04 season and the pathogen was again isolated from these cases. However, levels of pup mortality both in mid January and mid February were consistent with seasons prior to 2001/02 when the first of the epidemics occurred. This, in combination with the lack of a significant rapid change in the rates of mortalities (Fig. 3), compared to 2001/02 and 2002/03, suggest that 2003/04 can be considered a "normal season."

Mortality within the first six weeks of a normal season was estimated to be around 6%, while in years when *Klebsiella* impacts the population mortality could rise to three times this level ~18%. By mid February mortality in non-*Klebsiella* epidemic years can reach ~17%, with a comparative figure of 27% for the disease years. While the increase in mortality attributable to *Klebsiella* is higher in January, it was felt that the use of the 10.1% figure from mid February was more indicative given that the observed epidemics had subsided by that date.

Furthermore, despite the high mortality level seen in 1997/98, it was considered as a pre-*Klebsiella* year as there is no evidence to ascribe that event to this pathogen. By making this assumption the differential between pre-*Klebsiella* and *Klebsiella* mean mortalities has been reduced, thus reducing the additional cost on mortality attributable to disease. If the 1997/98 season were excluded the level of mortality would remain similar at six weeks of age, but increase from 10.1% to 18.2% by mid February. This would result in a reduced number of females recruiting.

Another important consideration was the empirical data used to derive survival rate. It is likely that survival rates used were overestimates due to the constant survival probabilities produced from the CJS models. This resulted from the lack of resight effort in the early years of each cohort and consequently survival probabilities were driven by numbers of animals seen at the tail of resight histories. In usual biological scenarios for *K* selected species such as pinnipeds, survival rates are lower among immatures than matures (Caughley 1977). A more likely scenario of a lower survival rate would reduce the number of females reaching maturity, and increase the cost (in absolute numbers) of the disease outbreak on that cohort.

Utilizing the available empirical survival data, the reduction in numbers of females reaching maturity as a result of the disease would range from 42 to 72 in 2006/07 when the 2001/02 cohort reach age five, while in 2007/08 when the 2002/03 cohort females reach five and the 2001/02 cohort have reached age six, the combined reduction of the two cohorts would range from 93 to 144 females.

As discussed above, if the 1997/98 data were excluded, the maximum increase in mortality from *Klebsiella* would reach 18.2% in mid February. Under this scenario, along with the previously utilized survival rates, the reduction in numbers of the 2001/02 cohort reaching age six and members of the 2002/03 cohort reaching five in 2007/08 would range from 143 to 270 females.

Absolute numbers of females removed from the population are important in management terms, as they relate directly to bycatch limits. In terms of the reduction in numbers as a proportion of the adult female population, the 2007/08 season is likely to be the first significantly affected by the combined *Klebsiella* outbreaks in 2001/02 and 2002/03. If the number of pups in 2007/08 is assumed to be the mean of the 1992/3-2003/04 seasons, i.e., 2,680 pups (see Appendix 1), the increased mortality associated with *Klebsiella* is 10.1%, and the proportion of females pupping ranges from 0.65 to 0.85 (I. Wilkinson unpubl. data), the reduction in numbers of females would range from 2.3 to 3.5% of the population at 65% fecundity and 2.9 to 4.6% at 85% fecundity. If the 18.2% figure is used for *Klebsiella* mortality the reductions in numbers of females would range from 3.5 to 6.5% at 65% fecundity and 4.5 to 8.6% at 85% fecundity.

The data in this study have shown that disease can play a significant role in the dynamics of pinniped populations. The epidemics observed in 2001/02 and 2002/03 in the New Zealand sea lion population will result in between 2.3% and 4.6% fewer adult females being present in the breeding population in 2007/08. In the case of threatened species such as the New Zealand sea lion, which are impacted by fisheries activities, it is vital to incorporate the effects of disease into management models to ensure that the effects of fishing related mortality on the population can be accurately determined, and appropriate bycatch limits set.

References

Baird, S.J. 1996. Non fish species and fisheries interactions working groups report, May 1996. New Zealand Fisheries Assessment Working Group Report 96/1, Ministry of Fisheries, Wellington.

Baker, A. (ed.). 1999. Unusual mortality of the New Zealand sea lion, *Phocarctos hookeri*, Auckland Islands, January-February 1998: A report of a workshop held 8-9 June 1998, Wellington, and a contingency plan for future events. Department of Conservation, Te Papa Atawhai, PO Box 10420, Wellington, New Zealand.

Borst, G.H.A., H.C. Walvoort, P.J.H. Reijnders, J.S. Van Der Kamp, and A.D.M.E. Osterhaus. 1986. An outbreak of a herpes virus infection in harbor seals (*Phoca vitulina*). J. Wildl. Dis. 22:1-6.

Broman, T., S. Bergstrom, S.L. On, H. Palmgren, D.J. McCafferty, M. Sellin, and B. Olsen. 2000. Isolation and characterization of *Campylobacter jejuni* subsp. *jejuni* from macaroni penguins *(Eudyptes chrysolophus*) in the subantarctic region. App. Env. Microbiol. 66:449-452.

Callan, R.J., G. Early, H. Kida, and V.S. Hinshaw. 1995. The appearance of H3N3 influenza viruses in seals. J. Gen. Virol. 76:199-203.

Caughley, G. 1977. Analysis of vertebrate populations. Wiley & Sons, New York. 234 pp.

Childerhouse, S., B. Dix, and N.J. Gales. 2001. Diet of New Zealand sea lions (*Phocarctos hookeri*) at the Auckland Islands. Wildl. Res. 28:291-298.

Doonan, I.J., and M.W. Cawthorn. 1984. Impacts of incidental mortality on the Hooker's sea lions. Internal report #6, Fisheries Research Division, New Zealand Ministry of Fisheries, Wellington.

Duignan, P.J. 1998. Morbillivirus infections of marine mammals. In: M. Fowler and R.E. Miller (eds.), Current therapy 4: Zoo and wildlife medicine IV. W.B. Saunders Co., Philadelphia, pp 497-501.

Duignan, P.J. 1999. Gross pathology, histopathology, virology, serology and parasitology. In: Baker, A. (ed.), Unusual mortality of the New Zealand sea lion, *Phocarctos hookeri*, Auckland Islands, January-February 1998: A report of a workshop held 8-9 June 1998, Wellington, and a contingency plan for future events. The Department of Conservation, Te Papa Atawhai, PO Box 10420, Wellington, New Zealand, pp. 29-33.

Duignan, P.J., J.T. Saliki, D.J. St. Aubin, G. Early, S. Sadove, J.A. House, K. Kovacs, and J.R. Geraci. 1995. Epizootiology of morbillivirus infection in North American harbor seals (*Phoca vitulina*) and gray seals (*Halichoerus grypus*). J. Wildl. Dis. 31:491-501.

Duignan, P.J., O. Nielsen, C. House, K.M. Kovacs, N. Duffy, G. Early, S. Sadove, D.J. St. Aubin, B.K. Rima, and J.R. Geraci. 1997. Epizootiology of morbillivirus infection in harp, hooded, and ringed seals from the Canadian Arctic and western Atlantic. J. Wildl. Dis. 32:7-17.

Dunn, L.J., J.D. Buck, and T.R. Robeck. 2001. Bacterial diseases of cetaceans and pinnipeds. In: L.A. Dierauf and F.M.D. Gulland (eds.), Marine mammal medicine, 2nd edn. CRC Press, Boca Raton, Florida, pp. 309-335.

Gales, N.J. 1995. New Zealand (Hooker's) Sea Lion Recovery Plan. Threatened Species Recovery Plan Series 17. Department of Conservation, Wellington.

Gales, N.J., and R.H. Mattlin. 1997. Summer diving behaviour of lactating New Zealand sea lions, *Phocarctos hookeri*. Can. J. Zool. 75:1695-1706.

Gales, N.J., and D.J. Fletcher. 1999. Abundance, distribution and status of the New Zealand sea lion, *Phocarctos hookeri*. Wildl. Res. 26:35-52.

Geraci, J.R., D.J. St. Aubin, I.K. Barker, R.G. Webster, V.S. Hinshaw, W.J. Bean, H.L. Ruhnke, J.H. Prestcott, G. Early, A.S. Baker, S. Madoff, and R.T. Schooley. 1982. Mass mortality of harbor seals: Pneumonia associated with influenza A virus. Science 215:1129-1131.

Gulland, F.M.D. 1995. The impact of infectious diseases on wild animal populations: A review. In: B.T. Grenfell and A.P. Dobson (eds.), Ecology of infectious diseases in natural populations. Cambridge University Press, Cambridge, pp. 20-51.

Gulland, F.M.D. 1999. Leptospirosis in marine mammals. In: M. Fowler and R.E. Miller (eds), Zoo and wildlife medicine IV. W.B. Saunders, Philadelphia, pp. 469-471.

Gulland, F., M. Koski, L.J. Lowenstine, A. Colagross, and L. Morgan. 1996. Leptospirosis in California sealions (*Zalophus californianus*) stranded along the central California coast. J. Wildl. Dis. 32:572-580.

Gulland, F.M.D., L.J. Lowenstine, J.M. Lapointe, T. Spraker, and D.P. King. 1997. Herpesvirus infection in stranded Pacific harbor seals of coastal California. J. Wildl. Dis. 33:450-458.

Harder, T.C., J. Plötz, and B. Liess. 1991. Antibodies against European phocid herpesvirus isolates detected in sera of Antarctic seals. Polar Biol. 11:509-512.

Harwood, J., and A. Hall. 1990. Mass mortality in marine mammals: Its implications for population dynamics. Trends Ecol. Evol. 5:254-257.

Heide-Jorgensen, M.P., T. Harkonen, and P. Aberg. 1992. Long term effects of epizootic in harbor seals in the Kattegat-Skaggerak and adjacent areas. Ambio 21:511-516.

Higgins, R. 2000. Bacteria and fungi of marine mammals: A review. Can. Vet. J. 41:105-116.

Jensen, T., M. van de Bildt, H. Dietz, T. Andersen, A. Hammer, T. Kuiken, and A.D.M.E. Osterhaus. 2002. Another phocine distemper outbreak in Europe. Science 297:209.

Kennedy, S., J.A. Smyth, P. Cush, P. Duignan, M. Platten, S.J. McCullough, and G.M. Allen. 1989. Histopathologic and immunocytochemical studies of distemper in seals. Vet. Pathol. 26:97-103.

Laws, R.M., and R.J.F. Taylor. 1957. A mass dying of crabeater seals, *Lobodon carcinophagus*, (Grey). Proc. Zool. Soc. Lond 129:315-325.

Leyland, M.J., P.J. Duignan, L. Rogers, J.H. Connolly, S. Fenwick, and C. Nicol. 2003. *Salmonella* infection in seals, pigs, and people in New Zealand. Third International Wildlife Management Congress, 1-5 December, Christchurch, New Zealand, Proceedings, pp. 456.

May, R.M. 1988. Conservation and disease. Cons. Biol. 2:28-30.

Molloy, J., and A. Davis. 1994. Setting priorities for the conservation of New Zealand's threatened plants and animals, 2nd edn. Department of Conservation, Wellington.

Munro, R., H. Ross, C. Cornwell, and J. Gilmour. 1992. Disease conditions affecting common seals (*Phoca vitulina*) around the Scottish mainland, September-November 1988. Sci. Total Env. 115:67-82.

Osterhaus, A.D.M.E., H. Yang, H.E. Spijkers, J. Groen, J.S. Teppema, and G. Van Steenis. 1985. The isolation and partial characterization of a highly pathogenic herpes virus from the harbour seal (*Phoca vitulina*). Arch. Virol. 86:239-251.

Osterhaus, A.D.M.E., J. Groen, P. De Vries, F.G.C.M. UytdeHaag, B. Klingeborn, and R. Zarnke. 1988. Canine distemper virus in seals. Nature 335:403-404.

Reijnders, P., S. Brasseur, J. van der Toorn, P. van der Wolf, I. Boyd, J. Harwood, D. Lavigne, and L. Lowry. 1993. Seals, fur seals, sea lions and walrus, status survey and conservation plan. IUCN/SSC Seal Specialist Group. IUCN, Gland, Switzerland.

Robertson, B.C., B.L. Chilvers, P.J. Duignan, I.S. Wilkinson, and N.J. Gemmell. 2006. Dispersal of breeding, adult male *Phocarctos hookeri*: Implications for disease transmission, population management and species recovery. Biol. Conserv. 127:227-236.

Smith, A.W. 1981. Marine reservoirs of caliciviruses. In: J.H. Steele (ed.), CRC handbook series in zoonoses, Sect. B, Vol. II. CRC Press, Boca Raton, Florida, pp. 182-190.

Smith, A.W., R.J. Brown, and D.E. Skilling. 1977. Naturally occurring leptospirosis in northern fur seals (*Callorhinus ursinus*). J. Wildl. Dis. 13:144-147.

Smith, A.W., D.E. Skilling, N. Cherry, J.H. Mead, and D.O. Matson. 1998. Calicivirus emergence from ocean reservoirs. Zoonotic and interspecies movements. Emerg. Infect. Dis. 4:13-20.

Stenvers, O., J. Plötz, and H. Ludwig. 1992. Antarctic seals carry antibodies against seal herpesvirus. Arch. Virol. 123:421-424.

Stratton, M., P.J. Duignan, N. Forester, J.S. Lumsden, and P. O'Toole. 2001. Prevalence of potentially pathogenic bacteria in New Zealand sea lions (*Phocarctos hookeri*). The Fourteenth Biennial Conference on the Biology of Marine Mammals, Nov. 28-Dec. 3, 2001, Vancouver, B.C., Canada. Proceedings, p. 207.

Taylor, R.H. 1971. Influence of man on vegetation and wildlife of Enderby and Rose Island, Auckland Islands. N.Z. J. Bot. 9:225-268.

Thompson, P.M., and A.J. Hall. 1993. Seals and epizootics: What factors might influence the severity of mass mortalities? Mamm. Rev. 23:149-154.

Vedros, N.A., A.W. Smith, and J. Schonweld. 1971. Leptospirosis epizootic among California sea lions. Science 172:1250-1251.

White, G.C., and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46(Suppl.):120-138.

Wilkinson, I.S., J. Burgess, and M.W. Cawthorn. 2003. New Zealand sea lions and squid: Managing fisheries impacts on a threatened marine mammal. In: N. Gales, M. Hindell, and R. Kirkwood (eds.), Marine mammals: Fisheries, tourism and management issues. CSIRO Publishing, Melbourne, pp. 192-207.

Woodly, T.H., and D.M. Lavigne. 1993. Potential effects of incidental mortalities on the Hooker's sea lions (*Phocarctos hookeri*) population. Aquat. Conserv. Mar. Freshw. Ecosyst. 3:139-148.

Young, T.P. 1994. Natural die-offs of large mammals: Implications for conservation. Conserv. Biol. 8:410-418.

Zarnke, R., T.C. Harder, H.W. Vos, J.M. Ver Hoef, and A.D. Osterhaus. 1997. Serologic survey for phocid herpesvirus 1 and 2 in marine mammals from Alaska and Russia. J. Wildl. Dis. 33:459-465.

Appendix 1. New Zealand sea lion pup production estimates at each of the four rookeries, and the combined total, at the Auckland Islands, 1992/93-2003/04.

	Rookery				
Season	Sandy Bay	Dundas Island	Figure of Eight Island	South East Point	Total
1992/93	424	1,870	69	26	2,389
1994/95	467	1,837	143	71	2,518
1995/96	455	2,017	144	69	2,685
1996/97	509	2,260	143	63	2,975
1997/98	477	2,373	120	51	3,021
1998/99	513	2,186	109	59	2,867
1999/2000	506	2,163	137	50	2,856
2000/01	562	2,148	94	55	2,859
2001/02	403	1,756	96	27	2,282
2002/03	489	1,891	95	43	2,518
2003/04	507	1,869	87	52	2,515
Mean					2,680

Modeling Spatial Dynamics of Steller Sea Lions (*Eumetopias jubatus*) Using Maximum Likelihood and Bayesian Methods: Evaluating Causes for Population Decline

Gavin Fay and André E. Punt
University of Washington, School of Aquatic and Fishery Sciences, Seattle, Washington

Abstract

The timing and extent of the negative population trend in the abundance of the western stock of Steller sea lions has not been geographically uniform. A stochastic metapopulation dynamics model is developed for Steller sea lions. This model allows for geographical differences in factors affecting population processes, and can be parameterized to represent a wide range of hypotheses for the decline in Steller sea lion abundance. Bayesian and maximum likelihood methods are used to fit this model to pup and non-pup count data, age structure samples, and survival estimates. Inferences from model selection criteria highlight the spatial variability in the types of impact deemed to provide most parsimonious representation of the data. Bayesian posteriors for the estimated model parameters show that many combinations of parameter values are able to provide similar fits to the data, even given a specific hypothesis for the decline. This highlights the uncertainty in the precise nature of the impact of these hypotheses. Indeed, while pup production is generally estimated consistently among models, estimates of the size of other components of the Steller sea lion population (such as total population size) depend greatly on the assumptions regarding the cause of the decline. The results demonstrate that future simulation modeling approaches will require more formal, spatial, and mechanistic descriptions of the manner in which specific hypotheses for the decline affect the population.

Introduction

Data from counts conducted by the National Marine Fisheries Service (NMFS) and the Alaska Department of Fish and Game (ADFG) of pups at rookeries, and of non-pups at rookeries and nonbreeding haul-out sites, suggest that the Alaskan population of Steller sea lions (Otariidae: *Eumetopias jubatus*) declined by approximately 85% between 1956 and 1998 (York et al. 1996, Sease and Loughlin 1999). In 1997, the population of Steller sea lions to the west of 144ºW (the western stock) was declared "endangered" under the Endangered Species Act, with the population to the east of this (the eastern stock) remaining "threatened" (Loughlin 1997).

Several reasons for the decline of the western stock of Steller sea lions have been postulated. York (1994) examined changes in the age-composition of samples collected in 1975-1978 and 1985-1986, and concluded that a 20% decline in the annual survival of juvenile females was the simplest explanation for the reduction in abundance. Pascual and Adkison (1994) analyzed several possible reasons for the decline in Steller sea lion abundance, and concluded that transient age-structure dynamics, historical pup harvesting, and short-term environmental stochasticity were unlikely causes, and that long-term environmental changes or a catastrophe of some sort were probably responsible. Other hypotheses regarding the decline of the western stock involve a reduction in birth rate, nutritional stress, predation, direct and indirect competition with fisheries, migration, disease, pollution, and the impact of a regime shift or trophic cascade (Calkins and Pitcher 1982, Merrick et al. 1987, Calkins and Goodwin 1988, Hoover 1988, York 1994, Loughlin and Merrick 1989).

To date, it has not been possible to exclude any of these hypotheses definitively, although past research efforts have eliminated redistribution, pollution, predation, subsistence harvest, disease, and natural fluctuations as the principal causes for the decline (NMFS 1992). Several authors suggest that the cause of the decline may be a combination of various factors (Loughlin and York 2000, Hunter and Trites 2001), and that the primary cause has likely changed over the period of decline (Loughlin and York 2000).

The timing and extent of the negative trend in the size of the western stock has not been uniform over the geographical range of the population. Trites and Larkin (1996) and York et al. (1996) both identified several spatially distinct trends in the abundance of Steller sea lions within the western stock. This suggests that the factors responsible for the decline have not been spatially homogeneous. The behavior of Steller sea lions does create distinct localized populations that may well enable spatial differences in the factors affecting population processes, such as survivorship and fecundity, to be expressed differentially within the overall population. In addition to evidence that Steller sea lions do not breed other than with their natal stock, Steller sea lions show a degree of tendency toward natal site fidelity in that females return to breed at either the site of birth, or at a site close to the natal site (Pitcher and Calkins 1981). At times other than the pupping and breeding season in the months of May to August, Steller sea lions disperse widely from their breeding areas, and may haul out at sites many hundreds of kilometers from these areas. Immature sea lions show a tendency to disperse even farther than mature animals (Raum-Suryan et al. 2002). Such a population structure, which is typical of otariids, is a good example of a metapopulation, whereby a set of distinct breeding populations are linked through dispersal of individuals, creating a "population of populations" (Hanski and Simberloff 1997).

The high degree of spatial structuring of Steller sea lion populations, and that of management decisions and other human influences likely to affect them, requires a population modeling approach that is spatially realistic. A stochastic, spatially structured, flexible modeling framework for Steller sea lions, which uses the metapopulation concept to account for spatial variability in population trend, is therefore developed. The population dynamics model is appropriate for Steller sea lions, and can be used to mimic the local dynamics of individual regions within the sea lion metapopulation. The implications of a number of different impact scenarios are considered, and model selection criteria used to compare among several different hypotheses regarding the type of impact on this sea lion population.

Methods

The population dynamics model (Appendix A) considers the western stock of Steller sea lions in Alaska as a metapopulation comprising six regions (Fig. 1), each of which includes one or more sea lion rookeries and a number of nonbreeding haul-out sites. Each region is considered within the modeling framework to represent an individual subpopulation in the metapopulation.

The sea lion population in a region is divided into the number of males, immature females, and mature females of each age. The numbers-at-age (by region) are updated each year by:

1. calculating the number of births;
2. allowing immature females to reach maturity; and
3. removing the deaths due to all causes.

Additional trends in birth and death rates can be implemented by imposing forcing functions on survival rate, pregnancy rate, and region-specific carrying capacity (see equations A.7-A.13). These forcing functions can be used to model the effect of unknown stressors on the Steller

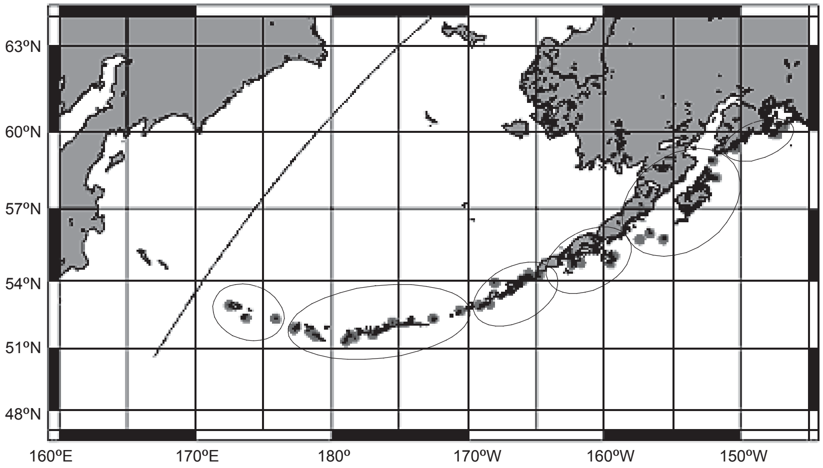


Figure 1. Map of the North Pacific Ocean showing the locations of the six regions of Steller sea lions comprising the Alaskan western stock metapopulation. The six regions are (from west to east): western Aleutian Islands, central Aleutian Islands, eastern Aleutian Islands, western Gulf of Alaska, central Gulf of Alaska, and eastern Gulf of Alaska.

sea lion population, which could result from one or more of the numerous hypotheses for the decline of the western stock. The model is flexible so that these functions can be parameterized to be region-specific, or global, so that one set of parameters determines the trends in survival and/or pregnancy rate in more than one region. The initial conditions (in 1945) correspond to a population at its pre-exploitation level, with the corresponding age-structure, as determined from the survival and maturity rates in Table A.1.

The model is fitted to four sources of data: (a) counts of the total number of pups in a region (which provides an index of the number of pregnant females in the region), (b) counts of non-pups at nonbreeding haul-out sites in a region (which provides a relative index of some component of the 1+ population in the region), (c) survival rates based on a tagging program, and (d) samples of the age-composition of the population in 1985. The survival rate and age-composition data are based on animals from the central Gulf of Alaska, and so these data are used only when estimating the values of the parameters of the population dynamics model for this region.

The parameters of the population dynamics model (Table 1) are either pre-specified based on auxiliary information for Steller sea lions, set to "guestimates" based on inferences from other species, or determined by fitting the population dynamics model to the available information on pup counts, non-pup counts, survival rate estimates, and the age-structure of the population inferred from collections. The parameters in the model that are related to density dependence are set at fixed values for the analyses of this paper. The resilience parameter, $\bar{A}$ is fixed at 0.22 and the parameter determining the degree of compensation, z, was fixed at 2.39, which corresponds to maximum pup production occurring when the regional non-pup population is at 60% of the equilibrium level.

The model fitting process involves either maximizing the likelihood function detailed in Appendix B (to provide the "best" estimates for the model parameters), or applying Bayesian methods to represent uncertainty in the model parameters and both current and historical population size.

Bayesian estimation

Bayesian estimation requires that prior distributions be placed on all of the "free" parameters of the model being fitted. The priors used when conducting the Bayesian analyses are listed in Table 1. Uniform prior distributions are assigned to all of the parameters except for the regional 1998 pup production (see below). The model is parameterized in such a way so as to be able to define as many estimable parameters as possible as fractions, thus taking values between zero and one. This enabled the placing of more objective uniform U[0,1] priors, and did not necessitate overly subjective choices regarding the bounds for the prior distributions. The parameters determining the reduction in the survival rate of pups and adults were chosen to be defined as fractions of the reduction in juvenile survival rate, because preliminary analyses showed that the survival rate of juveniles was reduced more than that of pups and adults.

The priors for the parameters that determine the year of maximum impact (smooth function), and the start year and impact duration (knife-edge function) are not specified in this manner. The bounds for these priors are constrained by the latest limit of the available data (2001), and either 1970 (for the knife-edge function) or 1980 (smooth function). These latter values reflect an understanding regarding the general timing of the Steller sea lion decline.

While the model is parameterized in such a way that the priors used encompass every possible value for many parameters, the method of parameterization is still somewhat subjective. For example, the impacts on survival rate are modeled with the maximum impact occurring on juveniles. While this is consistent with previous findings by York (1994), no account is made for the possibility that the reduction in the survival rates for adults and/or pups exceeded that for juveniles. Similarly, the years chosen for the bounds of the priors for the parameters determining the timing of the impact functions are arbitrary although they do encompass

Table 1. The parameters of the population dynamics model.

Parameter	Description	How specified	Prior
K^A	Regional pre-exploitation number of non-pups	Calculated	
	Pup production in 1998		$\text{Normal}\left[P_y^A,\left(\sigma_y^{A,P}\right)^2\right]$
X	Dispersal probabilities	Pre-specified	
Y	Mixing probabilities	Pre-specified	
M_a	Proportion mature at age	Pre-specified	
$\bar{A}$	Density-dependence (resilience) parameter	Pre-specified	
z	Degree of compensation	Pre-specified	
S_a	Age-specific survival rates	Pre-specified	
Parameters that determine the deterministic trend in pregnancy rate			
h_F^A	Maximum impact on pregnancy rate	Estimated	Uniform [0, 1]
y_F^A	Year of maximum impact on pregnancy rate	Estimated	1980 + Uniform [0,20]
$\sigma_{F1/2}^A$	Fraction of impact two years prior/post max.	Estimated	Uniform [0, 1]
υ_F^A	Year in which impact on pregnancy rate begins	Estimated	Uniform [1970, 2001]
l_F^A	Length of impact on pregnancy rate	Estimated	Uniform [0, 2002-υ_F^A]
Parameters that determine the deterministic trend in survival rate			
h_S^A	Maximum impact on juvenile survival rate	Estimated	Uniform [0, 1]
ϕ_1	Pup selectivity for survival impact	Estimated	Uniform [0, 1]
ϕ_2	Adult selectivity for survival impact	Estimated	Uniform [0, 1]
y_S^A	Year of maximum impact on survival rate	Estimated	1980+ Uniform [0, 20]
$\sigma_{S1/2}^A$	Fraction of impact two years prior/post max	Estimated	Uniform [0, 1]
υ_S^A	Year in which impact on survival rate begins	Estimated	Uniform [1970, 2001]
l_S^A	Length of impact on survival rate	Estimated	Uniform [0, 2002-υ_S^A]

Table 1. (continued.)

Parameter	Description	How specified	Prior
Parameters that determine the deterministic trend in carrying capacity			
ψ^A	Carrying capacity impact	Estimated	Uniform [0, 1]
y_ψ^A	Year in which impact on carrying capacity begins	Estimated	Uniform [1970, 2001]
l_ψ^A	Length of impact on carrying capacity	Estimated	Uniform [0, 2002- y_ψ^A]

the period for which data are available and the posterior distributions for these parameters show little evidence of probability density "piling up" at the boundaries.

The Bayesian calculations are implemented using the sampling-importance-resampling (SIR) algorithm (Rubin 1987, Gelman et al. 1995, Punt and Hilborn 1997). This algorithm samples parameter vectors from the Bayesian posterior distribution by generating a large number of parameter vectors from the prior probability distribution, and then re-sampling from these vectors with probability proportional to the likelihood. The backwards approach to Bayesian assessments (Butterworth and Punt 1995, Fay 2004) was implemented, with the value for the region-specific initial population size, K^A, (needed to compute the initial age structure), being determined by drawing from a prior distribution for the pup production in 1998, and then using Brent's method (Press et al. 1996) to solve for the value of K^A that would result in the selected pup production. The most recent pup count is then omitted from the likelihood function because the prior distribution has already been updated using this information. The 1998 pup counts were used when applying the backwards method, rather than the most recent pup count (often for the year 2000 or 2001). This was because maximum likelihood fits suggested that, for some regions, the model did not fit the more recent estimates of pup production very well (the MLE of the 2000-2001 pup count deviated by more than 1 standard error from the observation). The difference in using the count for 1998 rather than the most recent count is almost completely purely computational; the results would be essentially the same irrespective of the choice of year within the last few years.

The SIR algorithm was run until the maximum importance weight assigned to any single parameter vector was less than or equal to 0.5 percent of the total weight of all draws from the prior distributions. This convergence criterion ensured that there was a sufficiently large number of unique parameter vectors in the importance-weighted second sample of 1,000 parameter vectors to enable an investigation of the joint posterior distribution for the model parameters. However, for some regions the count data are highly informative, and very large numbers (several hundred million) of draws from the priors did not attain the convergence criterion.

Scenarios examined

The analyses of this paper consider the six regions of the western stock of Steller sea lions as distinct independent populations, with no movement of animals linking them. Impact functions (time-varying survival rates, changes in pregnancy rate/carrying capacity) in one region do not therefore affect the dynamics of the population in any other region. This assumption greatly simplifies the parameter estimation process because the estimation of the parameters governing the dynamics for each region can be conducted independently. A further simplification for the purposes of the analyses of this paper is that the dynamics are deterministic [$Bin(x,p)=xp$], i.e., no account is taken of demographic stochasticity; results in which demographic stochasticity is taken into account are not qualitatively different from those presented here. It is not presentationally feasible to provide the detailed results for all six regions, and so the results presented focus primarily on the central Aleutian Islands and western Gulf of Alaska regions. Observations resulting from concurrent analyses for the other four regions that are of particular interest are also discussed.

Table 2 lists the nine scenarios considered in this paper. These scenarios are based on different combinations of the impact functions. Table 2 also lists the parameters that are estimated for each scenario. These nine scenarios are compared for each region using maximum likelihood methods, and the Bayesian estimation framework outlined above. The results of the maximum likelihood estimation are compared using Akaike's Information Criteria corrected for small sample size (AIC_c) (Burnham and Anderson 1998). AIC_c allows for model selection among non-nested models, and includes penalties both for lack of fit to the data and model complexity (number of estimated parameters). The results of the Bayesian analyses are compared in a similar way, using the Deviance Information Criterion (DIC) (Spiegelhalter et al. 2002).

Results

Model selection based on AIC_c and DIC

Table 3 lists AIC_c and DIC values for the nine impact scenarios for the six regions and identifies the model with the lowest AIC_c/DIC for each region. Figure 2 shows the fits to pup and non-pup counts, and the estimates of the total number of non-pups for each region for the model selected using AIC_c, while Fig. 3 shows posterior distributions (medians and 95%

Table 2. The nine impact scenarios. The column "free parameters" lists the parameters that are estimated for each scenario in addition to the pre-exploitation number of non-pups, K^A and the parameters that determine the relative availability of non-pups.

	Impact			
Scenario	Survival rate	Pregnancy rate	Carrying capacity	Free parameters
1	Smooth impact	None	None	$h_S^A, \phi_1, \phi_2, y_S^A, \sigma_{S1/2}^A$
2	None	Smooth impact	None	$h_F^A, y_F^A, \sigma_{F1/2}^A$
3	Smooth impact	Smooth impact	None	$h_S^A, \phi_1, \phi_2, y_S^A, \sigma_{S1/2}^A, h_F^A, y_F^A, \sigma_{F1/2}^A$
4	Knife-edged impact	None	None	$h_S^A, \phi_1, \phi_2, \upsilon_S^A, l_S^A$
5	None	Knife-edged impact	None	$h_F^A, \upsilon_F^A, l_F^A$
6	Knife-edged impact	Knife-edged impact	None	$h_S^A, \phi_1, \phi_2, \upsilon_S^A, l_S^A, h_F^A, \upsilon_F^A, l_F^A$
7	None	None	Knife-edged impact	$\psi^A, y_\psi^A, l_\psi^A$
8	Smooth impact	Knife-edged impact	None	$h_S^A, \phi_1, \phi_2, y_S^A, \sigma_{S1/2}^A, h_F^A, \upsilon_F^A, l_F^A$
9	Knife-edged impact	Smooth impact	None	$h_S^A, \phi_1, \phi_2, \upsilon_S^A, l_S^A, h_F^A, y_F^A, \sigma_{F1/2}^A$

probability intervals) for the time-trajectories of total regional non-pups, pup production, and the fits to the non-pup counts for each region for the model selected using DIC.

The model selected by $\mathrm{AIC_c}$ varied among regions. Models with impacts on both survival and pregnancy rates were favored for four of the six regions (eastern and central Gulf of Alaska, and the eastern and central Aleutians). For the eastern Gulf of Alaska, the model with a knife-edged impact on both survival and pregnancy rate (model 6) was selected, whereas for the other three regions, the model that had a knife-edged impact on survival and a smooth impact on pregnancy rate (model 9) was selected. The "best" model for the western Gulf of Alaska was deemed to be that which only had a smooth impact function affecting pregnancy rate

Table 3. AICc and DIC values for the nine impact scenarios for each of the six regions. Values in bold for each region indicate the model with the lowest AICc/DIC value.

Scenario	Eastern GoA	Central GoA	Western GoA	Eastern Aleutians	Central Aleutians	Western Aleutians
			AICc			
1	95.40	83.47	53.55	73.68	63.15	42.46
2	82.92	75.94	**33.40**	83.35	61.26	56.00
3	62.21	58.96	51.11	54.94	60.81	89.02
4	94.31	145.23	68.94	99.03	80.22	**35.49**
5	69.95	1343.48	124.45	162.20	164.19	46.56
6	**40.71**	131.03	51.10	74.98	86.08	48.63
7	70.53	1496.99	169.34	174.04	187.41	86.54
8	45.97	91.87	67.20	80.13	79.40	65.27
9	54.01	**57.22**	47.12	**52.91**	**55.44**	64.75
			DIC			
1	80.57	69.48	40.88	61.28	49.35	23.93
2	75.79	70.03	26.96	77.87	44.33	38.16
3	23.59	38.53	17.8	32.54	32.06	15.17
4	77.11	121.73	51.79	83.86	68.55	20.82
5	65.27	1338.67	116.58	156.52	149.16	37.62
6	**16.77**	54.70	24.53	57.05	**28.98**	**10.73**
7	64.33	1494.38	151.75	159.59	173.71	30.58
8	18.13	70.19	43.38	59.21	43.80	14.31
9	45.89	**35.41**	**13.14**	**30.81**	30.42	16.74

(model 2), while for the western Aleutian Islands region, the model with a knife-edged reduction in survival rate (model 4) was selected.

For the regions toward the center of the range of the western stock, the models selected using DIC are similar to those selected using AIC_c. Model 9 was chosen as the "best" model for the central and western Gulf of Alaska, and the eastern Aleutian Islands regions. For the eastern Gulf, central Aleutians and western Aleutian Islands regions, model 6 (knife-edged reductions in both survival and pregnancy rate) was chosen as the "best" model. The impact scenarios selected by AIC_c therefore differ from those selected by DIC for the central and western Aleutians, and also for the western Gulf of Alaska.

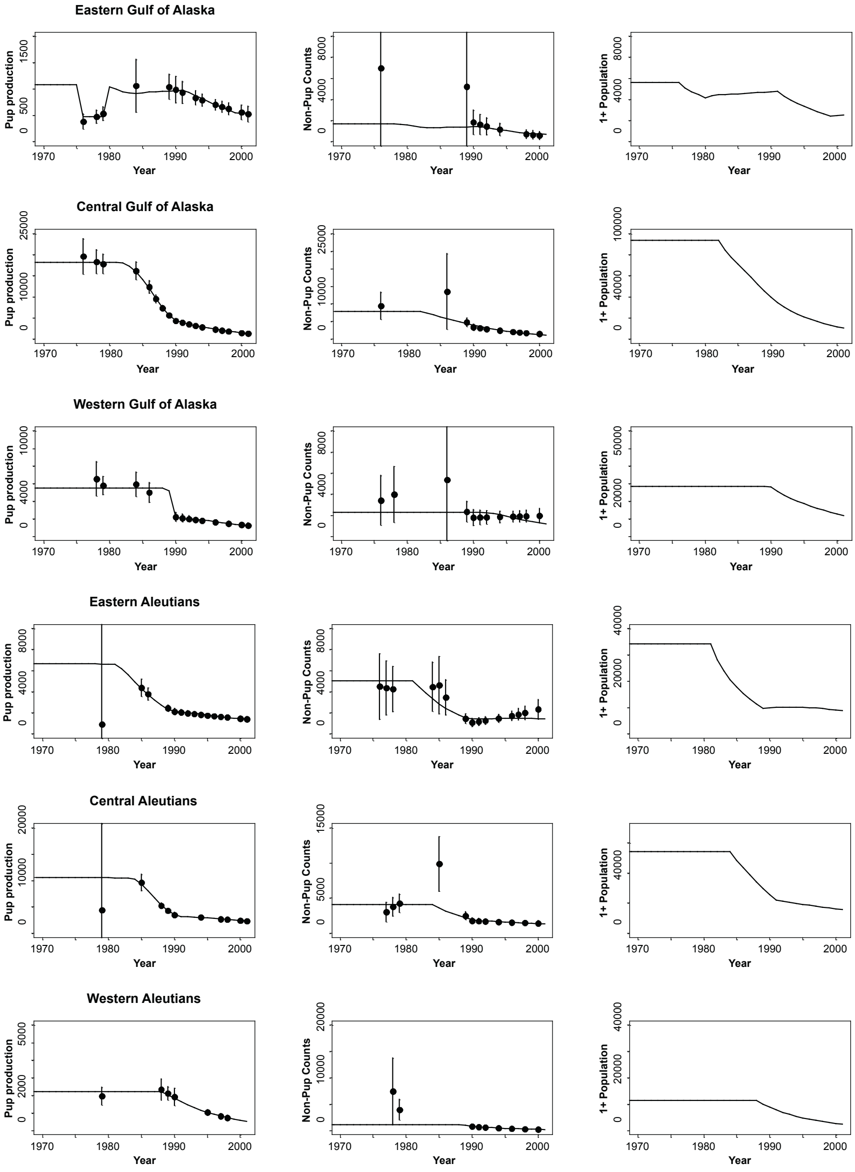


Figure 2. Fits to the pup and non-pup count data, and estimates of total non-pups, corresponding to the maximum likelihood estimates obtained from the models selected by AIC$_c$ for all six regions.

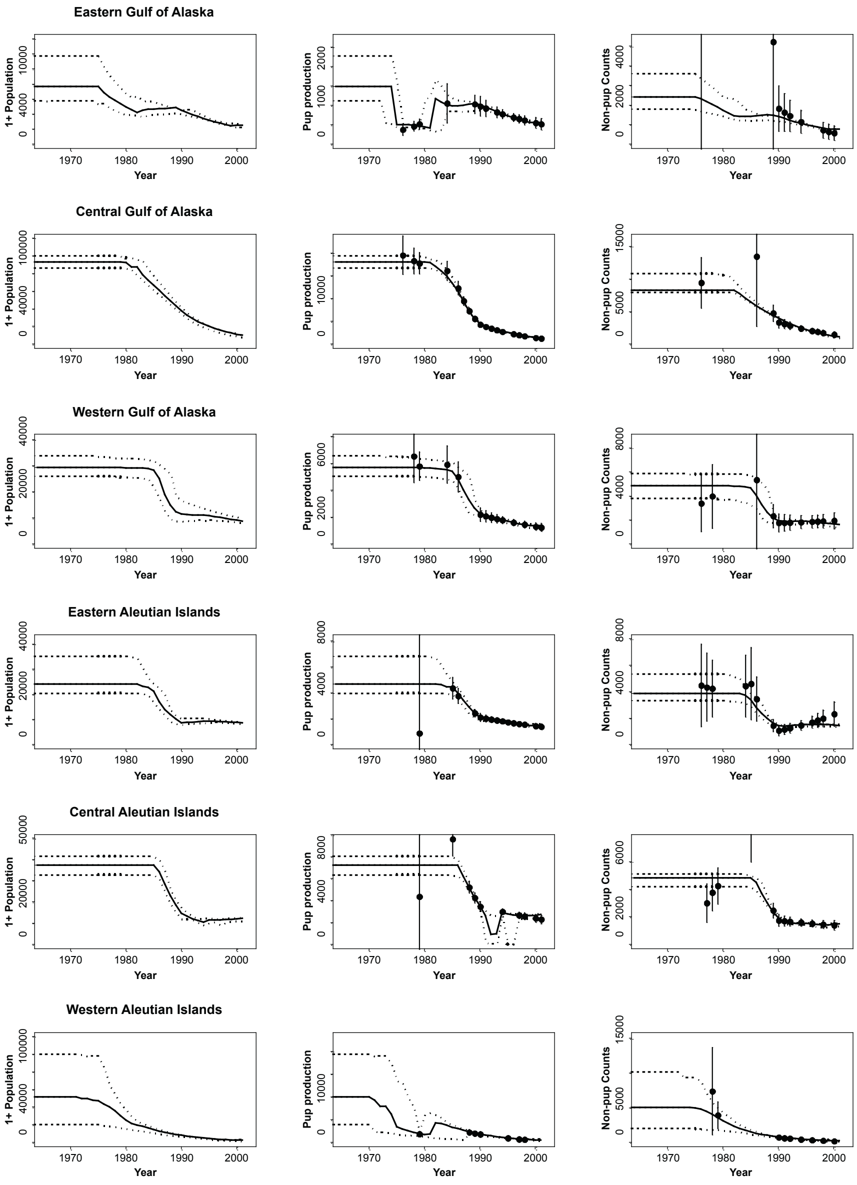


Figure 3. Median and central 95% probability intervals for the time trajectories of total regional non-pups, pup production, and estimated non-pup counts on haul-outs, for all six regions, for the models selected by DIC.

The models in which there is only a knife-edged reduction in pregnancy rate (model 5), or a knife-edged reduction in carrying capacity (model 7)—which implies a density-dependent increase in pregnancy rate—provided markedly poorer fits to the pup and non-pup count data than the other models for all six regions (Table 3).

The differences in AIC_c/DIC values between the "best" model and the next best model are not very large for some of the regions. This is particularly apparent for the central Gulf of Alaska, where model 3, the model with a smooth impact function on both survival and pregnancy rate, has an AIC_c value of 58.96 compared to a value of 57.22 for the "best" model (model 9). The importance of this is that, under a model-averaging procedure using AIC weights (Burnham and Anderson 1998), this "second best" model would receive almost as much weight as the "best" model. The other regions in which model 9 was selected by AIC_c as the "best" model (the eastern and central Aleutian Islands) also had an AIC_c value for model 3 that was close to the minimum value corresponding to model 9 (Table 3).

Region-specific results

Western Gulf of Alaska

The model selected by AIC_c for the western Gulf of Alaska as the "best" model was model 2, the impact scenario in which pregnancy rate (only) declined smoothly (Table 3; Fig. 2, third row of panels). There is no obvious trend in non-pup counts for this region after 1990, and there is little information in the non-pup counts for this region prior to 1990 (all estimates for the years pre-1990 for this region have very high CVs) (Fig. 2, third row). Consequently, there is little information that would suggest a reduction in survival as the cause of the decline in pup production inferred by the pup count data for this region, as opposed to a reduction in pregnancy rate.

The two impact scenarios selected by AIC_c and DIC for the western Gulf of Alaska lead to very similar estimates of historical (1945) numbers of non-pups; the central 95% of the posterior probability for this size lies between 25,924 and 33,764 sea lions for model 9, and between 26,280 and 32,910 for model 2 (Figs. 3 and 4). Inspection of the posterior distributions for the impact parameters for model 9 (Fig. 5a) reveals that the primary cause of the decline was a large impact on the survival rate of juveniles in the mid-late 1980s. The posteriors for the survival impacts on juveniles, pups, and even adults, span a wide range of values, suggesting that different combinations of relative impacts on these three classes of animals can provide almost equally good fits to the data. The posterior for y_F^A ("y F" in Fig. 5a) suggests that the pregnancy rate had to be reduced toward the end of the time series to fit the data for this model.

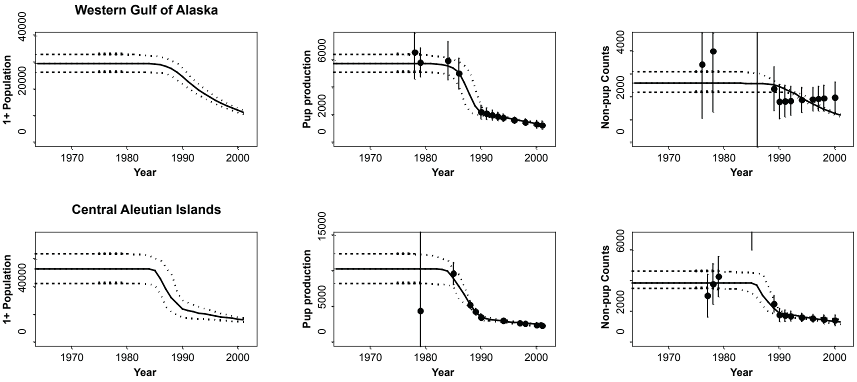


Figure 4. Median and central 95% probability intervals for the time trajectories of total regional non-pups, pup production, and estimated non-pup counts on haul-outs, for the models selected by AIC$_c$ when the results of AIC$_c$ differed to those of DIC: model 2 (western Gulf of Alaska), and model 9 (central Aleutian Islands).

For the model that assumed only a smooth reduction in pregnancy rate (model 2), the posteriors indicate that a 50-60% reduction in pregnancy rate occurred during the late 1980s, and that the pregnancy rate is still depressed (see the posteriors for h_F^A -"h F" and σ_{F2}^A - "sigma F2" in Fig. 5b). The wide posterior for the parameter determining the shape of the left-hand side of the smooth pregnancy rate function (σ_{F1}^A- "sigma F1" in Fig. 5b) indicates that, although the mode of the posterior for the year of maximum impact is around 1990, pregnancy rate was reduced for much of the late 1980s for all parameter vectors in the posterior. The magnitude of the impact on pregnancy rate is correlated with regional non-pup carrying capacity (Fig. 6), and interestingly, the magnitude of the impact in pregnancy rate did not change with the timing of the impact (Fig. 6, lower panels).

Central Aleutian Islands

The model selected by DIC for the central Aleutian Islands region was model 6, which differed from that selected by AIC$_c$ (model 9). Unlike the situation for the western Gulf region, the fits to the data and the 95% posterior intervals for the time trajectory of non-pups for the central Aleutians region for the models selected using AIC$_c$ and DIC differ appreciably (Figs. 3 and 4). The nine models imply quite different trends in the size of the regional population prior to the decline. Estimates of both the number of non-pups in 1945 for this region and the width of the central 95% posterior intervals of this quantity vary greatly among models. For

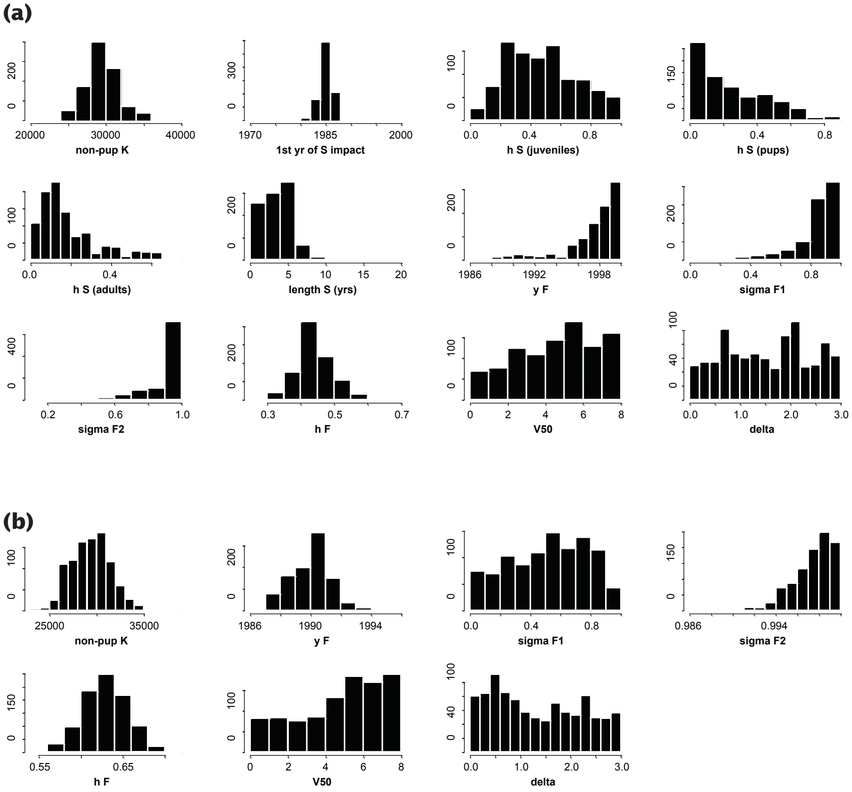


Figure 5. Posterior distributions for some of the model parameters based on fitting (a) model 9, and (b) model 2 to the data for western Gulf of Alaska. Parameter labels on panels are the same as those used in Table 1, except for "1st yr of S impact" (v_S^A), and "length S (yrs)" (l_S^A).

example, with the exception of model 9 (the model selected by AIC$_c$), the models that included a reduction in survival rate predict that the Steller sea lion population in this region is currently either stable or increasing (Fig. 7) while the models that just considered a reduction in pregnancy rate (models 2, 5, and 8), as well as model 9, suggest otherwise, with the 95% probability intervals for the trend in non-pups in the recent years showing a further decline (Fig. 7).

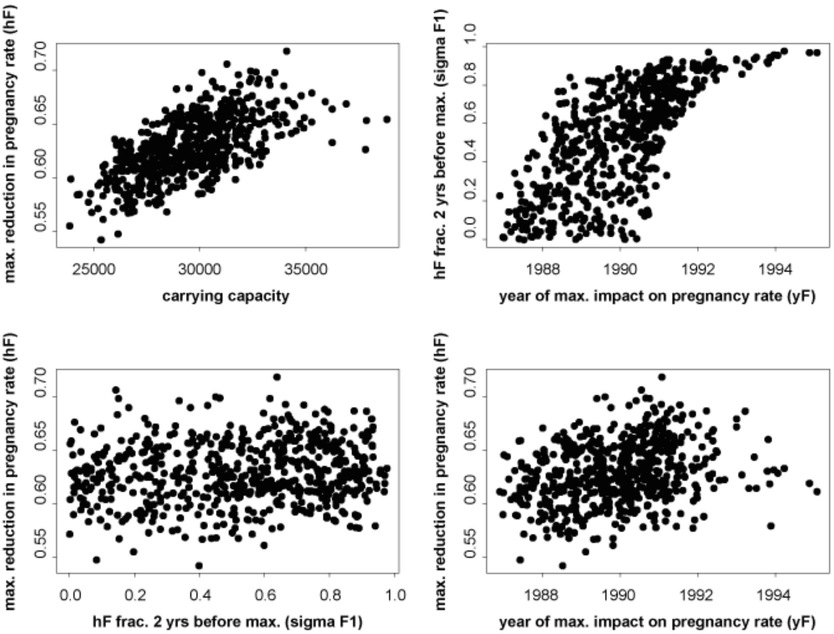


Figure 6. Correlation plots of some of the model parameters from the posteriors obtained for the western Gulf of Alaska region for model 2, the model with a smooth reduction in pregnancy rate only.

Discussion

Estimation of trends and population size

The current and pre-decline pup production was generally estimated consistently regardless of the impact scenario considered as the cause of the decline (perhaps with the exception of models 5 and 7, knife-edged reductions in pregnancy rate and carrying capacity respectively, although these models tended to provide poorer fits to the data than the alternative models). The pup count data were generally mimicked very well (e.g., Figs. 2-4). In contrast, the models were often very inconsistent when estimating the sizes of other population components, such as the total number of non-pups (e.g., Fig.7). In some regions, the estimated number of non-pups at equilibrium differed by up to two orders of magnitude depending on the impact scenario. This clearly reflects the nature of the assumed impact on the population, as this will determine how the relationship between the pups and the non-pups changes over time. As the non-pup counts are assumed to be relative indices of female abundance,

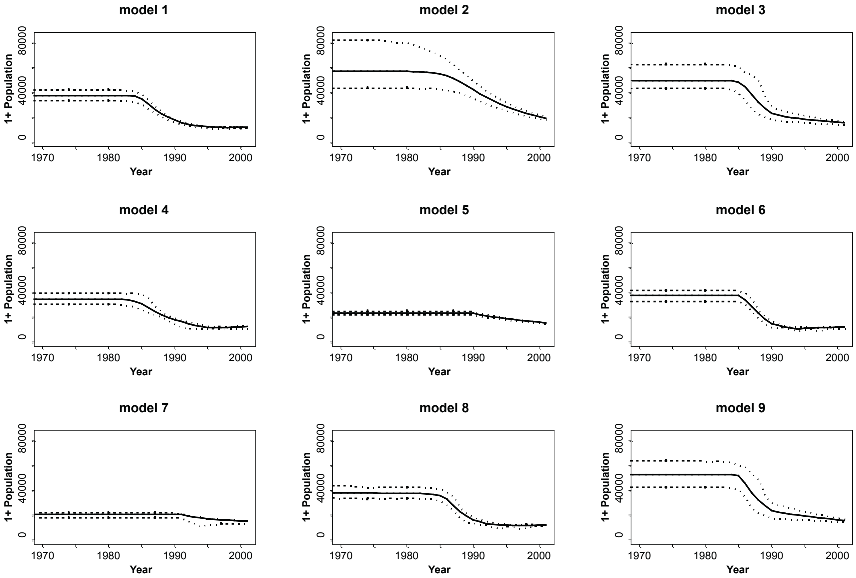


Figure 7. Median and central 95% probability intervals for the time-trajectory of the total number of non-pups for the central Aleutian Islands region for each of the nine models.

estimates of the numbers of non-pups will change depending on how the impact affects changes in pup production. The results of the Bayesian analyses demonstrate further the level of uncertainty associated with estimating regional total non-pup population sizes.

Model selection results, along with model predictions, were also observed by Fay (2004) to be sensitive to the choice of data set. Analyses for the central Gulf of Alaska that omitted the estimates of survival rates resulted in model 2 (smooth reduction in pregnancy rate), being selected by AIC_c as the "best" model, as opposed to models that included a survival impact (Table 3). This is unsurprising, because the estimates of survival rate are lower than those assumed under equilibrium (Table A.1).

The selection by AIC_c and DIC of different models depending on the region being analyzed demonstrates the benefits of adopting a spatial approach over one in which no account is made for differing impacts among regions. For those regions where the same type of impact scenario was selected as the most parsimonious representation of the data, the estimates of the values for the parameters providing that representation were markedly different. If the same impact scenario is assumed to apply to all regions and those regions are parameterized using the same

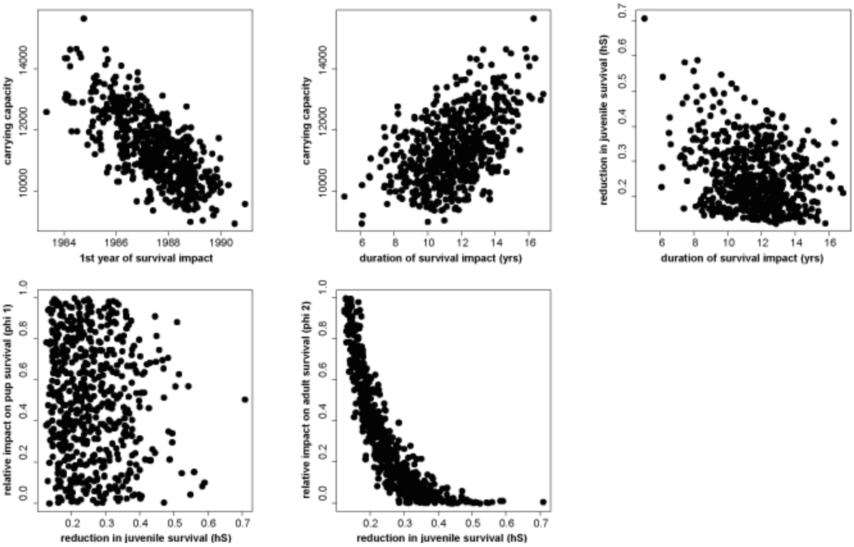


Figure 8. Correlation plots of some of the model parameters from the posteriors obtained for the western Gulf of Alaska region for model 9, the model with a knife-edged reduction in survival and a smooth reduction in pregnancy rate.

values for the parameters of the impact functions, then the fit to the data is extremely poor compared to that obtained when it is assumed that the values for the parameters are region-specific. For example, fitting model 9 to the data for all regions leads to a negative log-likelihood of 43.94 when the impact parameters are allowed to vary by region, and a value of 654.35 when the values for the model parameters related to impacts are assumed to be the same across all regions. The AIC_c resulting from this example is 299.93 for the independently parameterized version of the model compared to 1343.5 for the "global" scenario. This demonstrates that adopting a spatially heterogeneous view enables more of the trend in the data to be explained, supporting the spatially explicit parameter estimation procedure adopted here.

Can the existing data identify the population processes that caused the decline?

Even given the assumption of a certain impact scenario as the cause of the decline in Steller sea lion abundance for a region, the Bayesian posteriors demonstrate that there are many parameter combinations that are consistent with the data (Figs. 6 and 8). That is, the way in which a given impact scenario may be expressed within the population is not necessarily easily determined. This is particularly true for the survival impacts, where the relative impact on the survival rate of adults is correlated with that for juveniles for some regions (e.g., Fig. 8), implying a number of different ways in which an impact perturbs the population while providing similar predictions of model quantities such as total number of non-pups.

The lack of correlation among some of the other parameters (Fig. 8) also presents challenges, as this suggests that a very large number of combinations of parameter values can provide adequate fits to the data. The results show that there is a distinct inability to elucidate from the count data the precise nature in which a type of impact could affect the population, even given a particular impact scenario. In the instance of an adult survival impact versus a juvenile survival impact, additional data on the age structure of the population would probably assist in determining the real cause of the observed trend.

Several authors suggest it is likely that a number of factors were/are responsible for the decline in abundance of the western stock (Loughlin and York 2000, Hunter and Trites 2001). The scenarios considered in the analyses above assume only one type of each impact (i.e., one reduction in survival, along with one reduction in pregnancy rate), and assume that the vital rates affected by these impacts will return to their pre-impact levels following the cessation of the impact. Allowing for more than one forcing function affecting, for example, survival could allow the population dynamics model to accommodate a larger number of possible causes for the decline. However, prior knowledge regarding the likely effects of the modeled hypotheses would be required to prevent confounding among the parameters of these impact functions.

While the analyses of this paper have considered a number of different impact scenarios, little effort has been made to relate these to the various mechanistic hypotheses for the cause of the Steller sea lion decline. That the results of these investigations suggest a number of ways in which it is possible to fit the data means that, to properly assess the likelihood/importance of a given hypothesis for the decline, a mechanistic understanding of the manner in how that hypothesis could affect vital rates (such as survival and pregnancy rates) of Steller sea lions is necessary. This is important, as many of the postulated causes of the decline may ultimately express themselves in the Steller sea lion population in the same way (e.g., by a reduction in survival). However, the spatial and temporal trends in such an expression may be sufficiently different among hypotheses to enable isolation of a particular cause from another. As such, it will be necessary to obtain a detailed idea of the likely spatial/temporal effect of a given hypothesis, in addition to the section of the population likely impacted, before any final conclusions can be drawn. The flexible nature of the modeling framework presented in this paper does, however, enable the incorporation of such detailed information, should it be available.

Acknowledgments

Funding for this work was provided by NOAA Fisheries and the North Pacific Universities Marine Mammal Research Consortium. The comments by Milo Adkison (University of Alaska) are gratefully acknowledged.

References

Burnham, K.P., and D.R. Anderson. 1998. Model selection and inference: A practical information-theoretic approach. Springer-Verlag, New York.

Butterworth, D.S., and A.E. Punt. 1995. On the Bayesian approach suggested for the assessment of the Bering-Chukchi-Beaufort seas stock of bowhead whales. Rep. Int. Whal. Comm. 45:303-311.

Calkins, D.G., and E. Goodwin. 1988. Investigation of the declining sea lion population in the Gulf of Alaska. Alaska Department of Fish and Game. 76 pp.

Calkins, D.G., and K.W. Pitcher. 1982. Population assessment, ecology and tropic relationships of Steller sea lions in the Gulf of Alaska. Alaska Department of Fish and Game, Final Report RU243. 128 p.

Calkins, D.G., D.C. McAllister, K.W. Pitcher, and G.W. Pendleton. 1999. Steller sea lion status and trend in southeast Alaska: 1979-1997. Mar. Mamm. Sci. 15:462-477.

Fay, G. 2004. A Bayesian stochastic metapopulation model for Steller sea lions in Alaska. M.S. thesis, University of Washington, Seattle. 253 pp.

Gelman, A., B.P. Carlin, H.S. Stern, and D.B. Rubin. 1995. Bayesian data analysis. Chapman and Hall, London.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. In: I. Hanski and M.E. Gilpin (eds.), Metapopulation biology: Ecology, genetics and evolution. Academic Press Inc., San Diego, pp. 5-26.

Hoover, A.A. 1988. Steller sea lion, *Eumetopias jubatus*. In: J.W. Lentfer (ed.), Selected marine mammals of Alaska: Species accounts with research and management recommendations. Marine Mammal Commission, Washington, D.C., pp. 159-193.

Hunter, A.M.J., and A.W. Trites. 2001. An annotated bibliography of scientific literature (1751-2000) pertaining to Steller sea lions (*Eumetopias jubatus*) in Alaska. Fish. Res. Centre Res. Rep. 9(1):1-45.

Loughlin, T.R. 1997. Using the phylogeographic method to identify Steller sea lion stocks. In: A. Dizon, S.J. Chivers, and W.F. Perrin (eds.), Molecular genetics of marine mammals. Soc. Mar. Mammal. (Spec. Publ. 3), pp. 159-171.

Loughlin, T.R., and R.L. Merrick. 1989. Comparison of commercial harvest of walleye pollock and northern sea lion abundance in the Bering Sea and Gulf of Alaska. In: Proceedings of the International Symposium on the Biology and Management of Walleye Pollock. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 679-700.

Loughlin, T.R., and A.E. York. 2000. An accounting of the sources of Steller sea lion, *Eumetopias jubatus*, mortality. Mar. Fish. Rev. 62:40-45.

Merrick, R.L., T.R. Loughlin, and D.G. Calkins. 1987. Decline in abundance of the northern sea lion, *Eumetopias jubatus*, in Alaska, 1956-86. Fish. Bull. US. 85:351-365.

NMFS. 1992. Final Recovery Plan for the Steller sea lion (*Eumetopias jubatus*). Prepared by the Steller Sea Lion Recovery Team for the National Marine Fisheries Service (NMFS), Silver Spring, Maryland. 92 pp.

Pascual, M.A., and M.D. Adkison. 1994. The decline of the Steller sea lion in the Northeast pacific: Demography, harvest or environment. Ecol. Appl. 4:393-403.

Pitcher, K.W., and D.G. Calkins. 1981. Reproductive biology of Steller sea lions in the Gulf of Alaska. J. Mammal. 62:599-605.

Press, W.H., B.P. Flannery, S.A. Teukolsky, and W.T. Vetterling. 1996. Numerical recipes in FORTRAN. 2nd edn. Cambridge University Press, Cambridge.

Punt, A.E., and R. Hilborn. 1997. Fisheries stock assessment and decision analysis: The Bayesian approach. Rev. Fish Biol. Fish. 7:35-63.

Raum-Suryan, K.L., K.W. Pitcher, D.G. Calkins, J.L. Sease, and T.R. Loughlin. 2002. Dispersal, rookery fidelity, and metapopulation structure of Steller sea lions (*Eumetopias jubatus*) in an increasing and a decreasing population in Alaska. Mar. Mamm. Sci. 18:746-764.

Rubin, D.B. 1987. Comment: The calculation of posterior distributions by data augmentation. J. Am. Statist. Assoc. 82:543-546.

Sease, J.L., and T.R. Loughlin. 1999. Aerial and land-based surveys of Steller sea lions (*Eumetopias jubatus*) in Alaska, June and July 1997 and 1998. NOAA Tech. Memo. NMFS-AFSC-100. 61 pp.

Spiegelhalter, D.J., N.G. Best, B.R. Carlin, and A. van der Linde. 2002. Bayesian measures of model complexity and fit. J.R. Statist. Soc. B. 64:583-616.

Trites, A.W., and P.A. Larkin. 1996. Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: How many were there? Aquat. Mamm. 22:153-166.

Trites, A.W., and B.T. Porter. 2002. Attendance patterns of Steller sea lions (*Eumetopias jubatus*) and their young during winter. J. Zool. Soc. (Lond.) 256:547-556.

Winship, A.J., A.W. Trites, and D.G. Calkins. 2001. Growth in body size of the Steller sea lion (*Eumetopias jubatus*). J. Mammal. 82:500-519.

York, A.E. 1994. The population dynamics of northern sea lions, 1975-1985. Mar. Mamm. Sci. 10:38-51.

York, A.E., R.L. Merrick, and T.R. Loughlin. 1996. An analysis of the Steller sea lion metapopulation in Alaska. In: D.R. McCullough (ed.), Metapopulations and wildlife conservation. Island Press, Covela, pp. 259-292

Appendix A. The population dynamics model

Basic dynamics

The dynamics of animals aged 1 and older are governed by the equations[1]:

$$\begin{aligned}
N^{\mathrm{m},A}_{y+1,a+1} &= \tilde{N}^{\mathrm{m},A}_{y,a} + \sum_{A'\neq A} Bin(\tilde{N}^{\mathrm{m},A'}_{y,a}, X^{\mathrm{m},A',A}_{y,a}) - \sum_{A'\neq A} Bin(\tilde{N}^{\mathrm{m},A}_{y,a}, X^{\mathrm{m},A,A'}_{y,a})\\
N^{\mathrm{I},A}_{y+1,a+1} &= \tilde{N}^{\mathrm{I},A}_{y,a} + \sum_{A'\neq A} Bin(\tilde{N}^{\mathrm{I},A'}_{y,a}, X^{\mathrm{I},A',A}_{y,a}) - \sum_{A'\neq A} Bin(\tilde{N}^{\mathrm{I},A}_{y,a}, X^{\mathrm{I},A,A'}_{y,a})\\
N^{\mathrm{M},A}_{y+1,a+1} &= \tilde{N}^{\mathrm{M},A}_{y,a} + \sum_{A'\neq A} Bin(\tilde{N}^{\mathrm{M},A'}_{y,a}, X^{\mathrm{M},A',A}_{y,a}) - \sum_{A'\neq A} Bin(\tilde{N}^{\mathrm{M},A}_{y,a}, X^{\mathrm{M},A,A'}_{y,a})
\end{aligned} \qquad \text{(A.1)}$$

where

$N^{\mathrm{m/I/M},A}_{y,a}$ is the number of males, immature females, and mature females of age a in region A at the start of year y[2],

$\tilde{N}^{\mathrm{m/I/M},A}_{y,a}$ is the number of males, immature females, and mature females of age a in region A at the end of year y (after mortality and maturation but before dispersal):

$$\begin{aligned}
\tilde{N}^{\mathrm{m},A}_{y,a} &= \overline{N}^{\mathrm{m},A}_{y,a} && \text{Males}\\
\tilde{N}^{\mathrm{M},A}_{y,a} &= \overline{N}^{\mathrm{M},A}_{y,a} + (\overline{N}^{\mathrm{I},A}_{y,a} - \tilde{N}^{\mathrm{I},A}_{y,a}) && \text{Mature females}\\
\tilde{N}^{\mathrm{I},A}_{y,a} &= \overline{N}^{\mathrm{I},A}_{y,a} - Bin(\overline{N}^{\mathrm{I},A}_{y,a}, \beta_{a+1}) && \text{Immature females}
\end{aligned} \qquad \text{(A.2)}$$

$$\overline{N}^{\mathrm{m/I/M},A}_{y,a} = \sum_{A'=1}^{R} Bin(N^{\mathrm{m/I/M},A}_{y,a} Y^{\mathrm{m/I/M},A,A'}_{y,a}, S^{\mathrm{m/I/M},A'}_{y,a}) \qquad \text{(A.3)}$$

$X^{\mathrm{m/I/M},A,A'}_{y,a}$ is the probability during year y that a male, immature female, or mature female of age a in region A at the end of the year disperses to region A',

$Y^{\mathrm{m/I/M},A,A'}_{y,a}$ is the probability during year y that a male, immature female, or mature female of age a belonging to the population in region A is found in region A' and thus experiences the survival impacts specific to region A',

$S^{\mathrm{m/I/M},A}_{y,a}$ is the survival rate for males, immature females, and mature females of age a in region A during year y,

β_a is the probability that an immature animal of age a-1 maturates at age a, and equals $(M_a - M_{a-1})/(1 - M_{a-1})$ where

---

[1] Equation A.1 is modified appropriately for age x, which is treated as a plus-group. This plus group is defined as being at age 6 because all females are mature at this age.

[2] The "start" of the year refers to the start of the model "year," which begins with the pupping season, which occurs in June, in the middle of the calendar year.

M_a is the probability that an animal of age a is mature,

$Bin(x,p)$ is a $(x,\ p)$ binomial random variable with expectation xp, and variance $xp(1-p)$, and

R is the number of regions in the model.

Equation (A.3) allows for demographic variability in the probability of suffering mortality, and equation (A.1) allows for demographic variability in the dispersal rate.

Pups

The number of pups (immature animals of age $a = 0$) in region A at the start of year y, B^A_y, depends on both the number of mature females in that region and the pregnancy rate:

$$\begin{aligned} B^A_y &= \sum_{a=1}^{x} B^A_{y,a}; \qquad & B^A_{y,a} &= Bin(N^{\mathrm{M},A}_{y,a}, b^A_y) \\ N^{\mathrm{m},A}_{y,0} &= \sum_{a=1}^{x} Bin(B^A_{y,a}, 0.5); \qquad & N^{\mathrm{I},A}_{y,0} &= B^A_y - N^{\mathrm{m},A}_{y,0} \end{aligned} \tag{A.4}$$

where

$B^A_{y,a}$ is the number of pups produced by mature females of age a, and

b^A_y is the probability, during year y, that a mature female in region A pups.

The pregnancy rate in region A during year y is given by:

$$b^A_y = f^A_0 (1 + \bar{A}(1 - P^A_y / \tilde{P}^A_y)^z) h^A_y \tag{A.5}$$

where

f^A_0 is the pregnancy rate/infant survival rate at pre-exploitation equilibrium for region A, determined by the expected age structure at pre-exploitation equilibrium, which, given the values for survival and maturity in Table A.1, results in a value of 0.63,

$\bar{A}$ is the (resilience) parameter that determines the extent of density-dependence in birth rate,

z is the parameter that determines the degree of compensation,

h^A_y is a factor to impose a trend over time in the pregnancy rate in region A,

P^A_y is the number of mature females at the start of year y:

$$P_y^A = \sum_{a=1}^{x} N_{y,a}^{\mathrm{M},A} \tag{A.6}$$

$\tilde{P}_y^A$ is the carrying capacity for mature females in region A during year y.

Equation (A.5) allows for density dependence in the pregnancy rate, and is the only manner in which a density-dependent response is incorporated into the general modeling framework. This density dependence can be viewed as being expressed in either the pregnancy rate, or early infant mortality.

Trend in survival rate

The probability that an animal of stage m/I/M and age a in region A survives the impact of natural mortality, $S_{y,a}^{\mathrm{m/I/M},A}$, is given by:

$$S_{y,a}^{\mathrm{m/I/M},A} = S_a \, k_{y,a}^A \tag{A.7}$$

where

S_a is the survival rate for animals of age a at pre-exploitation equilibrium (Table A.1).

Equation (A.7) includes the factor $k_{y,a}^A$ to impose an impact on survival rate over time, which could represent impacts from a number of different sources, depending on the hypotheses being modeled for the decline. The functional forms of the impact on survival rate allow for different impacts on pups (age 0), juveniles (ages 1-4) and adults (ages 5+):

$$k_{y,a}^A = \begin{cases} 1 - \phi_1 \tilde{k}_y^A & \text{if } a = 0 \\ 1 - \tilde{k}_y^A & \text{if } 1 \le a \le 4 \\ 1 - \phi_2 \tilde{k}_y^A & \text{otherwise} \end{cases} \tag{A.8}$$

where

ϕ_1 is the parameter that determines the relative impact of changes in survival rate for pups compared to that for juveniles,

ϕ_2 is the parameter that determines the relative impact of changes in survival rate for adults compared to that for juveniles, and

$\tilde{k}_y^A$ is the impact during year y on the expected survival rate of juveniles.

The impact in a given year $\tilde{k}_y^A$ can be determined from two different functional forms:

a) An asymmetrical smooth forcing function which allows the maximum impact on survival to be approached at a different rate to that at which survival rate is returned to the level prior to the impact.

$$\tilde{k}_y^A = \begin{cases} h_S^A \exp\left(\ln\left(\sigma_{S1}^A\right)[y - y_S^A]^2 / 4\right) & \text{if } y \le y_S^A \\ h_S^A \exp\left(\ln\left(\sigma_{S2}^A\right)[y - y_S^A]^2 / 4\right) & \text{otherwise} \end{cases} \tag{A.9}$$

h_S^A is the parameter that determines the magnitude of the impact on the survival rate,

y_S^A is the year in which the impact on survival rate is greatest,

σ_{S1}^A is the fraction of the maximum impact on the survival rate two years prior to year y_s^A, and

σ_{S2}^A is the fraction of the maximum impact on the survival rate two years after year y_s^A.

b) A knife-edge function, whereby survival is reduced by a fixed amount for the duration of the impact.

$$\tilde{k}_y^A = \begin{cases} 0 & \text{if } y < \upsilon_S^A \\ h_S^A & \text{if } \upsilon_S^A \le y < \left(\upsilon_S^A + l_S^A\right) \\ 0 & \text{if } \left(\upsilon_S^A + l_S^A\right) \le y \end{cases} \tag{A.10}$$

υ_S^A is the year in which the impact on survival rate begins, and

l_S^A is the duration of the impact on survival.

Trend in pregnancy rate

As with the survival rate, an impact on pregnancy rate can be modeled using either a smooth function, or a knife-edge reduction.

a) Smooth forcing function:

$$h_y^A = \begin{cases} 1 - h_F^A \exp\left(\ln\left(\sigma_{F1}^A\right)[y - y_F^A]^2 / 4\right) & \text{if } y \le y_F^A \\ 1 - h_F^A \exp\left(\ln\left(\sigma_{F2}^A\right)[y - y_F^A]^2 / 4\right) & \text{otherwise} \end{cases} \tag{A.11}$$

where

h_F^A is the parameter that determines the magnitude of the impact on pregnancy rate,

y_F^A is the year in which the impact on pregnancy rate is greatest,

σ_{F1}^A is the fraction of the maximum impact on pregnancy rate two years prior to year y_F^A, and

σ^A_{F2} is the fraction of the maximum impact on pregnancy rate two years after year y^A_F.

b) Knife-edge forcing function:

$$h^A_y = \begin{cases} 1 & \text{if } y < \upsilon^A_F \\ 1 - h^A_F & \text{if } \upsilon^A_F \le y < \left(\upsilon^A_F + l^A_F\right) \\ 1 & \text{if } \left(\upsilon^A_F + l^A_F\right) \le y \end{cases} \tag{A.12}$$

where

υ^A_F is the year in which the impact on pregnancy rate begins, and

l^A_F is the duration of the impact on pregnancy rate.

Changes in carrying capacity

The population dynamics can also be impacted by a region-specific change in carrying capacity:

$$\tilde{P}^A_y = \begin{cases} \tilde{P}^A & \text{if } y < y^A_\psi \\ \psi^A \tilde{P}^A & \text{if } y^A_\psi \le y < \left(y^A_\psi + l^A_\psi\right) \\ \tilde{P}^A & \text{if} \left(y^A_\psi + l^A_\psi\right) \le y \end{cases} \tag{A.13}$$

where

ψ^A is the parameter that determines the extent of the change in carrying capacity for region *A*,

y^A_ψ is the year in which there is a change in carrying capacity for region *A*, and

l^A_ψ is the duration of the change in carrying capacity for region *A*.

Table A.1. Expected survival probabilities for females, and the probability of being mature as a function of age (source: York 1994, Table 1).

	Age (yrs)						
	0	1	2	3	4	5	6+
Survival S_a	0.782	0.782	0.782	0.93	0.909	0.895	0.851
Maturity M_a	0	0	0	0.32	0.57	0.83	1.00

Appendix B. Likelihood function

Pup counts

The pup counts are assumed to be unbiased, normally distributed indices of the total numbers of pups (both sexes) by region at the start of the year concerned. The contribution of the pup count data to the likelihood function for region *A* is therefore given by:

$$\prod_y \frac{1}{\sqrt{2\pi}\sigma_y^{A,P}} \exp\left(-\frac{\left[P_y^A - (N_{y,0}^{\mathrm{m},A} + N_{y,0}^{\mathrm{I},A})\right]^2}{2(\sigma_y^{A,P})^2} \right) \tag{B.1}$$

where

P_y^A is the pup count for region *A* and year *y*, and

$\sigma_y^{A,P}$ is the standard deviation of the pup count for region *A* and year *y*.

The product in equation (B.1) is restricted to those years for which pup counts are actually available.

Non-pup counts

In contrast to the pup counts, it is not reasonable to assume that the non-pup counts are unbiased indices of the number of animals aged 1 and older. This is because some (unknown) fraction of the non-pups will be on the sites that are surveyed, and this fraction is likely to be age-specific (Calkins et al. 1999, Trites and Porter 2002). Therefore, the non-pup counts are assumed to be relative indices of the total number of females aged 1 and older, adjusted for the probability of being sighted by age. The use of the non-pup count data in this manner is somewhat questionable. For example, the non-pup count data include data for both males and females. Unfortunately, the age-specific survival rate estimates (Table A.1) pertain only to females—assuming the same values for males (particularly the older males) is questionable as large males are expected to have a lower survival rate than equivalently aged females (Calkins and Pitcher 1982, Winship et al. 2001). The validity of assuming that the non-pup counts index the number of females therefore depends on how the number of females changes relative to how the number of males changes. Other problems with the use of the non-pup counts as indices of "available females" include that the haul-out probabilities may differ between the sexes and older females may be less likely to be counted on nonbreeding haul-outs during the breeding season as they will be involved in breeding activities on rookeries.

The contribution of the non-pup counts to the likelihood function is given by:

$$\prod_y \frac{1}{\sqrt{2\pi}\sigma_y^{A,Q}} \exp\left(-\frac{(Q_y^A - \hat{Q}_y^A)^2}{2(\sigma_y^{A,Q})^2}\right) \tag{B.2}$$

where

Q_y^A is the non-pup index for region *A* and year *y*,

$\hat{Q}_y^A$ is the model-estimate corresponding to Q_y^A:

$$Q_y^A = \sum_{a>1} V_a (N_{y,a}^{\mathrm{I},A} + N_{y,a}^{\mathrm{M},A}) \tag{B.3}$$

V_a is the relative probability of an animal of age a being available to be sighted:

$$V_a = \frac{V_\infty}{1+\exp\left(-\left[a - V_{50}\right]/\delta\right)} \tag{B.4}$$

V_∞ is an overall scaling factor,

V_{50} is the age at which 50% of the animals are available (relative to the age that is most available),

δ is a parameter which determines the width of the age-specific availability ogive, and

$\sigma_y^{A,Q}$ is the standard deviation of the non-pup index for region *A* and year *y*.

The logistic equation (B.4) was chosen as opposed to a dome-shaped function, which would indicate that availability on haul-outs declines with age. While this is a reasonable assumption (older animals are more likely to be mothers nursing pups on rookeries), a parameter that determines the extent to which availability declines with age would be confounded with the reduction in survival rate with age. Given the paucity of the data, the simpler functional form was deemed more preferable.

Survival rates

Estimates of survival rates based on tagging are available for the animals pupped in 1987 and 1988 (i.e., the 1987 and 1988 cohorts) (Anne York, NMML, pers. comm.). Separate survival rates are available for ages 0-5 (both cohorts) and ages 5^+ (separately by cohort). The contribution of the estimates of survival rate to the likelihood function is based on the assumption that these estimates are normally distributed about their expected values.[3] The survival rates were determined from animals tagged at Marmot Island and so are used only for the analyses for the central Gulf of Alaska.

---

[3] The assumption of normality is unlikely to impact the qualitative outcomes of any analysis as the standard errors for the survival estimates are fairly low.

Age composition data

The age-composition data for 1976-1981 (ADFG, unpubl. data) were used to calculate the survival rates in Table A.1, and are consequently not included in the likelihood function. The contribution of the (female) age-composition data for 1985[4] to the likelihood function is based on the assumption that the age-composition data are a random sample from the 3^+ component of the population that is available to being sighted/sampled (see equation B.4). The contribution of the 1985 age-composition data to the likelihood function (ignoring constants independent of the model parameters) is therefore:

$$\prod_{a\geq 3}(\hat{p}_a^A)^{N_{\mathrm{age}}\, p_a^{\mathrm{obs}}} \tag{B.5}$$

where

p_a^{obs} is the proportion which females of age *a* made up of the 1985 age-composition sample of 3^+ animals,

N_{age} is the weight assigned to the age-composition data (the effective sample size, taken to be 100—largely unimportant as age data are available for only one year), and

$\hat{p}_a^A$ is the model-estimate of the proportion which females of age *a* made up of the available population in 1985:

$$\hat{p}_a^A = \frac{V_a(N_{y,a}^{\mathrm{M},A} + N_{y,a}^{\mathrm{I},A})}{\sum_{a'\geq 3} V_{a'}(N_{y,a'}^{\mathrm{M},A} + N_{y,a'}^{\mathrm{I},A})} \tag{B.6}$$

---

[4] Age-composition data are also available for 1986 but these data are ignored because the sample size is very small.

Can Experimental Manipulation Be Used to Determine the Cause of the Decline of Western Stock of Steller Sea Lions (*Eumetopias jubatus*)?

André E. Punt and Gavin Fay
University of Washington, School of Aquatic and Fishery Sciences, Seattle, Washington

Abstract

A variety of reasons have been postulated for the decline of Steller sea lions (Otariidae: *Eumetopias jubatus*) in the Northeast Pacific. To date, however, it has proved impossible to distinguish among these reasons given the available data. In principle, experimental management based on spatial replication of treatments could be used to discriminate among some of these hypotheses. A simulation protocol was developed and applied to evaluate the power of a set of potential experiments to distinguish between whether the cause of the decline was fishing-induced or due to other factors. The simulations are based on an operating model that is individual-based and spatially explicit, and can be parameterized to represent the implications of a range of possible causes for the decline. This model can be used to generate the types of data typically available for the western stock of Steller sea lions. Experiments based on splitting four of the regions identified for past analyses of population dynamics information into sectors that are either open to some fishing or completely closed are considered. The performance of these experiments is, however, poor, owing to the impact of movement, different historical trends in different areas, demographic stochasticity, and the likely size of the effect that the experiments are attempting to detect. These results suggest that the currently available information imply that large-scale experimental manipulation by means of additional spatial closures, where the results are analyzed by examining trends in pup counts, is unlikely to provide

an effective means of discriminating among alternative hypotheses for the decline in Steller sea lions in Alaska.

Introduction

Steller sea lions (Otariidae: *Eumetopias jubatus*) are distributed across the North Pacific rim from the Kuril Islands, through the Aleutian Islands, to the Channel Islands in southern California (Loughlin et al. 1984). Assessments of the status and trends of Steller sea lion populations in Alaska are based on the results of visual counts of pups at rookeries and of non-pups at rookeries and non-breeding haul-out sites (e.g., Sease and Loughlin 1999). Data from these counts suggest that the Alaska population of Steller sea lions declined by approximately 85% between 1956 and 1998 (York et al. 1996, Sease and Loughlin 1999). Concerns over the decline in abundance inferred primarily from these counts led the Steller sea lion to be declared as *threatened* under the U.S. Endangered Species Act (ESA) in 1990 (NMFS 1992). Evidence that temporal trends in Steller sea lion abundance were not geographically uniform (e.g., York et al. 1996), listing by the International Conservation Union of the Steller sea lion as endangered, and genetic evidence of distinct breeding populations led to the classification of Steller sea lions into two stocks. In 1997, the population of Steller sea lions to the west of 144ºW (the western stock) was declared *endangered* under the ESA, with the population to the east of this (the eastern stock) remaining *threatened* (Loughlin 1997).

Many reasons for the decline of the western stock of Steller sea lions have been postulated. York (1994) examined changes in the age-composition of samples collected in 1975-1978 and 1985-1986, and concluded that a 20% decline in the annual survival of juvenile females was the simplest explanation for the reduction in abundance. Pascual and Adkison (1994) analyzed several possible reasons for the decline in Steller sea lion abundance, and concluded that transient age-structure dynamics, historical pup harvesting, and short-term environmental stochasticity are unlikely causes, and that long-term environmental changes or a catastrophe of some sort were probably responsible. Other hypotheses regarding the Steller sea lion decline involve reduction in birth rate, nutritional stress, predation, competition with fisheries, migration, disease, pollution, and the impact of a regime shift or trophic cascade (e.g., Calkins and Pitcher 1982, Merrick et al. 1987, Calkins and Goodwin 1988, Hoover 1988, Loughlin and Merrick 1989, York 1994). To date, it has not been possible to exclude any of these hypotheses definitively, although past research efforts have eliminated redistribution, pollution, predation, subsistence harvest, disease, and natural fluctuations as the principal causes for the decline (NMFS 1992). Several authors suggest that the cause of the decline may be a combination of various factors (Loughlin and York 2000, Hunter and Trites 2001), and that the primary cause has likely changed over the period of decline (Loughlin and York 2000).

The timing and extent of the negative trend in the size of the western stock has not been uniform over the geographical range of the population. Trites and Larkin (1996) and York et al. (1996) both identified several spatially distinct trends in the abundance of Steller sea lions within the western stock. This suggests that the factors responsible for the decline have not been spatially homogeneous. The behavior of Steller sea lions does create distinct localized populations that may well enable spatial differences in the factors affecting population dynamic processes, such as survivorship and pregnancy rate, to be expressed differentially within the overall population. In addition to evidence that Steller sea lions do not breed other than with their natal stock, Steller sea lions show some tendency toward natal site fidelity in that females return to breed at either the site of birth, or at a site close to the natal site (Pitcher and Calkins 1981).

It is possible that manipulative experiments designed specifically for Steller sea lions in Alaska may be capable of discriminating among at least some of the competing hypotheses. Specifically, such experiments may be able to resolve the question whether the decline in Steller sea lion abundance was caused solely by the fishing-related impacts or some other impacts. This study uses Monte Carlo simulation methods to evaluate the power of alternative experiments to address the question. Similar methods have been used to evaluate experiments to resolve key uncertainties regarding the dynamics of benthic communities off Australia's North West Shelf, following the introduction of fishing (e.g., Sainsbury et al. 1997), and to estimate quantities needed to evaluate management strategies for the exploitation of coral trout on the Great Barrier Reef, Australia (e.g., Mapstone et al. 1996, Punt et al. 2001).

Methods

The following steps are used to evaluate the power of alternative manipulative experiments based on spatial replication of treatments to select among alternative hypotheses.

1. Selection of the hypotheses (in this case whether fishing-related impacts were the sole reason for the decline in the abundance of the western stock of Steller sea lions).

2. Development of a model of the system of interest (the operating model), which can be used to generate data typical of those that would result from field experiments.

3. Parameterization of the operating model for the various alternative hypotheses, for example, by fitting it to the existing data.

4. Identification of alternative spatial experimental regimes and the approaches that would be used to analyze the data from the experiments.
5. Simulation of the process of conducting experiments and analyzing the results using the methods selected at step 4.
6. Evaluation of the success of different experimental regimes, in terms of whether the probabilities associated with the hypotheses for the Steller sea lion decline are updated in the correct direction.

Overview of the operating model

The operating model is age- and sex-structured and individual-based. The information available for each animal includes its age, sex, mother, whether it is mature, its rookery of birth (all animals are assumed to home to their natal sites), and where it is in the North Pacific at any given time. The spatial configuration includes 32 rookeries and 104 haul-out sites, and the model has a monthly time-step to allow within-year movement to be represented. Animals can be located anywhere in the North Pacific during the year, although the model forces females that will give birth to return to their natal rookeries at the time of the pupping season.

The mathematical specifications of the operating model are provided by Punt and Fay (2003) and are consequently not repeated in full here. The following steps are carried out each month to project the model forward:

1. Generate the number of pups if the month is July (the start of the modeled year and the assumed pupping season). For each mature female, there is a rookery-specific probability of giving birth (see equation 1 below). Pups are located on their natal rookeries at birth and the probability of a newborn being male or female is assumed to be 0.5.
2. For immature females, whether they mature during the current year is determined using data on the fraction of females of each age that are mature (York 1994).
3. Whether each animal dies during the current time-step is determined. The probability of death depends on age and location (an animal need not be at a haul-out or rookery, but could be anywhere in the North Pacific). Allowance is made for density-dependence in the mortality rate for pups during their first month of life, and the expected survival rate is multiplied by age-, year-, and location-specific factors (see equations 2 and 3 below) to mimic the consequences of the hypotheses regarding the causes for the decline.

Table 1. Probability of an animal moving to a location as a function of its depth.

Depth range	<50 m	50-100 m	100-200 m	200-500 m	>1,000 m
Probability	0.90	0.50	0.3	0.1	0.01

4. Each animal is allowed to move from its current location. The algorithm applied to determine the location of an animal at the start of month $m + 1$, given its location at the start of month m, is based on movement that is random in terms of bearing and distance, but takes into account the depth to which an animal moves (Table 1) and the need for animals to move back toward their natal rookeries so that they are at the rookeries at the time of the pupping season. The distance moved each month (before modification to account for depth and the need to return to the rookery for pupping) is generated from the normal distribution, $N(\bar{D},\sigma_D^2)$, where $\bar{D}$ is the average net distance moved during each month, and σ_D is a measure of the variation in the net distance moved during each month. The probability of an animal moving to a generated location is then based on the values in Table 1. This involves selecting a random number from U[0,1]; if the random number is less than the value for the depth range, the animal moves to the generated location; if not, a new distance and bearing are generated and the process is repeated. The values in Table 1 are "guestimates" that lead to the distribution of Steller sea lions by depth that conform with known, albeit largely anecdotal, information.
5. If it is the end of the year, the age of each animal is incremented by one.

The initial conditions (nominally year $y = 1950$) are defined to be a population in an equilibrium state. The input parameters that determine the number of animals at each rookery at the start of 1950 are the numbers of pups by rookery at the start of 1950. The value of pup survival at equilibrium is computed given specifications for the survival rates of animals age 1 and older, and the pregnancy rates by age (assumed, in absence of data to the contrary, to be independent of rookery) in an equilibrium state.

Modeling impacts on pregnancy and survival rate

The model outlined above includes demographic stochasticity in birth and death rates and individual variation in movement rates. However, to be able to mimic the observed population trajectory for Steller sea lions in Alaska even qualitatively, it is necessary to have model formulations

Table 2. The rookeries and the regions to which they are assigned.

Rookeries	Region
Seal rocks, Wooded	Eastern Gulf of Alaska
Chirikof, Chowiet, Marmot, Outer, Sugarloaf	Central Gulf of Alaska
Atkins, Chernabura, Clubbing Rocks, Lighthouse Rocks, Pinnacle Rock	Western Gulf of Alaska
Adugak, Akun/Billing Head, Akutan/Cape Morgan, Bogoslof/Fire Island, Ogchul, Ugamak Complex	Eastern Aleutian Islands
Adak, Amchitka/Column Rock, Ayugadak, Gramp Rock, Kasatochi/North Point, Kiska/Cape St. Stephen, Kiska/Lief Cove, Seguam/Saddleridge, Tag, Ulak/Hasgox Point, Yunaska	Central Aleutian Islands
Agattu, Attu/Cape Wrangell, Buldir	Western Aleutian Islands

that capture hypotheses for the decline in the population. The hypotheses can be divided into those in which some unknown (but perhaps spatially determined) process (or processes) impact the pregnancy rate of females; those in which some unknown process(es) impact the survival rate of pups, juveniles, and adults (again possibly with spatial differences in the size of the effect); and those in which some unknown process(es) impact both pregnancy and survival rates. At present, there is no way to identify how the (possible) impacts on pregnancy rate and survival rate may have changed over time, so the analyses of this paper consider a generalized functional form for the time-dependence in the impacts on pregnancy and survival rate.

The pregnancy rate of mature animals is defined to be the product of an average pregnancy rate (0.65) and a factor that allows for reductions in pregnancy rate on rookery r due to unknown causes, h_y^r (see Table 2 for the rookeries and the regions to which each rookery is assigned). The factor modifying pregnancy rate is assumed to depend on rookery according to the equation:

$$h_y^r = \begin{cases} 1 - h_F \exp\left(-[y - y_F]^2 / \sigma_F^1\right) & \text{if } y \le y_F \\ 1 - h_F \exp\left(-[y - y_F]^2 / \sigma_F^2\right) & \text{otherwise} \end{cases} \qquad (1)$$

where

h_F is the parameter that determines the magnitude of the impact on pregnancy rate,

y_F is the year in which the impact on pregnancy rate is greatest,

σ_F^1 is the parameter that determines the rate at which the impact on the pregnancy rate changes with time prior to year y_F, and

σ_F^2 is the parameter that determines the rate at which the impact on the pregnancy rate changes with time after year y_F.

The survival rate for an animal of age a in region A during year y is assumed to be the product of an expected survival rate ($S_{y,a}^A$) and an age- and location-specific time-dependent reduction in survival rate, $k_{y,a}^A$, i.e.:

$$k_{y,a}^A = \begin{cases} 1-\phi_1 \tilde{k}_y^A & \text{if } a=0 \\ 1-\phi_2 \tilde{k}_y^A & \text{if } 1 \le a \le 4 \\ 1-\tilde{k}_y^A & \text{otherwise} \end{cases} \tag{2}$$

where

ϕ_1 is the relative impact of changes in adult survival rate compared to that for pups,

ϕ_2 is the relative impact of changes in adult survival rate compared to that for juveniles,

$\tilde{k}_y^A$ is the impact during year y on the expected survival rate of adults:

$$\tilde{k}_y^A = \begin{cases} h_S \exp\left(-[y-y_S]^2 / \sigma_S^1\right) & \text{if } y \le y_S \\ h_S \exp\left(-[y-y_S]^2 / \sigma_S^2\right) & \text{otherwise} \end{cases} \tag{3}$$

h_S is the parameter that determines the magnitude of the impact on survival rate,

y_S is the year in which the impact on survival rate is greatest,

σ_S^1 is the parameter that determines the rate at which the impact on the survival rate changes with time prior to year y_S, and

σ_S^2 is the parameter that determines the rate at which the impact on the survival rate changes with time after year y_S.

The model for the impact on survival rate therefore allows for different impacts on pups (age 0), juveniles (ages 1-4), and adults (ages 5+). The values for the parameters in equations 1-3 are determined by fitting the population dynamics model to the actual data for Steller sea lions in Alaska (Fay and Punt 2006).

Using experiments to select among causes for the decline

Two types of experimental management regime are considered. Both involve closing additional areas to fishing, and then monitoring changes in pup production at rookeries in the areas in which some fishing is permitted and in which it is completely prohibited. There are few rookeries in the easternmost and westernmost regions ("Eastern Gulf of Alaska" and "Western Aleutian Islands" respectively; Table 2) so the experimental "treatments" are assumed to be applied to the central four regions only. There are two types of experimental management regime (A and B), and both involve defining longitudinal sectors and restricting or prohibiting fishing in some of these sectors. Regime A closes all fishing within the "closed" longitudinal sectors (i.e., the area closed is defined by two lines of longitude and all fishing is assumed to cease between those longitudes), while regime B closes all fishing within 37 km of the rookeries in the "closed" longitudinal sectors throughout the year. These closure regimes therefore extend the current restrictions on fishing at or near Steller sea lion rookeries.

There are three implementations of each management regime, depending on the choice of the longitudinal sectors and which of these sectors are designated to be closed to fishing (Table 3). The two sets of longitudinal sectors arise from (a) grouping rookeries so that the dis-

Table 3. The longitudinal sectors, and whether fishing is "open" or "closed," allowed within each for the six alternative experiments. Experiment type A prohibits fishing within the entire longitudinal sector, while experiment type B prohibits fishing within 37 km of each of the rookeries within the sector.

Experiments 1A/1B		Experiments 2A/2B and 3A/3B		
Longitude range	Status	Longitude range	Status 2A/2B	Status 3A/3B
160°E-175°	Open	160°E-176°34E	Open	Open
175°E-180°	Open	176°34E-178°W	Open	Closed
180°-171°W	Closed	178°W-169°28W	Closed	Open
171°W-166°W	Open	169°28W-167°30W	Open	Closed
166°W-163°W	Closed	167°30W-164°05W	Closed	Open
163°W-160°W	Open	164°05W-161°W	Open	Closed
160°W-158°W	Closed	161°W-157°23W	Closed	Open
158°W-153°W	Open	157°23W-155°W	Open	Closed
153°W-150°W	Closed	155°W-150°19W	Closed	Open
150°W-145°W	Open	150°19W-145°W	Open	Open

tance between rookeries within a sector is small relative to the distance between rookeries in adjacent sectors (experimental regimes 1A and 1B), and (b) splitting the existing regions approximately into two and placing the sector boundaries so that only rookeries from one region are in each sector (experimental regimes 2A, 2B, 3A, and 3B).

The results from the experiment are counts of pups. The experiment is assumed to start in 2003 and pup counts are assumed to be available for the years for which they are actually available (Fay 2004), and for all rookeries every year after 2001. These pup counts are assumed to be lognormally distributed with a coefficient of variation that is independent of rookery.

The pup counts are grouped into longitudinal sectors (Table 3) and analyzed by fitting the following model:

$$P_y^{r,s} = \begin{cases} \hat{P}_{1979}^{r,s} e^{-\lambda^r (y-1979)} & \text{if } y \le 2003 \\ \hat{P}_{1979}^{r,s} e^{-\lambda^r (2003-1979)} e^{-\gamma^{r,s}(y-2003)} & \text{otherwise} \end{cases} \tag{4}$$

where

$P_y^{r,s}$ is the pup counts summed over the rookeries with status s (status = in the sector in which some fishing is permitted or in the sector completely closed to fishing) in region r for year y,

λ^r is a measure of the rate of change in pup numbers from 1979 to 2003 for region r, and

$\gamma^{r,s}$ is a measure of the rate of change in pup numbers for the rookeries with status s in region r after 2003.

Two variants of equation 4 are considered. The first variant (model 1) estimates five parameters for each region (two $\hat{P}_y^{r,s}$s, two $\gamma^{r,s}$ s, and one λ^r) and the second variant (model 2) estimates four parameters for each region (two $P_y^{r,s}$ s, one γ^r, and one λ^r), i.e., γ is assumed to be independent of the status of a rookery for model 2. Model 1 is based on the assumption that the trend after 2003 depends on the status of a rookery (i.e., closing an area changes the factors that determine additional mortality and reduced pregnancy rate) while model 2 is based on the assumption that closing an area has no impact on the magnitude of these factors (because fishing is not the cause of the decline). The fits of models 1 and 2 to the pup count data are compared using AIC$_c$ (Burnham and Anderson 1998) and one of these is selected.

The ability of experimental treatments to distinguish whether fishing is the cause for the decline can be evaluated (i) by the frequency of time that model 1 is selected when fishing is really the cause for the decline (and hence closing areas does change the trend in population size in the area closed to fishing, implemented in the model by setting $h_y^r = 0$ and

$\tilde{k}_y^A = 0$ for $y > 2002$ for the closed areas) and (ii) by the frequency of time that model 2 is selected when fishing is not the cause for the decline (and hence closing areas does not change the trend in population size in the area closed to fishing). Note that when an area is not closed, the values for h_y^r and $\tilde{k}_y^A$ are determined using equations 1 and 3, i.e., the impact on the population continues to decline over time given the values for the parameters of the functional forms.

Specifications for the operating model

The impact on pregnancy rate is assumed to be related to the status of the rookery (i.e., whether pregnancy rate for a particular rookery is affected by an experiment depends on whether fishing is permitted in the area near the rookery). Note that closing the area around a rookery will not necessarily prevent an animal from that rookery from dying perhaps due to fishing, because the animal may move during the year to an area that is not closed and hence suffer the mortality associated with that area.

The movement patterns of Steller sea lions remain highly uncertain, with data available for only a relatively small number of animals and over a relatively short duration (e.g., Merrick and Loughlin 1997, Loughlin et al. 2003). For ease of simplification, and in absence of hard data to model movement, two scenarios regarding movement are considered: $\bar{D} = 100$, and $\bar{D} = 50$. For both of these scenarios σ_D is set equal to 40. Figure 1 shows the time-trajectories of pup numbers, numbers of mature females, and relative numbers on haul-outs by region for one of the scenarios. Results are shown in Fig. 1 when the impact on mortality and pregnancy rate is not modified (i.e., any future closures have no impact on the population trajectories).

Results

Table 4 lists the probability of selecting the model in which the trend in pup numbers differs depending on the status of a sector (model 1). Results are shown for two hypotheses regarding the biological processes impacted, for two hypotheses regarding the extent to which Steller sea lions move ($\bar{D} = 100, 50$), and for whether the cause of the decline was due to fishing. The results in this table correspond to the case in which future (post-2002) pup counts have a coefficient of variation of 0.05 and a decision between models 1 and 2 is made in 2010. The results in Table 4 are based on 200 simulations (20 replicates of 10 projections of the model).

For the experiment in which rookeries are grouped by distance (experiments 1A and 1B in Table 4), the probability of selecting model 1 (different trends in the areas in which some fishing is permitted and in which fishing is prohibited) is 100% irrespective of whether fishing is

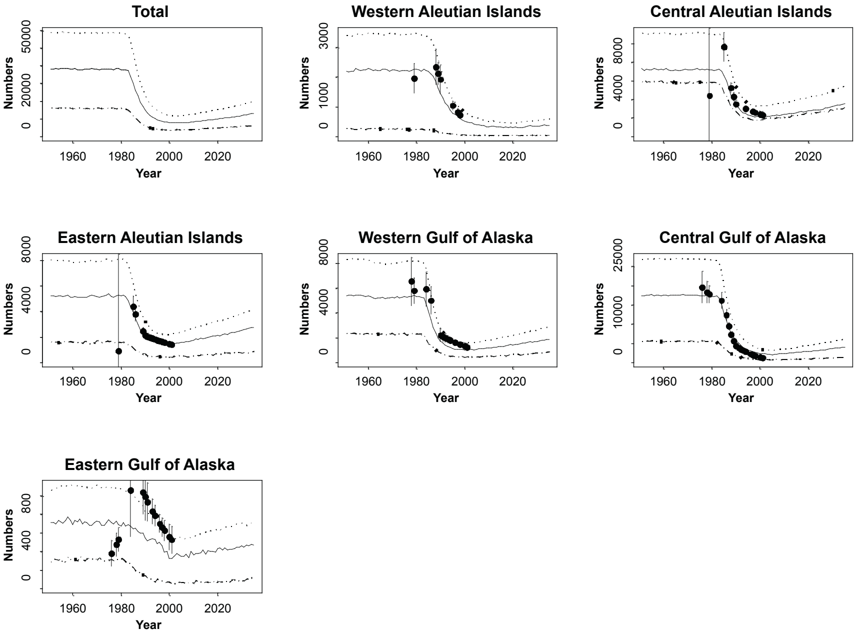
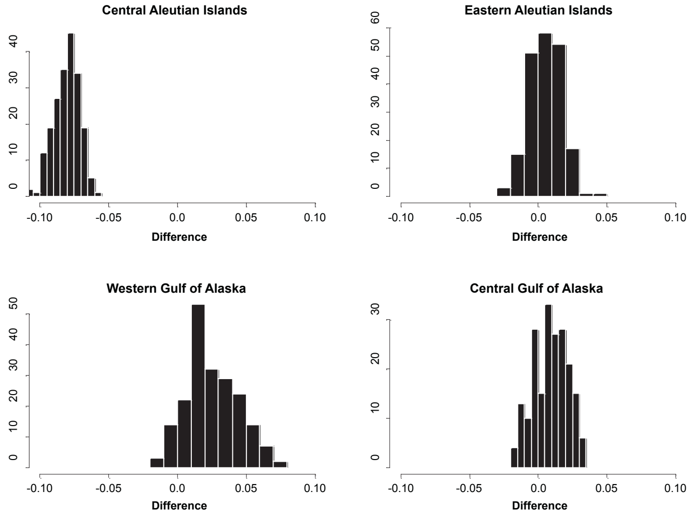


Figure 1. Time-trajectories of pup production (solid lines), mature females (dotted lines), and relative numbers on haul-outs (dashed lines) for six regions when the decline is due to a reduction in survival rate. The solid dots are the pup counts.

the true cause of the decline. This result arises because the two sectors within each region exhibit different trends even when fishing is not the cause of the decline. Figure 2 illustrates this by histograms over the 200 simulations of the difference between γ (see equation 4) for the two sectors by region for one of the scenarios in Table 4. Ideally, the difference should be zero when fishing is not the cause for the decline (i.e., closing areas has no impact on the magnitude of the additional mortality) and should be negative when fishing is the cause for the decline. However, this is not the case. For example, the histograms for the Central Aleutian Islands and the Western Gulf of Alaska regions are not clustered about zero even in the case when fishing is not the cause of the decline.

The above results are illustrated further in Fig. 3 by the time-trajectories of pup production by sector. It would have been anticipated that the trends for the “open” (O) and “closed” (C) sectors would have been similar when the fishing was not the cause for the decline. However, this is not the case, particularly for the Central Aleutian Islands region. Furthermore, the impact of closing a sector to fishing does not seem to be particularly

(a) Fishing is not the cause of the decline.



(b) Fishing is the cause of the decline.

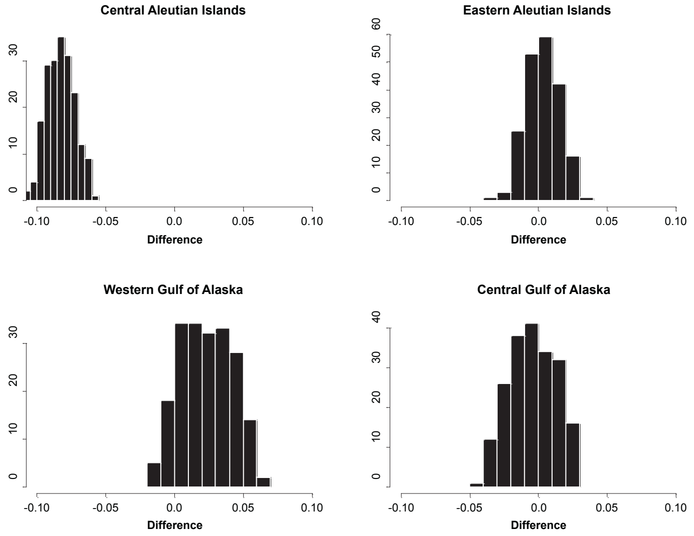


Figure 2. Estimated differences between the two sectors within each of the four regions (i.e., a negative number indicates that the pup counts in the area closed to fishing are increasing relative to those for the area in which some fishing is permitted). The results in the figure are based on the scenario in which the cause of the decline is additional mortality and $\bar{D}$ = 100.

large (Fig. 3), i.e., the assumed effect size for the experiment seems to be quite low. One reason for the different trends in the "open" and "closed" sectors is that the sector boundaries do not always correspond with the boundaries of the regions for experiments 1A and 1B, so some sectors include rookeries that have exhibited different trends historically.

Figures 4 and 5 provide the same model outputs as Fig. 3, except that they pertain to experiments 2A and 3A. The differences in trends in pup production between the two sectors for each region when fishing is not the cause of the decline are much smaller in Figs. 4 and 5 than in Fig. 3, confirming that the major differences in trend evident in Fig. 3 were due to the sector boundaries not always corresponding to the boundaries of the regions. However, performance is poor even for these experiments. For example, in only a very few cases is model 1 rejected more frequently when the decline is caused by fishing than when it is not (Table 4). One reason for this is that the trends in pup production still differ between the sectors "open" and "closed" to fishing even when fishing is not the cause of the decline, due to mixing of animals from rookeries associated with one sector into an adjacent sector (and hence experiencing the additional mortality in that sector).

A reason for the difference in the trend in pup production in the two sectors of the Western Gulf of Alaska region is that the population size in the sector open to fishing is small so there is an impact of demographic uncertainty (note that the time-trajectories of pup production for sec-

Table 4. Percentage of simulations in which the trend in pup numbers is estimated to depend on the rookery status selected (open or closed) (model 1). Results are shown for two hypotheses regarding the process impacted, regarding the extent to which Steller sea lions move ($\bar{D}$ = 100, 50), and for whether the cause of the decline was due to fishing.

Process impacted	Caused by fishing	$\bar{D}$	Experiment type					
			1A	1B	2A	2B	3A	3B
Mort	No	100	100	100	81	81	89	89
Mort	Yes	100	100	100	94.5	75	85.5	82.5
Mort + Preg	No	100	100	100	100	100	66	66
Mort + Preg	Yes	100	100	100	94	94	100	100
Mort	No	50	100	100	60	60	100	100
Mort	Yes	50	100	100	81.5	81.5	68.5	79.5
Mort + Preg	No	50	100	100	86	86	100	100
Mort + Preg	Yes	50	100	100	64.5	64.5	100	66

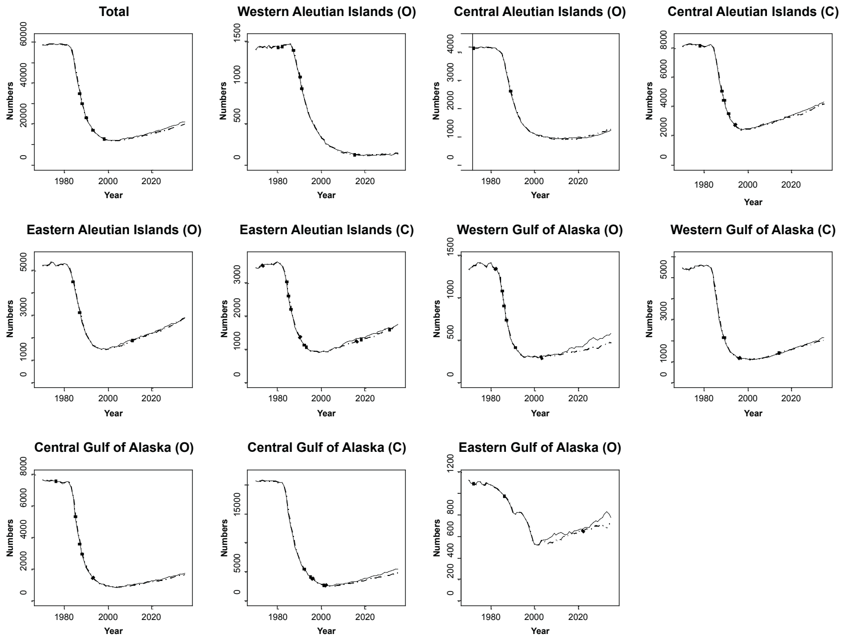


Figure 3. Time-trajectories (1970-2035) of pup production for the total population and for each of the sectors for experiments 1A and 1B (solid lines = fishing is not the cause of the decline; dashed lines = fishing is the cause of the decline). "O" indicates "open to some fishing" and "C" indicates "closed to fishing." The results in the figure are based on the scenario in which the cause of the decline is additional mortality and $\bar{D} = 100$.

tors with "small" population sizes (e.g., "Western Gulf of Alaska [O]" and "Eastern Gulf of Alaska") exhibit much more inter-annual variability than those with "large" population sizes).

Reducing the extent of movement to $\bar{D} = 15$ (Fig. 6) substantially reduces the impact of animals "wandering" into adjacent regions but cannot (by definition) impact the extent of demographic stochasticity. For example, reducing the extent of movement leads to somewhat more optimistic results for the "Central Aleutian Islands (O)" sector when fishing is not the cause for the decline (compare Figs. 4 and 6). Presumably this is because the reduction in survival in the Western Aleutian Islands region is still high during the projection years, and, when movement is higher, animals from the Central Aleutian Islands (O) sector die due to their mixing into the Western Aleutians region.

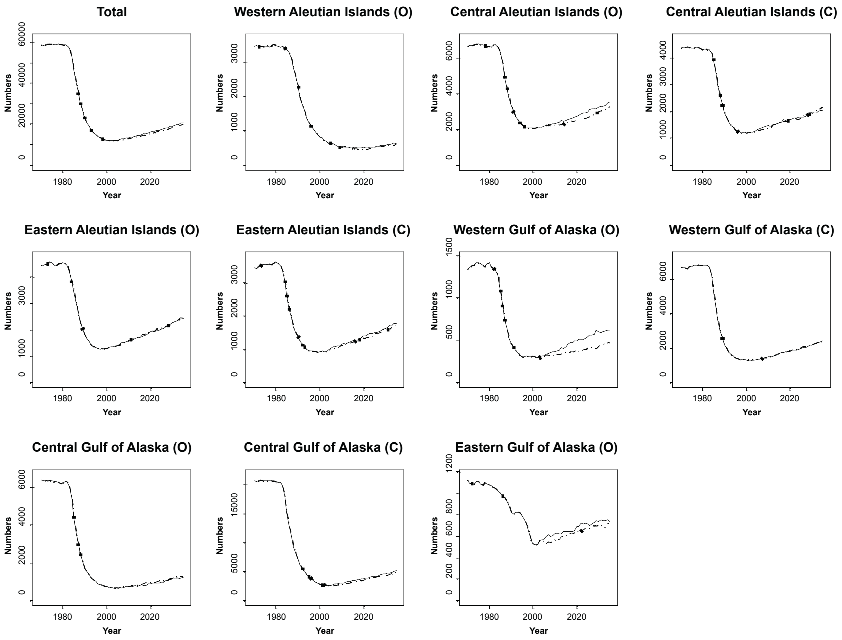


Figure 4. As for Fig. 3, except that the results pertain to experiment 2A.

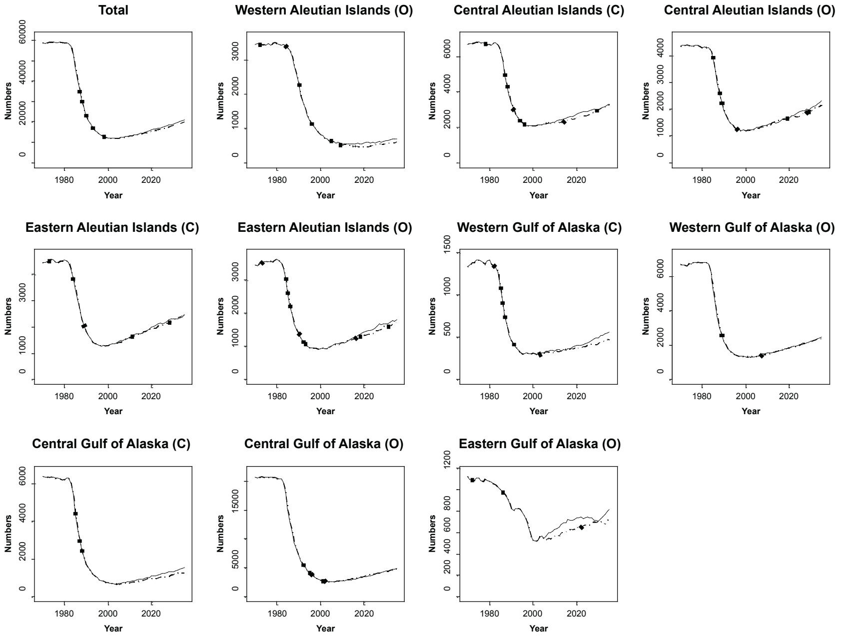


Figure 5. As for Fig. 3, except that the results pertain to experiment 3A.

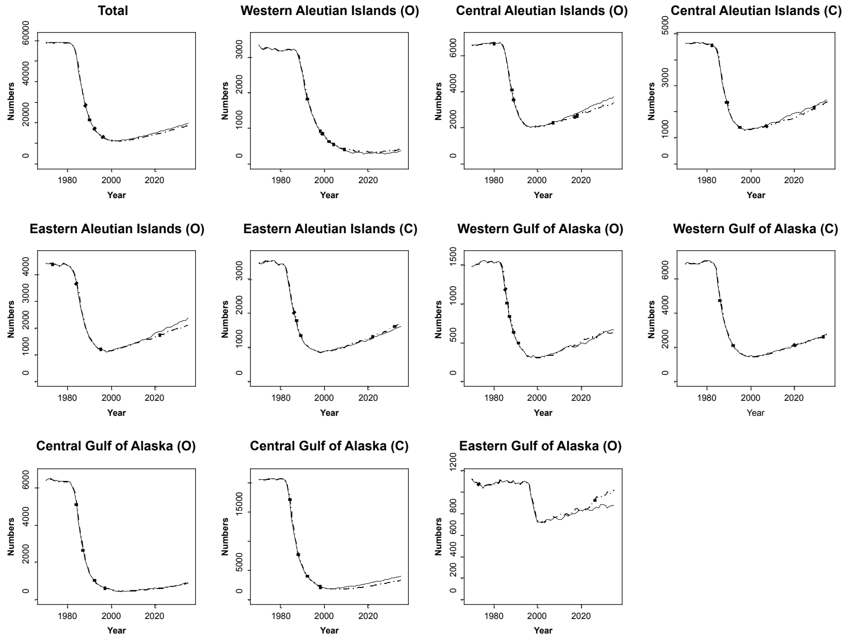


Figure 6. As for Fig. 4, except that $\bar{D}$ = 15.

The sensitivity of the results to changing the precision of the future pup counts and the year in which a decision between models 1 and 2 is made was examined, but these factors were found to be relatively inconsequential in terms of the qualitative features evident in Table 4 and Figs. 3-6.

Discussion

Although the idea of using (additional) spatial closures to resolve management-related uncertainties seems intuitively appealing, and large spatial closures have been implemented for this purpose elsewhere (e.g., Mapstone et al. 1996, Sainsbury et al. 1997), the results of this study highlight the need for a formal evaluation of the power of an experiment prior to its implementation. Unlike many other types of experiments, large-scale experiments in the marine environment are subject to many uncontrollable factors. Unfortunately, these factors may have quite a major impact on the power of experiments. The experiments considered in this study clearly performed very poorly in terms of resolving the question of whether the cause for the decline in Steller sea lions was due to fishing-related factors. There appear to be two main reasons for the poor performance of these experiments:

1. The trajectories of future pup production in longitudinal sectors in the North Pacific will exhibit different trends irrespective of whether additional closures are imposed because of (a) the effects of animals moving among regions (and hence being subject to different sources of mortality), (b) experimental units including rookeries that have exhibited different trends in the past (presumably because they were subject to different risks or magnitudes of risks), and (c) demographic stochasticity.
2. The effect size is low (i.e., the model predicts that the impact—whatever it was—was slowing down toward the end of the twentieth century so the impact of additional closures is low). In principle, the effect size could be increased by designing experiments that, say, return the situation to that estimated for a year such as 1991. This would correspond to the time when fishery management measures to protect Steller sea lions (initially 10 nm no-trawl zones surrounding rookeries in the western stock, although protection measures have become increasingly complex in years since) were first implemented. However, such an experiment might deliberately increase mortality on a species that is considered to be at risk of biological extinction (if fishing was indeed the cause of the decline). Furthermore, this experiment would not change the probability of incorrectly selecting model 1 if fishing were not the cause for the decline (see Table 4).

Although the performance of the experiments was poor, it should be noted that several of the assumptions underlying the evaluations should favor a successful experiment within the simulation framework of this paper. For example, the simulations are predicated on the assumption that there is only one major cause for the decline (fishing or something else). Clearly, the power to select between fishing and non-fishing causes will be reduced if there are several causes for the decline, and fishing is only one of them. The simulations are also predicated on the assumption that the coefficient of variation of the future pup count data is 0.05. While it appears to be the case that the pup counts for the central Gulf of Alaska region had coefficients of variation this low in recent years, the precision of the pup counts for the other regions is poorer than this (Fay 2004). The population projections also ignore environmental stochasticity. Inclusion of this source of uncertainty will add noise to the population trajectories, and likely further reduce the ability of differences in trends in pup production to distinguish between causes for the decline.

There are many unknown aspects of the population dynamics of Steller sea lions in Alaska. As such, there is uncertainty regarding the ability to assess the power of experiments to determine the cause of the decline in abundance. The uncertainty associated with some of these aspects could be reduced through the collection of additional data, and this may change the conclusion that experiments based on spatial closures have low power. Specifically, the factor that both substantially impacts uncertainty, and should be amenable to future research, is movement. The population dynamics model assumes that movement is random, and is subject to a depth preference and natal homing. Additional movement-related information could be used to improve this aspect of the model substantially. Movement-related information may also lead to a better basis for selecting the rookeries to monitor as part of any experiment. The method used to analyze the data from the experiment is fairly crude. It might be possible to improve the performance of the experiments by, for example, fitting population dynamics models to the data from the experiments and using the results of the population model fits as the basis for a decision on whether fishing was the cause for the decline.

In summary, the results of this paper suggest that the currently available information imply that large-scale experimental manipulation by means of additional spatial closures, where the results are analyzed by examining trends in pup counts, is unlikely to provide an effective means of discriminating among alternative hypotheses for the decline in Steller sea lions in Alaska.

Acknowledgments

Funding for this work was provided by the North Pacific Marine Research Consortium. The comments of two anonymous reviewers are gratefully acknowledged.

References

Burnham, K.P., and D.R. Anderson. 1998. Model selection and inference: A practical information-theoretic approach. Springer, New York.

Calkins, D.G., and E. Goodwin. 1988. Investigation of the declining sea lion population in the Gulf of Alaska. Alaska Department of Fish and Game. 76 pp.

Calkins, D.G., and K.W. Pitcher. 1982. Population assessment, ecology and trophic relationships of Steller sea lions in the Gulf of Alaska. Alaska Department of Fish and Game, Final Report RU243. 128 pp.

Fay, G. 2004. A Bayesian stochastic metapopulation model for Steller sea lions in Alaska. Master's thesis, University of Washington, Seattle. 253 pp.

Fay, G., and A.E. Punt. 2006. A Bayesian stochastic metapopulation model for Steller sea lions (*Eumetopias jubatus*): Evaluating changes in model fits with different assumptions about the causes for population decline. In: A.W. Trites, S.K. Atkinson, D.P. DeMaster, L.W. Fritz, T.S. Gelatt, L.D. Rea, and K.M. Wynne (eds.), Sea Lions of the World. Alaska Sea Grant College Program, University of Alaska Fairbanks.

Hoover, A.A. 1988. Steller sea lion—*Eumetopias jubatus*. In: J.W. Lentfer (ed.), Selected marine mammals of Alaska: Species accounts with research and management recommendations. Marine Mammal Commission, Washington, D.C., pp. 159-193.

Hunter, A.M.J., and A.W. Trites. 2001. An annotated bibliography of scientific literature (1751-2000) pertaining to Steller sea lions (*Eumetopias jubatus*) in Alaska. Fish. Res. Centre Res. Rep. 9(1):1-45.

Loughlin, T.R. 1997. Using the phylogeographic method to identify Steller sea lion stocks. In: A. Dizon, S.J. Chivers, and W.F. Perrin (eds.), Molecular genetics of marine mammals. Soc. Mar. Mammal. Spec. Publ. 3, pp. 159-171.

Loughlin, T.R., and R.L. Merrick. 1989. Comparison of commercial harvest of walleye pollock and northern sea lion abundance in the Bering Sea and Gulf of Alaska. In: Proceedings of the International Symposium on the Biology and Management of Walleye Pollock. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 679-700.

Loughlin, T.R., and A.E. York. 2000. An accounting of the sources of Steller sea lion, *Eumetopias jubatus*, mortality. Mar. Fish. Rev. 62:40-45.

Loughlin, T.R., D.J. Rugh, and C.H. Fiscus. 1984. Northern sea lion distribution and abundance: 1956-1980. J. Wildl. Manag. 48:729-740.

Loughlin, T.R., J.T. Sterling, R.L. Merrick, J.L. Sease, and A.E. York. 2003. Diving behavior of immature Steller sea lions (*Eumetopias jubatus*). Fish. Bull. U.S. 101:566-582.

Mapstone, B.M., R.A. Campbell, and A.D.M. Smith. 1996. Design of experimental investigations into the effects of line and spear fishing on the Great Barrier Reef. CRC Reef Research Centre Technical Report 7, Townsville. 86 pp.

Merrick, R.L., and T.R. Loughlin. 1997. Foraging behaviour of adult female and young-of-year Steller sea lions in Alaskan waters. Can. J. Zool. 75:776-786.

Merrick, R.L., T.R. Loughlin, and D.G. Calkins. 1987. Decline in abundance of the northern sea lion, *Eumetopias jubatus*, in Alaska, 1956-86. Fish. Bull. U.S. 85:351-365.

NMFS. 1992. Final Recovery Plan for the Steller Sea Lion (*Eumetopias jubatus*). Prepared by the Steller Sea Lion Recovery Team for the NOAA NMFS Office of Protected Resources, Silver Spring, Maryland. 92 pp.

Pascual, M.A., and M.D. Adkison. 1994. The decline of the Steller sea lion in the Northeast Pacific: Demography, harvest or environment. Ecol. Appl. 4:393-403.

Pitcher, K.W., and D.G. Calkins. 1981. Reproductive biology of Steller sea lions in the Gulf of Alaska. J. Mammal. 62:599-605.

Punt, A.E., and G. Fay. 2003. Estimation of Steller sea lion population dynamics parameters. Final report submitted to the North Pacific Marine Mammal Consortium. 48 pp.

Punt, A.E., A.D. Smith, A.J. Davidson, B.M. Mapstone, and C.R. Davies. 2001. Evaluating the scientific benefits of spatially explicit experimental manipulations of common coral trout (*Plectropomus leopardus*) on the Great Barrier Reef, Australia. G.H. Kruse, N. Bez, A. Booth, M.W. Dorn, S. Hills, R.N. Lipcius, D. Pelletier, C. Roy, S.J. Smith, and D. Witherell (eds.), Spatial processes and management of marine populations. Alaska Sea Grant College Program, University of Alaska Fairbanks, pp. 67-103.

Sainsbury, K.J., R.A. Campbell, R. Lindholm, and W. Whitelaw. 1997. Experimental management of an Australian multispecies fishery: Examining the possibility of trawl-induced habitat modification. E.L. Pikitch, D.D. Huppert, and M.P. Sissenwine (eds.), Global trends: Fisheries management. Am. Fish. Soc. Symp. 20:107-112.

Sease, J.L., and T.R. Loughlin. 1999. Aerial and land-based surveys of Steller sea lions (*Eumetopias jubatus*) in Alaska, June and July 1997 and 1998. NOAA Tech. Memo. NMFS-AFSC-100. 61 pp.

Trites, A.W., and P.A. Larkin. 1996. Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: How many were there? Aquat. Mamm. 22:153-166.

York, A.E. 1994. The population dynamics of northern sea lions, 1975-1985. Mar. Mamm. Sci. 10:38-51.

York, A.E., R.L. Merrick, and T.R. Loughlin. 1996. An analysis of the Steller sea lion metapopulation in Alaska. D.R. McCullough (ed.), Metapopulations and wildlife conservation. Island Press, Covela, California, pp. 259-292.

Conservation Management Issues and Status of the New Zealand (*Phocarctos hookeri*) and Australian (*Neophoca cinerea*) Sea Lion

R.A. Campbell
Department of Fisheries, Western Australia, North Beach, Australia

B.L. Chilvers and S. Childerhouse
Department of Conservation, Marine Conservation Unit, Wellington, New Zealand

N.J. Gales
Australian Antarctic Division, Hobart, Australia

Abstract

The two antipodean sea lion species are the rarest sea lions in the world. They are relatively similar in abundance and share common conservation management concerns. Recovery from commercial sealing in the eighteenth to twentieth centuries and ongoing interactions with commercial fishing activities are primary concerns. However, there are marked differences in distribution (number of breeding colonies) and life history traits, in particular the variation in breeding cycles and population genetic structure. These factors must be taken into consideration in addressing management concerns and are reflected in the current management actions being taken for both species in regard to interactions with commercial fishing activities.

Introduction

Conservation management of sea lions has been focused on the plight of the Steller sea lion, in light of the precipitous decline in abundance over the last 30 years (Loughlin 1998). Similar issues of incidental bycatch, direct harvesting, and resource competition are relevant for all species, including the Australian (*Neophoca cinerea*) and New Zealand sea lion (*Phocarctos hookeri*). These two species, while similar in abundance, differ markedly in aspects of biology and the issues confronting them. In this paper we will address the current issues of concern for these two species and provide an overview of the challenges facing managers of these resources.

New Zealand sea lion

Distribution and abundance

The endemic New Zealand sea lion, *Phocarctos hookeri* (also known as Hooker's sea lion) is one of the world's rarest pinnipeds, and has a highly localized distribution. The majority of the species is found in the New Zealand subantarctic, although some animals disperse as far as the New Zealand mainland and occasionally Macquarie Island. The breeding distribution of *P. hookeri* is centered on the New Zealand subantarctic islands with 87% of pup production for the species occurring at two

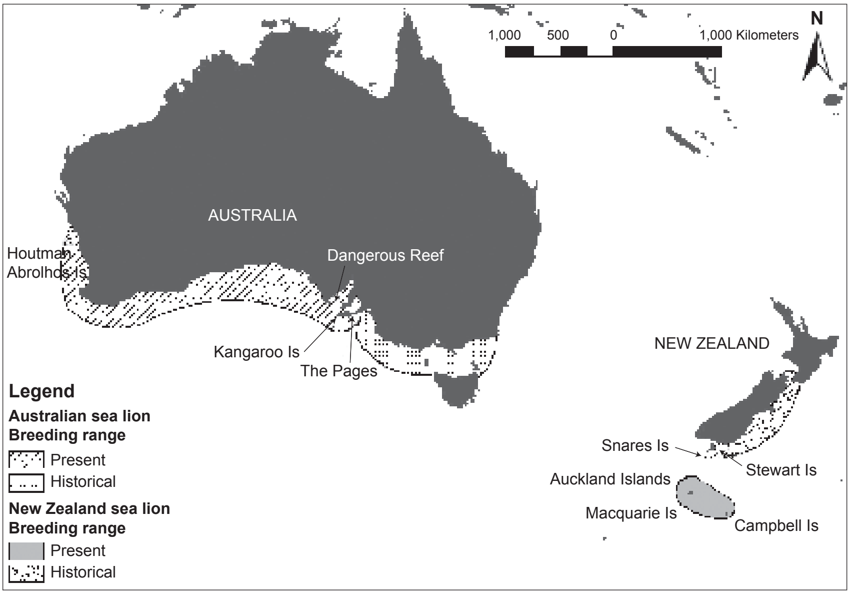


Figure 1. Historical breeding range was more extensive for both species prior to commercial exploitation and subsistence harvesting. Occasional breeding events have been reported on the South Islands of New Zealand; however, there has been no recolonization of this previous range by either species for over 100 years.

breeding areas in the Auckland Islands and the remaining 13% born at Campbell Island (Fig. 1; Childerhouse et al. 2005). Under New Zealand legislation, *P. hookeri* have been gazetted as a threatened species and are also listed as threatened by the IUCN (IUCN 2004, Hitchmough 2002). The species is designated as "vulnerable" as breeding is restricted to less than five locations (IUCN 1994). Occasional births have been recorded at the Snares (Crawley and Cameron 1972), Stewart Island (Childerhouse and Gales 1998) and Otago Peninsula (McConkey et al. 2002). The mean population size of New Zealand sea lions is estimated at 11,855 (95% confidence intervals 10,259-13,625) individuals for the 2004-2005 austral breeding season (B.L. Chilvers unpubl. data). The population appears to be undergoing a low-level decline in recent years from the population estimate of approximately 12,000-14,000 individuals in the mid 1990s (Gales and Fletcher 1999, Wilkinson et al. 2003, B.L. Chilvers unpubl. data). Pup production at Sandy Bay in the Auckland Islands has been approximately stable for at least the last three decades but is showing the same slow decline as the overall population (B.L. Chilvers unpubl. data). Records from other colonies are not sufficient to assess the long-term status. During the last decade there have been three unusually high mortality events recorded. In the 1997-1998 breeding season over 53% (n = 1,600) of pups and at least 70 adults died from an unidentified cause, speculated to have been a bacterial infection (Wilkinson et al. 2003). Two similar events, thought to be related to *Klebsiella pneumoniae* epidemics (Wilkinson et al. 2003) resulted in over 33% and 21% mortality in pups by 6 weeks of age during the breeding seasons 2001-2002 and 2002-2003 respectively. Although the impacts of these events on this species is not fully understood, it does indicate that disease can play a significant role in their dynamics (Wilkinson et al. 2003). The epidemics observed in 2001-2002 and 2002-2003 are expected to result in between 2.3% and 4.6% fewer adult females being present in the breeding population in 2007-2008 (Wilkinson et al. 2006).

The pristine abundance and distribution of the sea lion is unknown but it is clear from archaeological and commercial sealing records that significant exploitation for food and skins took place prior to the twentieth century. New Zealand sea lions had a substantially more widespread distribution before the arrival of humans in New Zealand and the distribution was significantly reduced by sealing and subsistence harvesting, which are the most likely causes of historical changes in distribution and abundance. The pre-exploitation distribution included the whole length of mainland New Zealand's coast, from the far north of the North Island through to Stewart Island and the subantarctic islands (Fig. 1; Childerhouse and Gales 1998, Gill 1998). The present breeding range is restricted to the Auckland Islands and Campbell Island, and a few individuals breeding irregularly outside of these areas. Within the last 10 years a few females (<10) have started to breed on mainland New Zealand and

Stewart Island, which may reflect a slow recolonization of earlier breeding grounds (McConkey et al. 2002).

Biology and ecology

New Zealand sea lions have marked sexual dimorphism: adult males weigh up to 450 kg and females up to 160 kg (Crawley 1995). At birth pups are 8-12 kg (Crawley 1995). Adult females vary from buff to creamy gray with darker pigment around the muzzle and flippers. Adult males are blackish-brown with a well-developed black mane of coarse hair reaching the shoulders (Crawley 1995). New Zealand sea lions breed and haul out on a diverse range of terrestrial habitat including sandy beaches, reef flats, grass and herb fields, dense bush and forest, and solid bedrock. They are polygynous breeders with colonial breeding occurring during the austral summer December-January. Adult males hold and defend physical territories on the breeding colonies. Challenges from peripheral males are regular and the tenure of territorial males is short (Robertson et al. 2006.). Post-parturient females exhibit estrus 7-10 days after birth of their pup and are mated by the territorial bull. Females become sexually mature as early as age 3 and can produce a pup the following year; however, current research indicates a low incidence of females breeding for the first time as either 4 or 5 year olds (I. Wilkinson, Department of Conservation, New Zealand, unpubl. data). Males become sexually mature at four years old but do not hold territories for a further 3-5 years. Maximum age recorded for both sexes is 23 years old. Foraging studies on lactating females at the Auckland Islands have found that they forage primarily on the shelf, up to 140 km from shore and mostly at depths of 100-200 m, but can dive to more than 500 m (Chilvers et al. 2005). Related studies have suggested that female New Zealand sea lions appear to be operating (diving) close to their physiological maximum (Costa et al. 1998, 2001; Crocker et al. 2001; Chilvers et al. unpubl. data). There have been no foraging studies for males. Sea lions forage on a wide variety of prey items including fish, cephalopods, and crustaceans and exhibit both benthic and midwater foraging patterns (Childerhouse et al. 2001).

Management issues

During the 1970s, a trawl fishery for arrow squid (*Nototodarus sloanii*) was established on the Auckland Island and Snares Island shelf. As the fishery developed, an accidental bycatch of sea lions became apparent (New Zealand Ministry of Agriculture and Fisheries 1991). Estimates of the sea lion bycatch in the squid fishery have varied from year to year, but official estimates range from 14 to 141 for the years 1988-2004. In total, it is estimated that 1,231 sea lions have been killed, at an average of 72 per annum. In addition to bycatch in the squid fishery, sea lions are also caught in other commercial fisheries including scampi, southern blue whiting, and orange roughy (Wilkinson et al. 2003). As a threatened species, the New Zealand sea lion–squid fishery interaction has been the subject of an ongoing management plan.

Management of the sea lion–fishery interaction has been undertaken in two main areas. The first included the implementation of closed areas to fishing to mitigate the risk accidental captures posed to the population. In 1986 the government imposed a 12 nautical mile exclusion zone around the Auckland Islands that prohibited trawling close to the major breeding areas of the New Zealand sea lion (Sharp-Brewer 1992). In 1994, the Auckland Islands Marine Mammal Sanctuary was established within this same area with the same controls on fishing; in 2004 this area became part of the Auckland Islands–Motu Maha Marine Reserve, extending the prohibition to all fishing activities within the 12-mile exclusion zone. However, foraging studies have shown that adult females range over 100 km from their breeding sites (Chilvers et al. 2005), thus limiting the mitigating effect of this measure.

In addition, fisheries controls were implemented to directly manage fishing effort. In an attempt to limit the potential impact of the sea lion bycatch a catch limit or fisheries related mortality level (FRML) of sea lions was set by the government in 1992, on the basis of draft guidelines from the United States National Marine Fisheries Service (e.g., potential biological removal, see Wade 1998). The estimated level of bycatch is monitored in season by government observers aboard the fishing vessels (normally covering about 20% of all vessels) and the fishery is closed for the remainder of that year when it is estimated that the FRML has been reached (Wilkinson et al. 2003).

An FRML is set each year based on population estimates and has been approximately 60-80 individuals a year since 1992. The squid fishery has been closed seven times over the last thirteen years when it was estimated that bycatch exceeded the FRML. While the approach has been successful, it has not always offered complete protection to the sea lions. Often the delay in reporting and closure of the fishery has led to estimated catches of sea lions exceeding the FRML for that year. In 2003 legal action by the fishing industry forced the reopening of the fishery after it was closed. In addition, recent modeling work (Breen et al. 2003) has suggested that the present method for setting an FRML is overly conservative and that more sea lions can be killed without impacting on the recovery of the population. Based on this modeling work, it is likely that the present method of setting an FRML will be altered to a so-called “adaptive rule” whereby the FRML will be set using a polynomial function at a rate proportional to the number of pups born and will be increased/ decreased according to changes in the status of pup production. It is argued that the use of the adaptive rule is the strategy best suited to optimize utilization of the squid fishery, recognizing information uncertainty and providing for the recovery of New Zealand sea lions. This method resulted in an FRML of 115 sea lions for the 2004-2005 season. The level of fishing-related mortality for the 2004-2005 season was assessed by calculating an average strike rate of capture per unit fishing effort and then monitoring the fishing effort expended, as opposed to using observers in previous years.

In addition to the setting of an FRML there has been ongoing development of a sea lion excluder device (SLED) that works on a similar principle to grids used in a number of trawl fisheries to exclude sea turtles and other large vertebrates (Seidel and McVea 1982). This device aims to eject sea lions through an escape panel before they enter the codend of the net, so that they do not get caught and drowned. To date results have been equivocal—there has been reasonable success in ejecting sea lions but many show signs of trauma that would more than likely lead to their death (Wilkinson et al. 2003). The development is ongoing and at present a 20% discount factor on the average strike rate is allocated to vessels that use an approved SLED, based on the assumption that 20% of the sea lions passing through it survive. This has the effect of increasing the FRML by 20% in relation to the fishing effort allowed under the adaptive rule.

There may also be indirect effects of commercial fishing on the New Zealand sea lion due to resource competition and ecosystem impact; however, the extent or level of this impact is currently unknown. It has been proposed that competition with commercial fishing is one of the causes of the precipitous decline in Steller sea lions (Calkins et al. 1999), and it is now recognized that ecosystem-based management of fisheries is a key strategy for the maintenance of all marine ecosystems (Pikitch et al. 2004).

Research and the future

Current research includes obtaining demographic and population status parameters, health status of populations, and foraging and diet analysis in relation to fisheries interactions. Given the restricted range and small population size of this species, it is vital that population and management models incorporate the effects of disease, data uncertainty, and other stochastic events into management models. This is needed to ensure that the effects of fishing-related mortality on the population can be accurately determined, and appropriate management strategies put in place to ensure the long-term survival of this species.

Australian sea lion

Distribution and abundance

Current population estimates of the Australian sea lion suggest there are approximately 12,000-14,000 animals, and the population is relatively stable (Gales et al. 1994, Goldsworthy et al. 2003). *Neophoca cinerea* breed nearly exclusively on offshore islands between the Houtman Abrolhos Islands (28.45ºS, 113.75ºE) and The Pages (35.78ºS, 138.28ºE) in South Australia, on over 70 individual breeding colonies (Fig. 1). Most colonies are relatively small, producing less than 50 pups, and approximately 40% of the pup production occurs at three colonies in South Australia (The Pages, Kangaroo Island, and Dangerous Reef). Historical commercial exploitation during the eighteenth to twentieth centuries reduced the range of this species with local and regional extinctions recorded (Fig. 1; Ling 1999). There have been no subsequent recolonizations of these breeding areas. Harvest records suggest that a minimum of 3,500 Australian sea lions were killed. However, recent examination of records for the south coast of Western Australia shows that a minimum of 2,000 animals were killed in this population alone (Campbell 2005), resulting in a minimum of 5,500 skins harvested across the range.

Trends in pup production vary across colonies with a low level decline reported at Kangaroo Island over the past 20 years, and an increase recorded for Dangerous Reef over the last six seasons (Shaughnessy et al. 2006). Populations on the west coast of Western Australia appear stable over the past 15 years, though there have been recorded declines in pup production at some of the south coast colonies (Gales et al. 1994, Campbell 2003). There are very limited data for most other colonies, and this is one of the fundamental challenges to be met for the effective management of this species.

This species has only recently been listed as “vulnerable” on the threatened species list under federal legislation (Environmental Protection and Biodiversity Conservation Act [EPBC Act] of 1999), based on the prospect that population declines are likely to continue. This listing requires a national recovery plan to be drafted that will identify key threatening processes. Under the EPBC Act, commercial fisheries are required to meet ecological sustainable development (ESD) guidelines that include mitigating impact with protected species to maintain their export license. The Australian sea lion is also afforded “special protection” status by Western Australia state legislation and classified as “rare” under South Australian legislation.

Biology and ecology

The Australian sea lion displays marked sexual dimorphism with males reaching a maximum weight of 350 kilograms and females averaging around 100 kg. Pups are around 5 kg at birth and postparturient females exhibit estrus around 7-10 days after giving birth. This species is a polygynous breeder with males defending a number of females sequentially over the course of the extended 4-5 month breeding season (Ling 1992, Gales et al. 1994).

This species is unique among pinnipeds in having a supra-annual, non-synchronous breeding cycle (Higgins 1993, Gales et al. 1994). It displays an elongated 17.5 month breeding cycle which includes a long active gestation phase of 13 months (Ling and Walker 1978, Higgins 1993, Gales et al. 1994). It was postulated that this system evolved in response to a low nutrient environment, allowing for the extension of active gestation and time until weaning to maximize pup survival (Gales and Costa 1997). Recent research suggests that this cycle may vary in length in relation to SST and possibly resource availability, adding yet another facet to the unique biology of the Australian sea lion (Goldsworthy et al. 2004).

It was suggested that the asynchronous nature of the breeding cycle was maintained by female natal site fidelity, and that the timing of estrus may be genetically regulated. Investigation of the patterns of mtDNA, which is maternally inherited, showed that there was indeed extremely high levels of female natal site fidelity (Campbell 2003), resulting in high levels of population subdivision on a finer scale than previously recorded for any marine mammal species (Maldonado et al. 1995, Lamont et al. 1996, Bernardi et al. 1998, Slade et al. 1998, Anderson and Born 2000, Goldsworthy et al. 2000, Trujillo et al. 2004). A comparable level of population structuring is evident in the California Channel Island fox, where sub-populations are geographically separated by island habitat (Gilbert et al. 1990). The consequence of this high level of population subdivision is that nearly each breeding colony is a separate population of locally recruiting females, with obvious consequences for conservation management in light of their small population size. Effectively, every distinct breeding colony is a "management unit" (see Moritz 1994). The lack of recolonization by *N. cinerea* to previously known breeding range reflects this trait, and is in contrast to the recolonization of previous breeding range by other otariids (e.g., New Zealand fur seals in Gales et al. 2000).

Examination of other genetic markers incorporating male and female mediated gene flow (i.e., microsatellites) suggests that there are distinct sub-populations that have minimal gene flow based on regional geography. Males exhibit greater dispersal capabilities than females but appear to be limited to a fairly narrow geographic range (~200-300 km, Campbell 2003). Low levels of genetic diversity in some sub-populations may also be of consequence to survival, as reduced diversity appears to influence pup survival in other pinnipeds (e.g., harbour seals in Coltman et al. 1998, grey seals in Bean et al. 2004).

High rates of pup mortality (40-50%) have been recorded occasionally at a number of breeding colonies (Shaughnessy 1999). Known causes of death are crushing by conspecifics, both accidental and intentional, disease, and starvation (Higgins and Tedman 1990; R. McIntosh, LaTrobe University, Melbourne, Australia, unpubl. data). Rates of mortality at some colonies appear to be greater for breeding seasons that occur primarily in the colder winter months than summer (Gales et al. 1992, Shaughnessy 1999). Positive density-dependent effects on pup mortality are evident at three breeding colonies on the west coast of Western Australia, which may act to limit population growth (Campbell 2005). Average pup mortality rates for the parapatric New Zealand fur seal are at least a magnitude lower, at approximately 2-4% (Gales et al. 2000). Increased levels of interaction in sea lion colonies are possible due to the extended breeding season (5 months) and the plasticity of male territories as they pursue and defend estrus females. It is likely that the peaks of pup mortality are due to a combination of factors but are not currently well understood.

The Australian sea lion is a generalist feeder with a wide array of prey items including rock lobster, cephalopods, shark, and benthic fishes (Gales and Cheal 1992). Lactating females appear to forage exclusively on the benthos on the continental shelf, between 10 and 120 meters, and are pushing their metabolic limit to a greater extent than any other otariid recorded (Costa and Gales 2003). Pups and juveniles are restricted to foraging in shallow waters, usually less than 60 meters, due to development of oxygen store capacity. Females have been reported ranging over 60 kilometers from the breeding colony during foraging trips whereas pups and juveniles are limited to shorter range trips up to 20 kilometers (Fowler and Costa 2004.). Adult males dive deeper (<300 m), ranging across the continental shelf and slope edges (D. Costa, University of California, Santa Cruz, pers. comm.).

Management issues

It is evident that even low levels of incidental mortality (e.g., from fisheries) may adversely affect the viability of the many small, genetically isolated colonies. In addition to this, the known foraging range of this species overlaps extensively with human activities across the continental shelf. This increases the risk of both direct and indirect effects of fishing on the sea lion population, especially for younger animals that are limited to foraging in close proximity to their natal site. Recorded impacts on *N. cinerea* include incidental capture and injury through entanglement and anecdotal reports of direct shooting (Mawson and Coughran 1999, Shaughnessy et al. 2003). Indirect effects may include trophic level disturbances through depletion of resources, resource competition, and possible top-down forcing effects by predators of sea lions due to reduced prey abundance. At present, there is little evidence of recruitment overfishing occurring in fisheries that operate within the range of *N. cinerea* (Penn et al. 2005), though this issue may be more relevant for pups and juveniles who are confined to foraging in shallow waters.

Understanding the rate of incidental catch in fishing operations and marine debris is poor at present, though indications are that this could be a significant cause of mortality especially among younger cohorts (Page et al. 2004). For example, on the west coast of Western Australia an interaction occurs with the pot-based rock lobster fishery. Sea lions forage from pots for lobster and bait and occasionally become stuck in the pot and drown (Shaughnessy et al. 2003, Western Australia Department of Fisheries 2004). Surveys of pup production in this area show that between 130 and 150 pups are born every breeding cycle, and preliminary estimates of the level of bycatch suggest that between 2 and 12 animals (pups and juveniles) are caught every fishing season (Campbell et al. unpubl.). On the basis of this level of bycatch it was decided by the fishery management authority to eliminate the bycatch by means of pot modification (Western Australia Department of Fisheries 2004). Anecdotal reports of significant levels of bycatch of Australian sea lions in other fisheries every season (e.g., demersal gillnets) suggest that there is considerable interaction (Shaughnessy 1999), and may represent a level of bycatch that is adversely affecting the viability of some populations of this species.

The Australian sea lion is also the focus of considerable tourism activities throughout its range and the impacts of this are unknown at present. Potential concerns are the disturbance of breeding colonies resulting in a reduction or loss of reproductive output, transmission of disease, and supplementary feeding. These concerns all have the potential to drastically impact the viability of small populations.

Research and the future

The issue of indirect effects of interaction with commercial fisheries is also of considerable concern given the spatial extent of foraging ranges and the consumption of commercially fished prey species. The broad range of the sea lion's diet may give them the ability to prey shift if required and thus mediate this effect. However, given the high metabolic effort expended by lactating females in foraging, a small change in resource abundance may impact foraging behavior and reduce pup survival rates and female reproductive rates. A number of research projects are currently under way to examine diet, interactions between commercial fishing activity and foraging behavior, and the impacts of marine protected areas on foraging ecology. Increased effort in long-term monitoring of pup production across the range is essential in the light of reported declines at some colonies. This is especially important given the large number of small, reproductively isolated colonies. Mitigation of incidental bycatch and other sources of anthropogenic mortality is a key issue in the effective conservation of this endemic species, and will require close cooperation between research scientists, fishery managers, and fishermen.

Conclusions

The antipodean sea lion species exhibit some similarities in population size and historical processes that affected their distributions, and there are common concerns in the management of interactions with commercial fishing operations. Future management of marine ecosystems will include the challenge of assessing the indirect effects of commercial fishing on top-order predators such as sea lions. There are knowledge gaps for both species, with regard to the ontogeny of foraging behavior and diet, that must be filled to successfully implement ecosystem management. There is also a paucity of life history data for *N. cinerea* in particular, and this knowledge may be of increasing importance in the future as the impacts of fisheries interactions are assessed. The development of research programs to assess the population decline in other species (e.g., Steller sea lions) provides an opportunity for Southern Hemisphere scientists to tailor their research efforts and provide effective conservation management for the Australian and New Zealand sea lion.

References

Anderson, L.W., and E.W. Born. 2000. Indications of two genetically different subpopulations of Atlantic walruses (*Odobenus rosmarus rosmarus*) in west and northwest Greenland. Can. J. Zool. 78:1999-2009.

Bean, K., W. Amos, P. Pomeroy, S.D. Twiss, T.N. Coulson, and I.L. Boyd. 2004. Patterns of parental relatedness and pup survival in the grey seal (*Halichoerus grypus*). Mol. Ecol. 13:2365-2370.

Bernardi, G., S.R. Fain, and J.P. Gallo-Reynoso. 1998. Genetic variability in Guadalupe fur seals. J. Hered. 89:301-305.

Breen, P.A., R. Hilborn, M.N. Maunder, and S. Kim. 2003. Effects of alternative control rules on the conflict between a fishery and a threatened sea lion (*Phocarctos hookeri*). Mar. Mam. Sci. 60:527-541.

Calkins, D.G., K. McAllister, K.W. Pitcher, and G.W. Pendleton. 1999. Steller sea lion status and trend in southeast Alaska: 1979-1997. Mar. Mam. Sci. 14:232-244.

Campbell, R.A. 2003. Demography and genetic population structure of the Australian sea lion (*Neophoca cinerea*). Ph.D. thesis, University of Western Australia, Department of Zoology, Perth.

Campbell, R.A. 2005. Historical distribution and abundance of the Australian sea lion (*Neophoca cinerea*) on the west coast of Western Australia. Fisheries Research Report No. 148, Department of Fisheries, Western Australia. 42 pp.

Childerhouse, S., and N. Gales. 1998. Historical and modern distribution and abundance of the New Zealand sea lion *Phocarctos hookeri*. N.Z.J. Zool. 25:1-16.

Childerhouse, S., B. Dix, and N. Gales. 2001. Diet of New Zealand sea lions (*Phocarctos hookeri*) at the Auckland Islands. Wildl. Res. 28:291-298.

Childerhouse, S., N. Gibbs, G. McAlister, S. McConkey, H. McConnell, N. McNally, and D. Sutherland. 2005. Distribution, abundance and growth of NZ sea lion, *Phocarctos hookeri,* pups on Campbell Island. N.Z.J. Mar. Freshw. Res. 39:889-898.

Chilvers, B.L., I.S. Wilkinson, P.J. Duignan, and N.J. Gemmell. 2005. Summer foraging areas for lactating New Zealand sea lions, *Phocarctos hookeri*. Mar. Ecol. Prog. Ser. 304:235-247.

Coltman, D., W. Bowen, and J. Wright. 1998. Birth weight and neonatal survival of harbour seal pups are positively correlated with genetic variation measured by microsatellites. Proc. R. Soc. Lond. Ser. B 265:803-809.

Costa, D.P., and N.J. Gales. 2003. The energetics of a benthic diver: Seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. Ecol. Monogr. 73:27-43.

Costa, D.P., N.J. Gales, and D.E. Crocker. 1998. Blood volume and diving ability of the New Zealand sea lions, *Phocarctos hookeri*. Physiol. Zool. 71:208-213.

Costa, D.P, N.J. Gales, and M.E. Goebel. 2001. Aerobic dive limit: How often does it occur in nature? Comp. Biochem. Physiol. 129:771-783.

Crawley, M.C. 1995. NZ sea lions. In: C.M. King, The handbook of New Zealand mammals. Oxford University Press, Auckland, pp. 256.

Crawley, M.C., and D.B. Cameron. 1972. New Zealand sea lions, *Phocarctos hookeri,* on the Snares Islands. N.Z.J. Mar. Freshw. Res. 6:127-132.

Crocker, D.E., N.J. Gales, and D.P. Costa. 2001. Swimming speed and foraging strategies of New Zealand sea lions (*Phocarctos hookeri*). J. Zool. (Lond.) 254:267-277.

Fowler, S., and D.P. Costa. 2004. Foraging in a nutrient limited environment: Development of diving in the threatened Australian sea lion. Presented at Sea Lions of the World: Conservation and Research in the 21st Century, Sept. 30-Oct. 3, 2004, Anchorage, Alaska. Alaska Sea Grant College Program, University of Alaska Fairbanks. Unpubl.

Gales, N.J., and A.J. Cheal. 1992. Estimating diet composition of the Australian sea lion (*Neophoca cinerea*) from scat analysis: An unreliable technique. Wildl. Res. 19:447-456.

Gales, N., and D. Costa. 1997. The Australian sea lion: A review of an unusual life history. In: M. Hindell and C. Kemper, Marine mammal research in the Southern Hemisphere. Volume 1: Status, ecology and medicine. Surrey, Beatty and Sons, Chipping Norton.

Gales, N.J., and D.J. Fletcher. 1999. Abundance, distribution and status of the New Zealand sea lion, *Phocarctos hookeri*. Wildl. Res. 26:35-52.

Gales, N.J., A.J. Cheal, G.J. Pobar, and P. Williamson. 1992. Breeding biology and movements of Australian sea lions, *Neophoca cinerea*, off the west coast of Western Australia. Wildl. Res. 19:405-416.

Gales, N.J., B. Haberley, and P. Collins. 2000. Changes in the abundance of New Zealand fur seals, *Arctocephalus forsteri*, in Western Australia. Wildlife Research 27:165-168.

Gales, N.J., P.D. Shaughnessy, and T.E. Dennis. 1994. Distribution, abundance and breeding cycle of the Australian sea lion, *Neophoca cinerea*. J. Zool. 234:353-370.

Gilbert, D.A., N. Lehman, S.J. O'Brien, and R.K.Wayne. 1990. Genetic fingerprinting reflects population differentiation in the California channel-island fox. Nature 344:764-767.

Gill, B.J. 1998. Prehistoric breeding sites of New Zealand sea lions (*Phocarctos hookeri*, Carnivora: Otariidae) at North Cape. Rec. Auckl. Mus. 35:55-64.

Goldsworthy, S., P.D. Shaughnessy, and R. McIntosh. 2004. Plasticity in gestation length in response to environmental conditions in Australian sea lions, *Neophoca cinerea*: New hypotheses to an enigmatic life history. Presented at Sea Lions of the World: Conservation and Research in the 21st Century, Sept. 30-Oct. 3, 2004, Anchorage, Alaska. Alaska Sea Grant College Program, University of Alaska Fairbanks. Unpubl.

Goldsworthy, S.W., C. Bulman, X. He, and C. Littnan. 2003. Trophic interactions between marine mammals and Australian fisheries: An ecosystem approach. In: N. Gales, M. Hindell, and R. Kirkwood (eds.), Marine mammals: Fisheries, tourism and management issues. CSIRO Publishing, Melbourne, pp. 62-99.

Goldsworthy, S., J. Francis, D. Boness, and R. Fleischer. 2000. Variation in the mitochondrial control region in the Juan Fernandez fur seal (*Arctocephalus philippii*). J. Hered. 91:371-377.

Higgins, L.V. 1993. The non-annual, non-seasonal breeding cycle of the Australian sea lion, *Neophoca cinerea*. J. Mammal. 74:270-274.

Higgins, L.V., and R.A. Tedman. 1990. Effects of attacks by male Australian sea lions, *Neophoca cinerea*, on mortality of pups. J. Mammal. 71:617-619.

Hitchmough, R.A. 2002. New Zealand threat classification systems list 2002. Department of Conservation, Threatened Species Occasional Publication 23, Wellington.

IUCN. 1994. Red list categories and criteria, V. 2.3. IUCN Species Survival Commission, Gland, Switzerland.

IUCN. 2004. Red list of threatened species. IUCN Species Survival Commission, Gland, Switzerland.

Lamont, M.M., J.T. Vida, J.T. Harvey, S. Jeffries, R. Brown, H.H. Huber, R. Delong, and W.K. Thomas. 1996. Genetic substructure of the Pacific harbor seal (*Phoca vitulina richardsi*) off Washington, Oregon and California. Mar. Mam. Sci. 12:402-413.

Ling, J. 1992. *Neophoca cinerea*. Mamm. Species 392:1-7.

Ling, J.K. 1999. Exploitation of fur seals and sea lions from Australian, New Zealand and adjacent subantarctic islands during the eighteenth, nineteenth and twentieth centuries. Aust. Zool. 31:323-350.

Ling, J.K., and G.E. Walker. 1978. An 18 month breeding cycle in the Australian sea lion? Search 9:464-465.

Loughlin, T.R. 1998. The Steller sea lion: A declining species. Biosphere Conservation 1:91-98.

Maldonado, J.E., F.O. Davila, B.S. Stewart, E. Geffen, and R.K. Wayne. 1995. Intraspecific genetic differentiation in California sea lions (*Zalophus californianus*) from southern California and the Gulf of California. Mar. Mamm. Sci. 11:46-58.

Mawson, P.R., and D.K. Coughran. 1999. Records of sick, injured and dead pinnipeds in Western Australia 1980-1996. J.R. Soc. West. Aust. 82:121-128.

McConkey, S.D., S. Heinrich, C. Lalas, H. McConnell, and N. McNally. 2002. Pattern of immigration of New Zealand sea lions, *Phocarctos hookeri*, to Otago, New Zealand: Implications for management. Aust. Mammal. 24:107-116.

Moritz, C. 1994. Applications of mitochondrial DNA analysis in conservation: A critical review. Mol. Ecol. 3:401-411.

New Zealand Ministry of Agriculture and Fisheries. 1991. Hooker's sea lion: Public discussion paper June 1991. Ministry of Agriculture and Fisheries and Department of Conservation, Wellington, New Zealand.

Page, B., J. McKenzie, R. McIntosh, A. Baylis, A. Morrissey, N. Calvert, T. Haase, M. Berris, D. Dowie, P. Shaughnessy, and S.D. Goldsworthy. 2004. Entanglement of Australian sea lions and New Zealand fur seals in lost fishing gear and other marine debris before and after government and industry attempts to reduce the problem. Mar. Pollut. Bull. 49:33-42.

Penn, J.W., W.J. Fletcher, and F. Head (eds.). 2005. State of the fisheries report 2003/04. Department of Fisheries, Perth, Western Australia.

Pikitch, E.K., C. Santora, E.A. Babcock, A. Bakun, R. Bonfil, D.O. Conover, P. Dayton, P. Doukakis, D. Fluharty, B. Heneman, E.D. Houde, J. Link, P.A. Livingston, M. Mangel, M.K. McAllister, J. Pope, and K.J. Sainsbury. 2004. Ecosystem-based fishery management. Science 305:346-347.

Robertson, B.C., B.L. Chilvers. P.J. Duignan, I.S. Wilkinson, and N.J. Gemmell. 2006. Dispersal of breeding, adult male *Phocarctos hookeri*: Implications for disease transmission, population management and species recovery. Biol. Conserv. 127:227-236.

Sharp-Brewer, E. 1992. The future management of the Hooker's sea lion/squid trawl fishery interaction around the Auckland Islands. Internal MAF [Ministry of Agriculture and Forestry] Memorandum. Wellington, New Zealand.

Shaughnessy, P.D. 1999. The action plan for Australian seals. Environment Australia.

Shaughnessy, P.D., R. Kirkwood, M. Cawthorn, C. Kemper, and D. Pemberton. 2003. Pinnipeds, cetaceans, and fisheries in Australia: A review of operational procedures. In: N. Gales, M. Hindell, and R. Kirkwood (eds.), Marine mammals: Fisheries, tourism and management issues. CSIRO Publishing, Melbourne, pp. 136-152.

Shaughnessy, P.D., R.R. McIntosh, S.D. Goldsworthy, T.E. Dennis, and M. Berris. 2006. Trends in abundance of Australian sea lions, *Neophoca cinerea*, at Seal Bay, Kangaroo Island, South Australia. In: A.W. Trites, S.K. Atkinson, D.P. DeMaster, L.W. Fritz, T.S. Gelatt, L.D. Rea, and K.M. Wynne (eds.), Sea lions of the world. Alaska Sea Grant College Program, University of Alaska Fairbanks.

Slade, R.W., C. Moritz, A.R. Hoelzel, and H.R. Burton. 1998. Molecular population genetics of the southern elephant seal *Mirounga leonina*. Genetics 149:1945-1957.

Trujillo, R.G., T.R. Loughlin, N.J. Gemmell, J.C. Patton, and J.W. Bickham. 2004. Variation in microsatellites and mtDNA across the range of the Steller sea lion, *Eumetopias jubatus*. J. Mammal. 85:338-346.

Wade, R.P. 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. Mar. Mam. Sci. 14:1-37.

Western Australia Department of Fisheries. 2004. Western rock lobster environmental management strategy July 2002-June 2006. Department of Fisheries, Western Australia.

Wilkinson, I.S., J. Burgess, and M.W. Cawthorn. 2003. New Zealand sea lions and squid: Managing fisheries impacts on a threatened marine mammal. In: N. Gales, M. Hindell, and R. Kirkwood (eds.), Marine mammals: Fisheries, tourism and management issues. CSIRO Publishing, Melbourne, pp. 192-207.

Wilkinson, I.S., P.J. Duignan, A. Castinel, A. Grinberg, B.L. Chilvers, and B.C. Robertson. 2006. *Klebsiella pneumoniae* epidemics: Possible impact on New Zealand sea lion recruitment. In: A.W. Trites, S.K. Atkinson, D.P. DeMaster, L.W. Fritz, T.S. Gelatt, L.D. Rea, and K.M. Wynne (eds.), Sea lions of the world. Alaska Sea Grant College Program, University of Alaska Fairbanks.

An Integrated Bayesian Evaluation of Hooker's Sea Lion Bycatch Limits

P.A. Breen and S.W. Kim
National Institute of Water and Atmospheric Research Ltd., Wellington, New Zealand

Abstract

This paper extends previous work on the effect of New Zealand's subantarctic squid fishery on the threatened Hooker's sea lion at the Auckland Islands. The management goal is to rebuild and maintain the population above 90% of carrying capacity, K, and to maintain the population above 90% of the unfished level in years when it is less than 90% K.

We fitted a fully age-structured model, with density-dependent pup births, to seven sets of population data, including time series of estimated births, tag/re-sighting data, pup mortalities, and population and bycatch age structures. From these data the model estimated posterior distributions for survival, maturity, vulnerability, and pupping rate parameters. A prior distribution on the intrinsic rate of increase, λ, a derived parameter, was necessary to obtain biologically reasonable estimates.

The population appears to be near K already. The bycatch control rule used in New Zealand before 2004, based on the Permitted Biological Removal approach and different policy objectives from the goal listed above, was very conservative and incurred a high cost to the fishery. Simple alternatives are safe to the sea lion population, meet the management goal, and incur much lower economic cost.

The Bayesian model is an ideal tool for incorporating multiple data sets and prior information in such evaluations.

Introduction

Near the Auckland Islands in the subantarctic waters south of New Zealand, the commercial trawl fishery for arrow squid (*Nototodarus sloanii*) incidentally catches some endemic New Zealand or Hooker's sea lions (*Phocarctos hookeri*). Because the sea lion population has a threat classification, the bycatch is treated as a serious conservation problem and the fishery is restricted. This study extends the work of Breen et al. (2003) and describes a new evaluation of decision rules or "management procedures" for controlling sea lion bycatch.

Sea lion biology and the history of exploitation are described by Childerhouse and Gales (1998) and Wilkinson et al. (2003). From 2,150 to 3,000 pups are born annually at four rookeries on the Auckland Islands, 385 were born in 2003 at Campbell Island (Childerhouse et al. 2005), and very few are born on the South Island (McConkey et al. 2002b). Sea lions were killed for their hides in the early nineteenth century, were depleted and then rebounded, but pre-exploitation numbers and severity of exploitation cannot be estimated (Childerhouse and Gales 1998). The species is classified as "vulnerable" by the International Union for the Conservation of Nature (IUCN) (Reijnders et al. 1993, IUCN 1996) because of the low number of breeding sites.

The Auckland Islands squid fishery (SQU 6T) begins in January or early February each year and usually finishes by June. Sea lions sometimes enter the trawl nets; some are caught and drowned (Table 1). The squid fishing industry is excluded from fishing closer than 12 nautical miles (22.2 km) from the islands; it uses sea lion excluder devices in the nets and a Code of Practice (Maunder et al. 2000), but the bycatch remains a cause for concern. Each year the New Zealand Ministry of Fisheries imposes a bycatch limit, estimates bycatch during the season with an observer program, and closes the fishery if the limit is approached (Table 1). Until 2004 the limit was based on the work of Wade (1998); in 2004 and 2005 it was based on this study.

Before 2004, Fisheries-Related Mortality Limits (FRMLs) were calculated as

$$FRML_y = 0.5 \frac{N_{y-1}^{vuln} + N_{y-2}^{vuln}}{2} \lambda F_r$$

where N_{y-1}^{vuln} is a conservative estimate of vulnerable sea lions in the previous year, λ ($R_{\max}$ in Wade 1998) is the maximum rate of population increase, and F_r is a "recovery factor." N_y^{vuln} was taken as the lower 20th percentile of the total population estimate, obtained from a simple model (Gales and Fletcher 1999) using estimates of pup births. Two years of population estimates were averaged.

Wade (1998) suggested that 0.12 would be a suitable default value for λ for pinnipeds, but 0.08 was adopted in New Zealand. The recovery factor, F_r, was set to 0.15 in New Zealand for reasons that were not recorded. This implementation, first used in 1992, will be called the 1992 rule.

This study was commissioned by the Ministry of Fisheries and guided by a Technical Working Group with representation from stakeholders. It modified and extended the model of Breen et al. (2003) to a variety of additional sea lion data. Bayesian results were used in simulations that

Table 1. Annual fishing effort, bycatch limits, estimated bycatch, dates of closing[a] and extrapolated effort[b] in area SQU 6T[c].

Year	Tows	Bycatch limit	Estimated bycatch	Closure date	Extrapolated tows
1988	1,737		33	–	1,737
1989	3,711		141	–	3,711
1990	5,318		117	–	5,318
1991	3,500		21	–	3,500
1992	2,216	32	82	–	2,216
1993	654	63	17	–	654
1994	4,571	63	32	–	4,571
1995	3,759	69	109	–	3,759
1996	4,160	73	104	4 May	4,160
1997	3,353	79	114	28 Mar	5,449
1998	1,413	63	63	27 Mar	2,296
1999	395	64	12	–	395
2000	1,206	65	70	8 Mar	3,136
2001	580	75	64	7 Mar	1,508
2002	1,653	79	84	13 Apr	2,149
2003	1,383	70	39	–	1,383

[a] Where the fishery was closed early because a bycatch limit was approached.
[b] Assuming a 13-week season for years when the season was closed early.
[c] From unpublished data held by the Ministry of Fisheries, Wellington, New Zealand, and Paul Starr, Starrfish, Nanaimo, B.C., Canada.

explored the effects of alternative management procedures (Butterworth and Punt 1999) on the sea lion population and on the fishery.

The New Zealand Department of Conservation (DoC) considers that new sea lion breeding colonies can be encouraged by maintaining the core population at a high percentage of its carrying capacity, *K* (cf. McConkey et al. 2002a). Their interim goal (Caroline Hart, DoC, 53 Boulcott St., Wellington, New Zealand, pers. comm.) is “to manage the recovery of the population to at least 90% of *K*, not delayed by more than 10% compared to the time that would be taken to achieve such a population status with zero fishing related mortality.”

Methods

Population data

Pup birth estimates were made annually by DoC at each of the four Auckland Islands rookeries since the 1994-1995 breeding season (1995); irregular estimates were made before then (Table 2) (Wilkinson et al. 2003). A reliability code was developed for each estimate: for this study only estimates with high reliability codes were used and a sensitivity trial showed that this restriction had little effect on results (Breen and Kim 2005).

Bycatch-at-age frequency was estimated from sea lions caught by the squid fishery, then autopsied and aged (Childerhouse et al. 2004) from tooth rings (Table 3) (DoC unpubl. data). We combined the 129 age estimates from 1998 and 2000-2002.

Remaining data were all provided by Ian Wilkinson (DoC pers. comm.). At the Sandy Bay rookery, biologists tagged breeding females in each of 1999, 2000, and 2001. They removed a tooth under anesthetic, and we combined the 822 estimated ages (Table 3) after comparing the individual years informally.

Female pups were tagged in 1987 and 1990-1993, and re-sightings were made in later years, especially in 1999 and later (Table 4). A similar but smaller data set comprised re-sightings of 135 breeding females branded in 2000 at Sandy Bay: numbers seen in 2001, 2002, and 2003 were 116, 107, and 94 respectively.

A small data set comprised the observed numbers of pups produced by these same 135 branded females in 2001, 2002, and 2003 (99, 69, and 77 respectively). The final data set (Table 5) comprised known pup mortalities on the combined Auckland Islands rookeries through mid-January from 1993 through 2003.

Estimation model

The Auckland Islands population model was implemented in AD Model Builder™ (Otter Research Ltd, otter-rsch.com/admodel.htm). The parent model, described by Breen et al. (2003), was altered by implementing a full age structure with ages 0-21 and assuming that all animals die after age 21. Model predictions and likelihood components were added for the six new data sets described above.

Survival-at-age was made a four-parameter function. Vulnerability-at-age (of sea lions to capture by trawls) and maturity-at-age functions were each estimated with two new parameters. The modified model is fully described by Breen and Kim (2005) (available from the first author). Males and females were not modeled separately: combined males and females were modeled. Maximum pupping rate of mature animals (*R0*) was bounded at 0.50, implying a 50:50 sex ratio. The main estimated parameters are as follows. For population size, an initial number of 1 year

Table 2. Annual pup birth estimates and their reliability codes[a] for the four Auckland Islands sea lion rookeries (Ian Wilkinson, DoC, pers. comm.).

	Sandy Bay		Dundas Island		Figure of Eight		Southeast Point	
Year	Estimate	Reliability	Estimate	Reliability	Estimate	Reliability	Estimate	Reliability
1943	350	4						
1966	465	2						
1973	525	2	1,000	4	29	3		
1975	420	2						
1976	481	2						
1977	428	2						
1978	434	2	2,077	2				
1980	193	4						
1981	471	2	2,468	3	51	3		
1982	523	2					21	3
1983	142	4						
1984	458	2						
1985	500	2	253	4	47	4		
1986	452	2	1,344	2				
1987	473	2	1,386	4	105	1		
1990	434	2			120	1		
1991	429	2	1,132	4				
1992	489	2	1,934	2				
1993	432	1	2,086	2	74	1	63	3
1995	464	1	1,837	1	132	1	71	1
1996	455	1	2,017	1	144	1	69	1
1997	509	1	2,259	1	143	1	63	1
1998	477	1	2,373	1	120	1	51	1
1999	513	1	2,186	1	109	1	59	1
2000	506	1	2,163	1	137	1	50	1
2001	562	1	2,148	1	94	1	54	1
2002	403	1	1,756	1	96	1	27	1
2003	489	1	1,891	1	94	1	43	1

[a] Reliability code 1 is a reliable modern estimate; code 4 denotes low reliability.

Table 3. Numbers-at-age in the bycatch autopsies and breeding female data sets.

Age	Bycatch	Breeding females
0	0	0
1	3	0
2	2	0
3	18	0
4	12	12
5	21	44
6	22	72
7	13	107
8	9	135
9	9	128
10	11	104
11	2	73
12	3	46
13	1	38
14	2	21
15	0	17
16	0	12
17	0	7
18	0	4
19	0	2
20	0	0
21	1	0

olds in 1965 is *N1* and the carrying capacity is *K* for mature animals. For maturity-at-age, m_{50} is the age at which 50% are mature and m_{95-50} is the difference between m_{95} and m_{50}. Similarly, v_{50} and v_{95-50} describe vulnerability-at-age.

Annual survival-at-age is based on four parameters: *S0* describes the survival of pups from birth to mid-January, *S1* describes the difference between mature and immature survival rates, including those for pups after mid-January, *S2* determines the base survival of mature animals and *S3* determines the rate at which survival declines with age for mature animals.

Table 4. Numbers of female pups tagged in each year at Sandy Bay (bold) and the number re-sighted in each subsequent year (Ian Wilkinson, DoC, pers. comm.).

	Year tagged					
Year re-sighted	1987	1990	1991	1992	1993	Total re-sighted
1987	**101**					
1988	0					0
1989	0					0
1990	0	**156**				0
1991	0	3	**193**			3
1992	2	12	8	**235**		22
1993	0	0	0	1	**205**	1
1994	0	0	0	1	0	1
1995	0	0	0	1	0	1
1996	0	8	10	6	14	38
1997	0	1	0	2	0	3
1998	0	2	6	4	1	13
1999	1	25	38	61	59	184
2000	3	24	48	62	70	207
2001	3	23	39	58	54	177
2002	3	16	27	66	58	170
2003	2	15	10	40	16	83

The model assumes that a constant proportion of the total population breeds on each rookery: it estimates three proportions Q_1 through Q_3 and determines the fourth by subtraction. The estimated bycatch (Table 1) is removed from the population each year, taking numbers- and vulnerability-at-age into account. All density-dependence was assumed to be in the pupping rate: this decreases from its maximum, *R0*, at low population size to a rate that produces equilibrium at *K*, with a shape determined by *z*.

Fitting procedure

The model was fitted simultaneously to each of the seven data sets. All error was assumed to be observation error; process error was not used in fitting but was introduced to forward projections. Estimated pup births

Table 5. Total numbers of estimated pup births, deaths by mid-January, and the percent mortality at all four Auckland Islands rookeries.

Year	Total	Alive	Dead	Mortality (%)
1993	2,389	2,304	83	3.5
1995	2,518	2,206	301	12.0
1996	2,685	2,389	296	11.0
1997	2,975	2,729	246	8.3
1998	3,021	2,350	671	22.2
1999	2,867	2,572	295	10.3
2000	2,856	2,689	167	5.8
2001	2,859	2,468	391	13.7
2002	2,282	1,826	456	20.0
2003	2,518	2,078	438	17.4

Source: Ian Wilkinson, DoC, pers. comm.

were fitted assuming normally distributed error and estimating standard deviations of observation error for each rookery (σ_1 through σ_4). Bycatch proportion-at-age was predicted from the model's numbers- and vulnerability-at-age for the relevant years; a normal likelihood was assumed and used a standard deviation function used in the New Zealand rock lobster and abalone assessments (e.g., Haist et al. 2005). The breeding-at-age data set was fitted in the same way.

The tagged female re-sightings data set was fitted with binomial likelihood and estimating a re-sighting probability, $P_t^{re-sight}$, for each year from 1991 through 2003. The branded breeding female re-sighting data set was fitted similarly except that re-sighting probability was assumed to be 100%. Pups produced by the branded females and the pup mortality rates were fitted with normal likelihood.

Likelihoods were constructed so that we could weight the individual data sets, and as in abalone and rock lobster assessments (e.g., Haist et al. 2005) a common component of error, $\tilde{\sigma}$, was estimated and applied to the standard deviations in each element of the normal fits. We estimated 33 parameters.

Bayesian priors were established for all parameters. Most were uniform distributions with wide bounds, intended to represent uninformative priors. Two non-uniform priors were used. The prior for the shape parameter z was a normal-log distribution with mean 2.5 and c.v. 0.3. A lognormal prior was used for the derived parameter λ, with a mean of 0.08 (the value used by the 1992 rule) and a c.v. of 0.4, chosen so that few of the posterior samples contained λ less than 0.02, a value thought to be unrealistically low.

Markov chain–Monte Carlo techniques (McMC) were used to estimate the posterior distributions of estimated and derived parameters. We ran a single chain of 30 million simulations, starting at the mode of the joint posterior distribution (MPD) estimates using no burn-in, and we saved 5,000 regularly spaced samples. We examined traces and simple diagnostic plots (running median and percentiles, moving mean) for each chain, but did not use more formal tests for convergence of the chains.

Projection methods

For each set of forward projections we made a 100-year run from each of the 5,000 posterior samples. From the parameter vector and data, the model generates a trajectory of numbers through the beginning of 2004. Additional information required for projections beyond 2004 is: a fishing submodel, a bycatch control rule to generate the annual bycatch limit, and stochastic error applied to population processes and the fishing and observation processes.

Bycatch control rules were applied as if they were management procedures: an input value was obtained from the population model, observed with error, and used to produce a bycatch limit under the rule, fishing was simulated, and the population was updated. This procedure was repeated in a 100-year loop, and the loop was repeated 5,000 times for each bycatch control rule, using each of the samples of the joint posterior distribution.

Fishing submodel

Each year's potential bycatch was modeled as the product of attempted fishing effort, the number of vulnerable sea lions, and an annual catchability coefficient. Attempted fishing effort was based on observed fishing effort (mean 2,871, standard deviation 1,567 tows) from 1988 to 2003, extrapolating in years when the fishery was closed early (Table 1) by assuming an undisturbed fishing season of 13 weeks. Projected effort in each year was randomly chosen from this distribution, but was not permitted to fall below the lowest observation of 395 tows.

The number of vulnerable sea lions each year was the sum of the element products of numbers- and vulnerability-at-age. Mean catchability and its standard deviation (both in log space) were calculated by the model for each of the 5,000 posterior samples from the vulnerable numbers, the observed effort, and the number caught. Projected catchability for each year was randomly chosen from this distribution.

The bycatch in a given year was then the product of vulnerable numbers, attempted tows, and the catchability coefficient. This was compared with the specified bycatch limit and the model bycatch was the lower value.

Bycatch control rules

The work described here used a family of variants of the 1992 rule. We examined the relation between pup births and the estimated vulnerable numbers, and used that relation with the other rule constants to form a simple proportional analog of the 1992 rule:

$$FRML_y = 0.02577\left(\frac{N_{0,y-1}^{proj} + N_{0,y-2}^{proj}}{2}\right)$$

where $N_{0,y-1}^{proj}$ is the pup count after simulated observation error has been applied. This was generalized to simple multiples of the 1992 PBR rule:

$$FRML_y = n0.02577\left(\frac{N_{0,y-1}^{proj} + N_{0,y-2}^{proj}}{2}\right)$$

where *n* is the multiplier and the name of the rule. Rule 0 allows no bycatch, rule 1 is the 1992 rule, rule 2 gives bycatch limits twice as high as the 1992 rule, and so on.

Stochastic error

Random observation error was applied to pup births and random process error to the fishing process and annual mortality and pupping rates. Lognormal error was applied to the mortality rate for each age, in each year using the same random deviate for all ages, but using a different error c.v. for pups and older animals (0.50 and 0.10 respectively). These were chosen after inspection of their effects; for instance, the c.v. for age 0

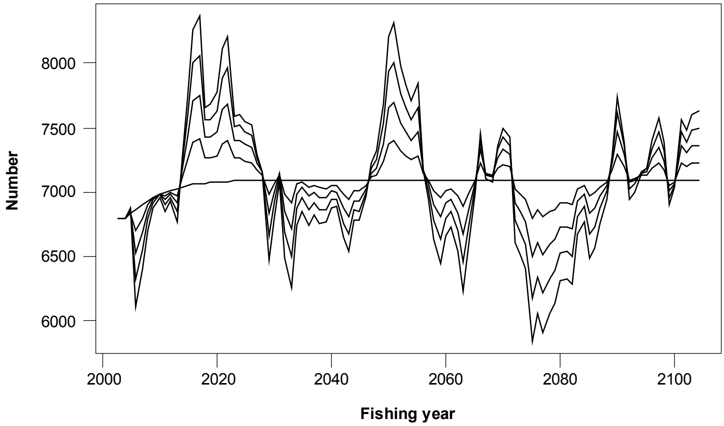


Figure 1. A randomly selected trajectory of projected mature numbers with no stochastic variation in survival (horizontal line) and with stochastic variation with c.v.s of 0.05, 0.10, 0.15, and 0.20 (concentric lines extending progressively farther from the deterministic trajectory).

allows pup mortality to be more than 50% about 3% of the time (Fig. 1). Survival rates were truncated at one-third of the deterministic value for each age to prevent extremely low values.

Each year's pupping rate was modified by lognormal error with a c.v. of 0.05, chosen after examination of its effects and comparison with the short series of observed pup counts. In sets of 5,000 projections, the sequence of stochastic errors was identical so that individual population trajectories from different bycatch control rules could be compared directly.

Indicators

We assessed whether the population was at least 90% of *K*, or at least 90% of the non-fished population, 90% of the time. Formally, this is

$$P\left(N_t^{fished} > \min\left(0.9N_t^{unfished}, 0.9K\right)\right) > 0.9$$

This was evaluated for all years in a set (the "100-year criterion") or for the first 20 years of each run (the "20-year criterion"). A third criterion was that the mean of mature numbers should be 90% of *K* in the second 50 years of each run, when averaged over the 5,000 runs (the "*Nmat/K*" criterion).

We also examined *effort lost*: the median (of the 5,000 runs) of the mean (over the 100 years in each run) of tows lost to the bycatch control rule during the run, *% closed*: the median percentage of seasons closed early by the bycatch control rule, *max catch* and *mean catch*: the median of maximum and mean annual bycatch in each run, *N100/K*: the median population at the end of 100 years, expressed as a proportion of *K* for that run, and *nadir/K*: the median of the lowest mature numbers from each run expressed as a proportion of *K*.

Results

Parameter estimation

The MPD estimate of *R0* was on its upper bound (Table 6), and the marginal posterior distribution (Table 6) was also near this bound. Shape of the density-dependent pupping function, *z*, was uncertain. The survival rate parameter *S2* was also near its upper bound of 1 in both the MPD and the posterior. These parameters being on their bounds caused poor McMC traces, but the traces and diagnostic plots for most other parameters were acceptable.

Fits to the pup birth estimates (Fig. 2) were flat and showed no overall trend in the residuals. The fit to bycatch-at-age (Fig. 3) showed considerable variation at ages 2-3, reflecting uncertainty in the vulnerability estimates. The fit to breeding female age frequency (Fig. 4) was generally good but showed problems at ages 8-10, reflected in the residuals. Fits to

Table 6. MPD estimates and summaries of posterior distributions from 5,000 Markov chain–Monte Carlo simulations[a].

Parameter	MPD	5%	Median	Mean	95%
$\tilde{\sigma}$	0.103	0.096	0.112	0.113	0.134
K	7,393	6,781	7,376	7,409	8,156
$N1$	2,137	1,337	1,959	2,009	2,860
$R0$	0.500	0.485	0.495	0.495	0.500
Z	3.085	1.850	3.065	3.191	4.995
$S0$	0.866	0.852	0.867	0.867	0.883
$S1$	0.084	0.042	0.080	0.080	0.117
$S2$	1.000	0.955	0.983	0.982	0.999
$S3$	0.018	0.013	0.016	0.016	0.019
m_{50}	6.018	4.817	5.645	5.616	6.311
$m_{95\text{-}50}$	1.821	0.950	2.069	2.135	3.566
v_{50}	2.86	1.91	2.60	2.61	3.42
$v_{95\text{-}50}$	0.18	0.12	1.21	1.42	3.50
σ_1	885	660	871	891	1194
σ_2	5,555	3,779	5,067	4,990	5,901
σ_3	622	442	644	678	1,017
σ_4	375	262	407	435	704
Q_1	0.177	0.170	0.178	0.178	0.186
Q_2	0.760	0.749	0.760	0.760	0.771
Q_3	0.042	0.038	0.042	0.042	0.047
Q_4	0.020	0.017	0.020	0.020	0.024
$P_{91}^{surv,re-sight}$	0.014	0.007	0.017	0.019	0.037
$P_{92}^{surv,re-sight}$	0.059	0.044	0.062	0.063	0.086
$P_{93}^{surv,re-sight}$	0.002	0.001	0.003	0.004	0.009
$P_{94}^{surv,re-sight}$	0.001	0.001	0.003	0.003	0.007
$P_{95}^{surv,re-sight}$	0.002	0.001	0.003	0.004	0.008
$P_{96}^{surv,re-sight}$	0.066	0.053	0.071	0.072	0.094
$P_{97}^{surv,re-sight}$	0.006	0.003	0.008	0.008	0.016

Table 6. (continued.)

Parameter	MPD	5%	Median	Mean	95%
$P_{98}^{surv,re-sight}$	0.027	0.019	0.031	0.032	0.049
$P_{99}^{surv,re-sight}$	0.440	0.399	0.485	0.489	0.590
$P_{00}^{surv,re-sight}$	0.569	0.519	0.630	0.635	0.769
$P_{01}^{surv,re-sight}$	0.541	0.493	0.601	0.607	0.742
$P_{02}^{surv,re-sight}$	0.663	0.599	0.734	0.739	0.895
$P_{03}^{surv,re-sight}$	0.393	0.340	0.434	0.439	0.555
λ (%)	3.3	2.2	3.2	3.3	4.5
N_{03}^{mat}/K (%)	96.2	91.5	95.6	95.3	97.7
$N_{0,03}/N_{03}^{mat}$ (%)	37.9	34.3	38.3	38.2	41.9

[a]All are estimated parameters except the last three lines, which are derived parameters.

the tagged female pup re-sightings were generally good (Fig. 5). Estimated re-sighting probabilities for the tagged female pups (Table 6) were low until 1999 and later, when they rose to 45-75%.

Summaries of marginal posterior distributions of the survival-, vulnerability-, and maturity-at-age are shown in Fig. 6. Variation in survival rate was largest for pups and the oldest animals and varied little for ages 1 to 10, suggesting that the data are highly informative about survival. Most females appear to mature between 4 and 7 years of age.

The marginal posterior distribution of mature numbers in 2003 (Table 6) suggests a current population at 96% of *K*. The marginal posterior distribution of λ had a median of 3.2% (Table 6) and was on the left-hand edge of the prior (Fig. 7). In an early fit with a uniform prior on λ, the posterior had most of its weight near zero and the posterior for *K* was very wide, with much weight near the upper bound of 200,000 animals. This was thought by the Technical Working Group to be biologically unrealistic.

The 2003 pupping rate (Table 6) was estimated between 34% and 38%. Correlations among parameters in their marginal posterior distributions showed some high correlations, especially among survival parameters, between survival and maturity parameters, and among the re-sighting probabilities. These suggest that parameterization was not optimal; we should perhaps not have assumed that survival and maturity were related.

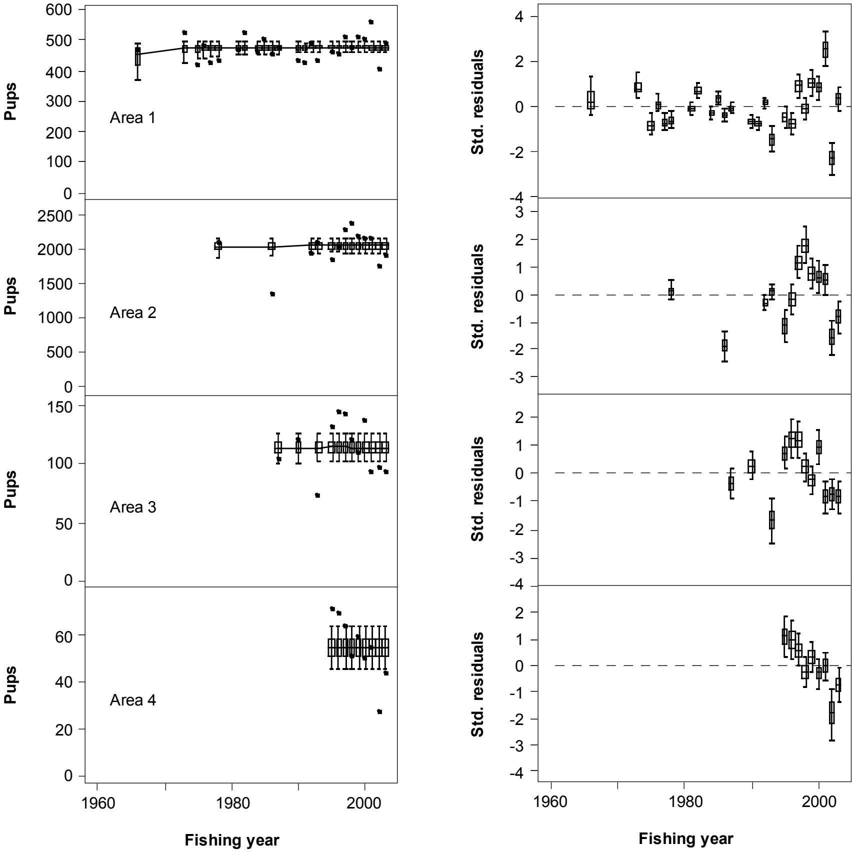


Figure 2. Posterior distributions of fits to the pup births data sets (left) and posterior distributions of residuals (right). From top to bottom the four areas are Sandy Bay, Dundas, Southeast Point, and Figure of Eight. In the left plots, solid dots indicate the observed value; box plots summarize the posterior distributions: the median is indicated with a horizontal line, the box encloses the 25th to 75th quantiles, and the outer horizontal lines show the 5th and 95th quantiles.

Projection results

The 20-year and *Nmat/K* criteria were satisfied for all the rules examined (Table 7). The 100-year criterion was satisfied until rule 9.23. Thus, the interim management goal of DoC was satisfied by nearly all rules examined.

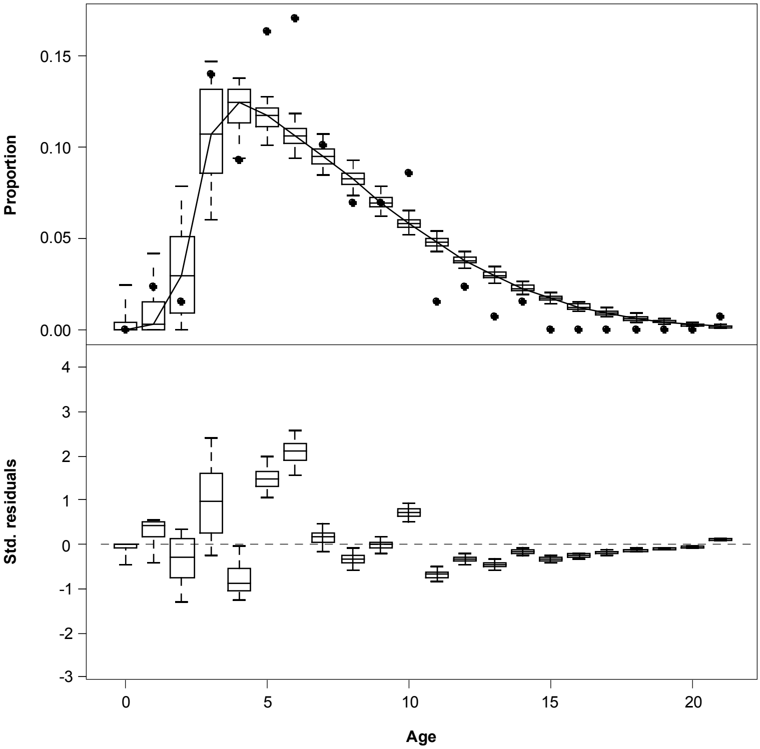


Figure 3. The posterior distributions of fits to the bycatch-at-age data set (upper) and their residuals (lower). In the upper plot, solid dots indicate the observed value; box plots are as for Fig. 2.

The *N100/K* indicator had a median of 98% with no fishing, and fell to 92% under rule 10. The lowest point, *nadir/K*, had a median of 85%, which fell to 79% under rule 10. The full distributions of *nadir/K* and *N100/K* are compared between rule 0 and rule 10 in Fig. 8. These represent the differences between complete restriction of the fishery at one end and nearly unrestricted fishing (assuming no increase in annual fishing effort) at the other; differences are small.

The median of *effort lost* under rule 1 was 904 (Table 7, Fig. 9), roughly one-third of attempted effort. This decreases to negligible values by rule 4. The *% closed* index (Fig. 9) was 52% under rule 1 and declined to less than 6% after rule 4.

Mean bycatch initially rose steeply with increasing multipliers (Table 7) but reached an asymptote of 99 by rule 8 (Fig. 10). Its value under rule 1 was 53. Maximum bycatch, with a value of 77 under rule 1, also

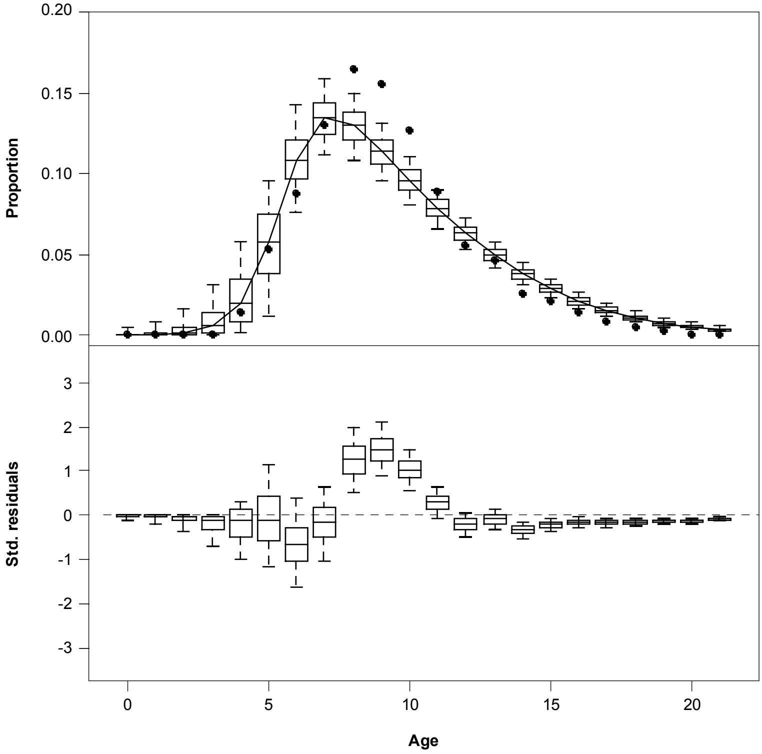


Figure 4. The posterior distributions of fits to the breeding-at-age data set (upper) and their residuals (lower).

rose steeply (Fig. 10) but was leveling out by rule 8 toward a maximum of 550.

Discussion

Population parameters

Compared with the two previous studies of this problem (Maunder et al. 2000, Breen et al. 2003), this study used far more population data. These data enabled estimation of maturity- and vulnerability-at-age schedules, current pupping rate, pup mortality, and a more elaborate survival-at-age function. Breen et al. (2003), fitting only to pup birth estimates, obtained highly uncertain population parameters only after confining the parameter space with a strong prior on adult survival. The data used in this study are much more informative, especially for survival rates, producing narrow posterior distributions for these parameters. Estimated survival

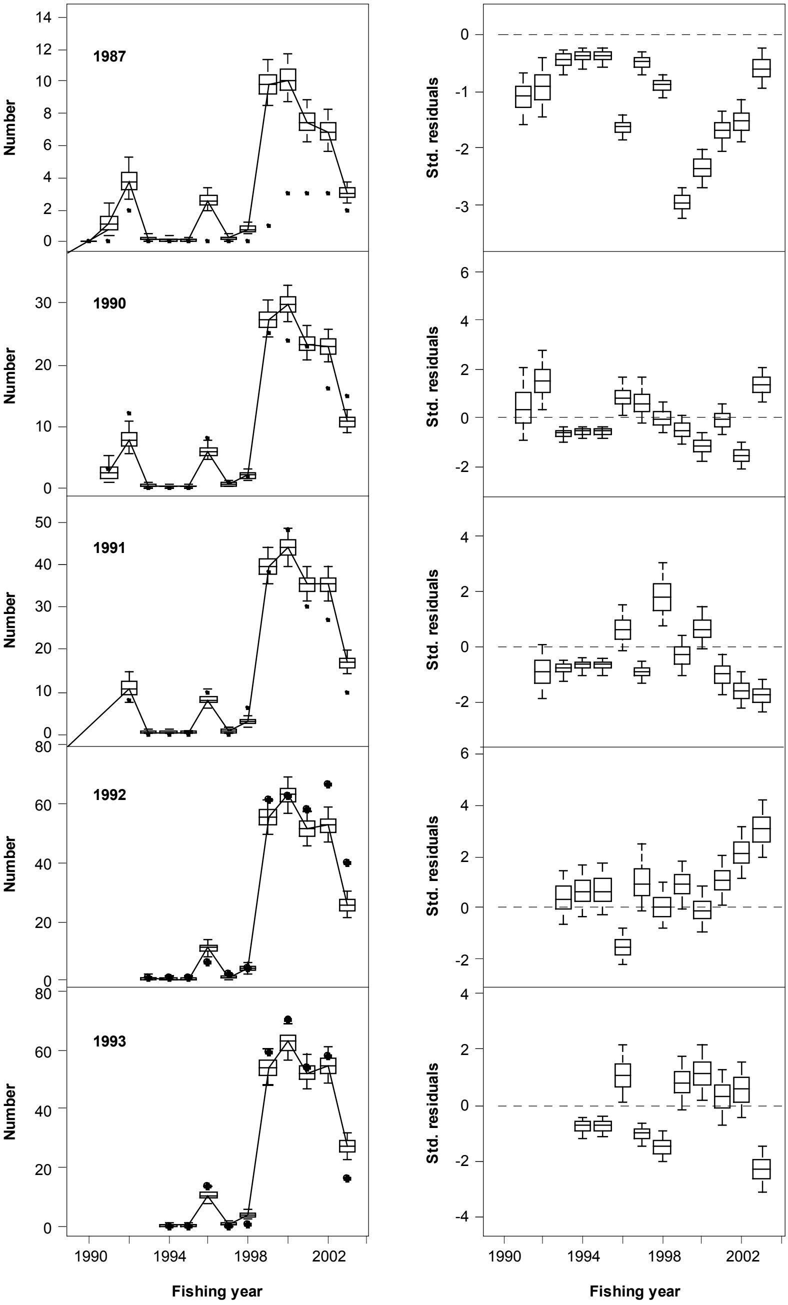


Figure 5. The posterior distributions of fits to the tagged female re-sightings data set (left) and their residuals (right). The year shown in each left plot indicates the year of tagging.

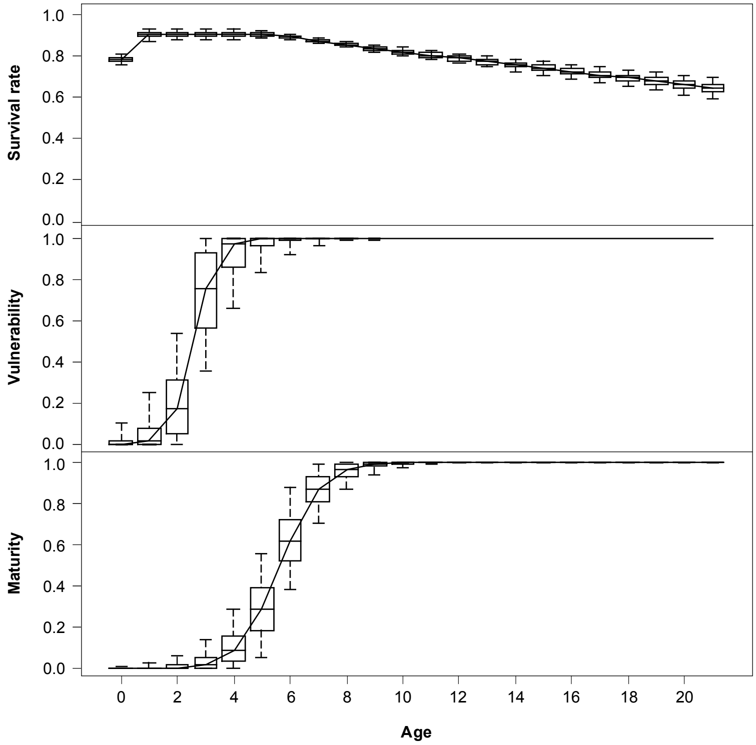


Figure 6. Summaries of the posterior distributions of estimated survival-at-age (top), vulnerability-at-age (center), and maturity-at-age (bottom).

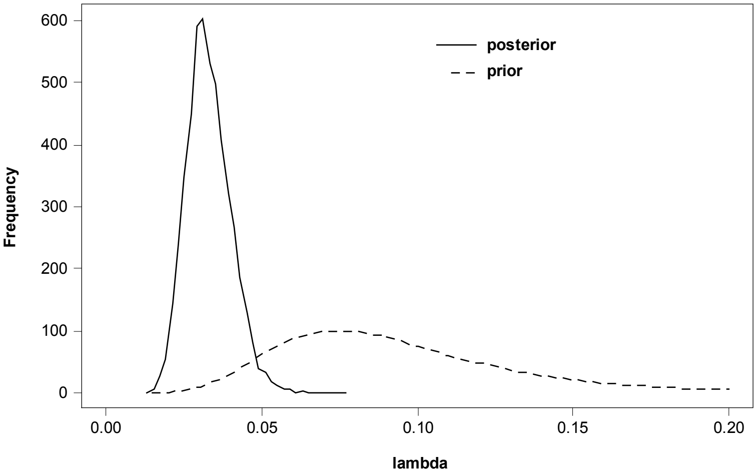


Figure 7. The posterior distribution for λ (solid line) compared with its prior distribution.

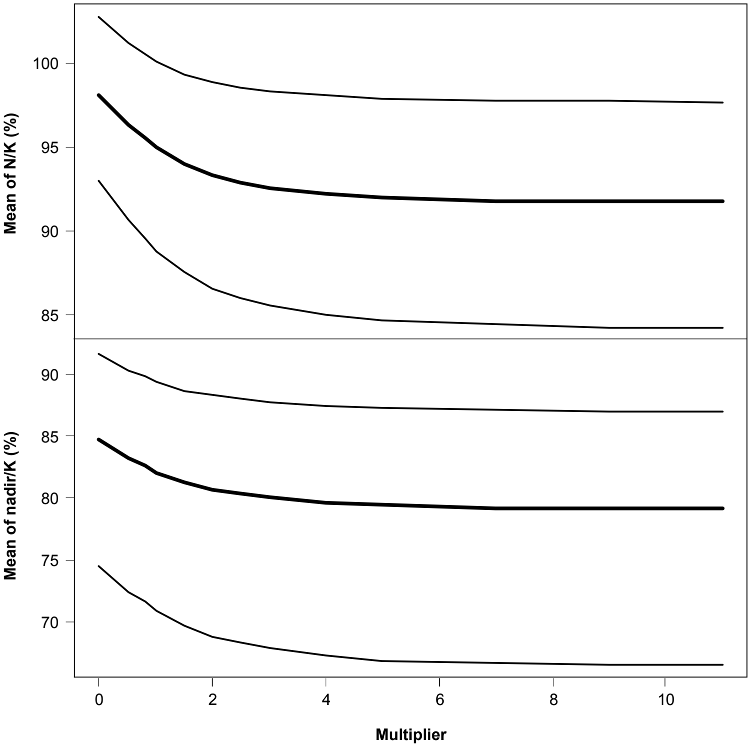


Figure 8. Summaries of the posterior distributions of mature numbers at the end of 100-year projections (upper) and the nadir (lower). The x-axis shows the multiplier of the 1992 rule used to produce the bycatch control rule. Thick lines show the medians of posterior distributions; thinner lines show 5th and 95th quantiles.

of ages 1-6 was near 90%, the mean used in the strong prior of Breen et al. (2003).

The pup births data set contained the only information from which the model could scale the population size and hence estimate *K* and *N1*. Pups produced by tagged females were the next most important observations; in a sensitivity trial without these data, estimated current pupping rate was lower, mature numbers were higher, and (because of increased scope for density-dependence) λ was higher.

We fit the model to all data sets at once, an "integrated" approach (Maunder 2001). A common alternative is to estimate population process parameters separately from the relevant data for use in a model, in a "segregated" approach. With an integrated model, the same assumptions are

Table 7. Summary of indicators from projections for each of the 1992 rule variants modeled[a].

Multiplier	0	0.5	1	2	3	4	5	8	9	9.23	10
20-yr criterion	100,000	100,000	100,000	99,989	99,810	99,409	99,006	98,264	98,131	98,115	98,053
100-yr criterion	500,000	500,000	499,052	487,109	473,902	464,642	458,702	451,181	450,181	450,003	449,508
Nmat/K (%)	98.2	96.4	95.0	93.4	92.6	92.2	92.0	91.8	91.8	91.8	91.7
Effort lost	2,910	1,614	904	328	138	64	31	0	0	0	0
% Closed	100.0	77.0	51.9	23.1	11.1	5.7	3.2	0.7	0.5	0.4	0.3
Max catch	0	39	77	151	222	290	355	516	540	542	545
Mean catch	0	31	53	76	87	92	95	98	98	98	99
Nadir	6,248	6,127	6,039	5,935	5,885	5,859	5,843	5,821	5,820	5,819	5,818
Nadir/K (%)	84.8	83.2	82.0	80.7	80.0	79.6	79.4	79.2	79.1	79.1	79.1
N100/K (%)	98.7	96.9	95.6	94.1	93.4	93.0	92.8	92.6	92.6	92.6	92.6

[a] For the 20-year and 100-year criteria the values shown are the sum of years in which the criterion was true; for *Nmat/K* the value is the mean of the posterior distribution; for all others the value is the median of the posterior distribution.

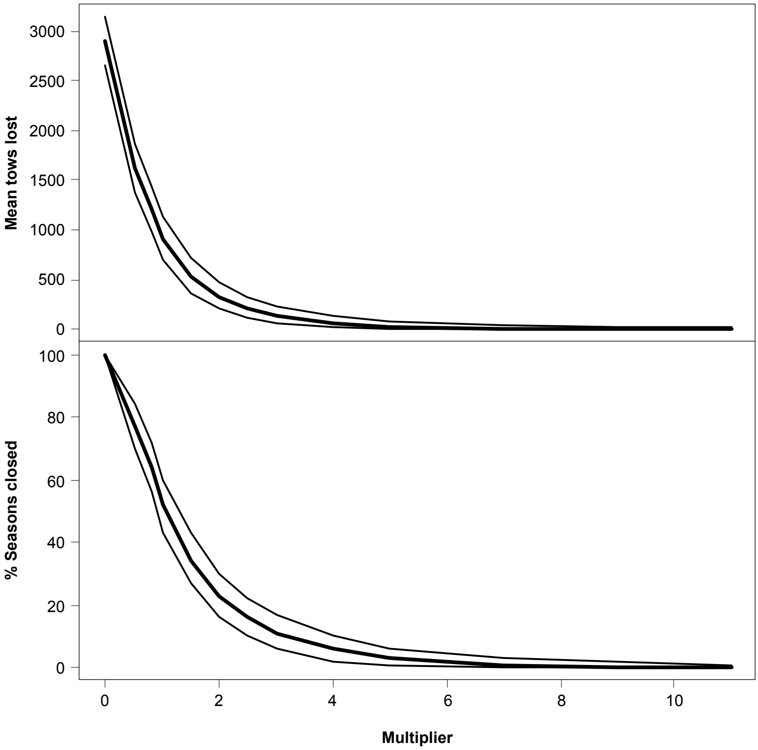


Figure 9. Summaries of the posterior distributions for the indicators *effort lost* (upper) and *% closed* from 100-year projections.

used in the estimation and projection models, parameters about which several data sets contain information (survival in this case) are estimated consistently with all data sets, and estimated parameter combinations are consistent with the data. In the segregated approach, assumptions may be contradictory, and some parameter combinations may have low likelihood even when estimated appropriately from the relevant data sets.

The tight estimates of survival-at-age (Fig. 6) suggest a high information content in the four relevant data sets, in turn suggesting that more parameters could be devoted to this function. The estimated parameter z and the derived parameter λ remained poorly determined despite the new data; the population studied has been stable over the period with data, so density-dependence has not been observed. Such parameters could be estimated only if the population were observed over a range of sizes.

For λ, the data evidently provided some restriction on the upper limit, as the posterior distribution did not extend far beyond 0.05. But

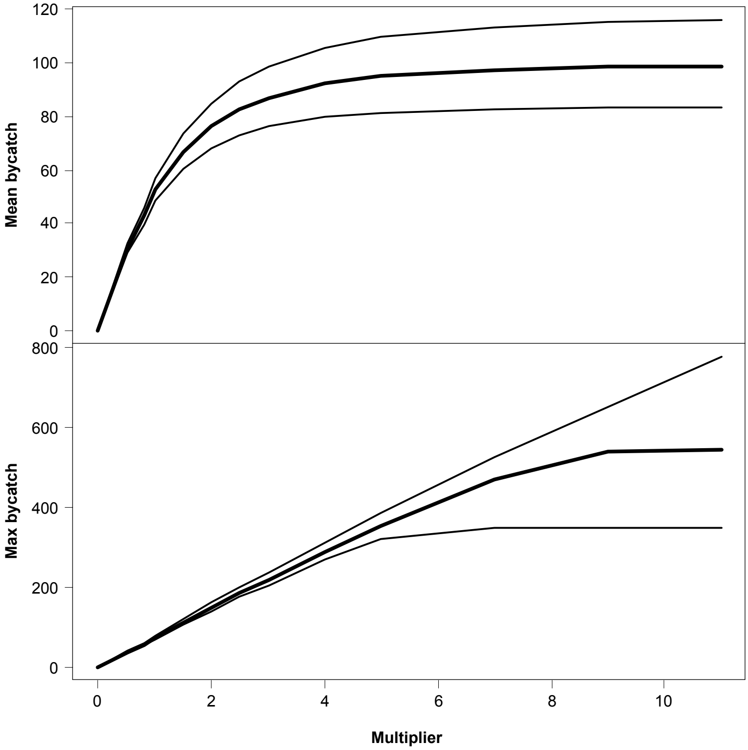


Figure 10. Summaries of the posterior distributions for the mean (upper) and maximum annual bycatch indicators from 100-year projections.

at the lower end, the data were consistent with a λ near zero. Thus two different results are consistent with the data: a population near *K* with a current rate of increase much less than λ, or a population much smaller than *K* with a small current rate of increase resulting from a very low λ. To the model, either reconstruction fits the data. To the Technical Working Group, the second situation is not credible: the population experienced some uncontrolled exploitation in the early nineteenth century, after which sea lions are thought to have been depleted compared with the present; then the population recovered, at least at the Auckland Islands (Childerhouse and Gales 1998). The same conclusion is reached by McConkey et al. (2002a). There is little evidence to suggest that the current Auckland Islands population is not near *K*.

A bycatch control rule giving 9 times the bycatch limit of the 1992 rule satisfied the management goal. Thus the 1992 rule was much more restrictive than was necessary, and a rule with a multiplier from 2 to 4 might give a more acceptable balance between conservation and fishery exploitation goals. However, both the total fishing effort and the catchability of sea lions must be monitored to detect any increases from the mean values used here. Although the high-multiplier rules give high bycatch limits, the median sea lion bycatch has an asymptote near 100; this compares with a mean of 69 sea lions caught annually since estimates were made (Table 1). However, the highest number of sea lions caught in 100-year runs has a median of 545 and a wide range. Such high bycatches would arise from the random coincidence of high fishing effort and high catchability. They would be politically unacceptable in New Zealand despite having a small effect on the population or population goal.

Conclusions are sensitive to the prior used for λ. Without the prior, unrealistically low values for λ were obtained, sometimes associated with high estimates of K. If projections were made from those, the effects of bycatch would be greater and the sustainable exploitation rate would be lower. This problem is related to the lack of data on density-dependence; the population appears to have been stable over the period when data were collected, leading the model to conclude that it is near K.

The model treats the Auckland Islands population as a homogeneous entity, divided in constant proportion into the four rookeries and the bycatch. Declines in pup births at Southeast Point suggest that the population is not divided among rookeries in constant proportion. If the bycatch is taken disproportionately from the rookeries, the fishery bycatch could have a greater effect on a single rookery than is suggested by our results.

Acknowledgments

This project was funded by the New Zealand Ministry of Fisheries. Thanks to Susan Waugh, Ian Wilkinson, and Simon Childerhouse for providing sea lion population data, and to Paul Starr for providing fishery data. The help from Aquatic Environment Working Group members was greatly appreciated: thanks to Kate Bartram, Richard Cade, Martin Cawthorn, Jim Cornelius, David Gilbert, Caroline Hart, Dave Sampson, Paul Starr, Kevin Stokes, Kevin Sullivan, Susan Waugh, Barry Weeber, and Ian Wilkinson. David Gilbert, Doug DeMaster, and two anonymous reviewers provided helpful comments on the draft manuscript.

References

Breen, P.A., and S.W. Kim. 2005. Exploring alternative management procedures for controlling bycatch of New Zealand or Hooker’s sea lions in the SQU 6T arrow or Wellington flying squid fishery. Final Research Report to the New Zealand Ministry of Fisheries, Wellington. May 2005.

Breen, P.A., R. Hilborn, M.N. Maunder, and S.W. Kim. 2003. Effects of alternative control rules on the conflict between a fishery and a threatened sea lion (*Phocarctos hookeri*). Can. J. Fish. Aquat. Sci. 60:527-541.

Butterworth, D.S., and A.E. Punt. 1999. Experiences in the evaluation and implementation of management procedures. ICES J. Mar. Sci. 56:985-998.

Childerhouse, S., and N. Gales. 1998. Historical and modern distribution and abundance of the New Zealand sea lion *Phocarctos hookeri.* N.Z. J. Zool. 25:1-16.

Childerhouse, S., G. Dickie, and G. Hessel. 2004. Ageing live New Zealand sea lions (*Phocarctos hookeri*) using the first post-canine tooth. Wildl. Res. 31:177-181.

Childerhouse, S., N. Gibbs, G. McAlister, S. McConkey, H. McConnell, N. McNally, and D. Sutherland. 2005. Distribution, abundance and growth of New Zealand sea lion *Phocarctos hookeri* pups on Campbell Island. N.Z. J. Mar. Freshw. Res. 39:889-898.

Gales, N.J., and D.J. Fletcher. 1999. Abundance, distribution and status of the New Zealand sea lion *Phocarctos hookeri*. Wildl. Res. 26:35-52.

Haist, V., P.A. Breen, S.W. Kim, and P.J. Starr. 2005. Stock assessment of red rock lobsters (*Jasus edwardsii*) in CRA 3 in 2004. N.Z. Fish. Assmt. Rep. 2005/38. 126 pp.

IUCN. 1996. IUCN red list of threatened animals. IUCN (International Union for the Conservation of Nature and Natural Resources), Gland, Switzerland.

McConkey, S.D., S. Heinrich, C. Lalas, H. McConnell, and N. McNally. 2002a. Pattern of immigration of New Zealand sea lions *Phocarctos hookeri* to Otago, New Zealand: Implications for management. Aust. Mamm. 24:107-116.

McConkey, S.D., H. McConnell, C. Lalas, S. Heinrich, A. Ludmerer, N. McNally, E. Parker, C. Borofsky, K. Shimanski, and G. McIntosh. 2002b. A northward spread in the breeding distribution of the New Zealand sea lion *Phocarctos hookeri*. Aust. Mamm. 24:97-106.

Maunder, M.N. 2001. A general framework for integrating the standardization of catch per unit of effort into stock assessment models. Can J. Fish. Aquat. Sci. 58:795-803.

Maunder, M.N., P.J. Starr, and R. Hilborn. 2000. A Bayesian analysis to estimate loss in squid catch due to implementation of a sea lion population management plan. Mar. Mamm. Sci. 16:413-426.

Reijnders, P.S., S. Brasseur, J. van der Toorn, P. van der Wolf, I. Boyd, J. Harwood, D. Lavigne, and L. Lowry. 1993. Seals, fur seals, sea lions, and walrus, status survey and conservation plan. IUCN/SSC Seal Specialist Group. IUCN, Gland, Switzerland.

Wade, P. 1998. Calculating limits to the allowable human caused mortality of cetaceans and pinnipeds. Mar. Mamm. Sci. 14:1-37.

Wilkinson, I., J. Burgess, and M. Cawthorn. 2003. New Zealand sea lions and squid: Managing fisheries impacts on a threatened marine mammal. In: N. Gales, M. Hindell, and R. Kirkwood (eds.), Marine mammals: Fisheries, tourism and management issues. CSIRO Publishing, Collingwood, Victoria, pp. 192-207.

Status and Conservation of Otariids in Ecuador and the Galápagos Islands

Juan Jose Alava
School of Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia, Canada; and Fundación Ecuatoriana para el Estudio de Mamíferos Marinos, Guayaquil, Ecuador

Sandie Salazar
Fundación Ecuatoriana para el Estudio de Mamíferos Marinos, Guayaquil, Ecuador; Centro Interdisciplinario de Ciencias Marinas, La Paz, México; and Charles Darwin Research Station, Puerto Ayora, Galápagos Islands, Ecuador

Abstract

Three species of otariids are found in the coastal zone and marine area of Ecuador and the Galápagos Islands. Two species, Galápagos sea lion (*Zalophus wollebaeki*) and Galápagos fur seal (*Arctocephalus galapagoensis*), are endemic to the Galápagos. The South American sea lion (*Otaria flavescens*) has been recorded several times on the Ecuadorian coast, and even small semi-permanent or resident male groups (~10-30 animals) have frequently been observed in two southern locations (Santa Clara Island and Punta Brava-Salinas). The most recent estimates of Galápagos sea lion and fur seal populations, conducted in November 2001 by the Charles Darwin Foundation around the Galápagos Islands, were 14,000-16,000 and 6,000-8,000 animals, respectively. In the last two decades, anthropogenic impacts and natural phenomena have affected both Galápagos pinniped populations. Anthropogenic effects include oil spills (e.g., *Jessica*), fishery interactions, and illegal hunting (sea lions used for trade in reproductive organs). Natural events such as the 1982-1983 and 1997-1998 El Niños caused large reductions in populations, and diseases are being monitored to try to prevent negative impacts on the islands. Sightings of *O. flavescens* on the coast of Ecuador have been linked to El Niños since the displacement of this species from Peruvian colonies is

caused by oceanographic changes (e.g., reduction of prey). Research and conservation of marine mammals, including rescue of sea lions, have been conducted by the Charles Darwin Foundation and the Ecuadorian Foundation for the Study of Marine Mammals in the last two decades.

Introduction

Otariid pinnipeds are a significant group of marine mammals among the neotropical mammals in Ecuador. At least three species of otariids inhabit marine areas of both Ecuador and the Galápagos Islands, two of which are endemic to the Galápagos Islands: the Galápagos fur seal (*Arctocephalus galapagoensis*) and the Galápagos sea lion (*Zalophus wollebaeki*). The third species is the South American sea lion (*Otaria flavescens*), which has been identified several times along the Ecuadorian coast and recently recorded as a temporal or semi-permanent resident. Natural history and ecological studies of the two Galápagos pinnipeds was conducted and documented over 20 years ago by Trillmich (1979, 1984); however, there are several gaps in the population dynamics, current trends, and health status that still need to be elucidated. In this manuscript, we review the conservation, population status, and records of three otariid species in Ecuador and the Galápagos Islands. In particular, we detail the impact of natural events and anthropogenic activities on Galápagos sea lions.

Otariids in the Galápagos Islands

Population

The two endemic species of otariids (*Z. wollebaeki* and *A. galapagoensis*) residing in the Galápagos Islands have different habitat preferences, as well as reproductive and feeding strategies. Due to the unique characteristics of their tropical habitat, both pinniped species in Galápagos have developed important features of endemism, including body size reduction, physiological adaptations for thermoregulation, and specific behavioral characteristics (Trillmich 1984, Limberger et al. 1986). These sympatric species have been successful in surviving due to the upwelling of cold, nutrient-rich water, which supports rich food resources. While the Galápagos sea lion has diurnal feeding habits, the Galápagos fur seal has nocturnal feeding habits. Locations of major reproductive colonies for both species are shown in Fig. 1. Galápagos fur seals are found in the northeastern islands of Isabela, Fernandina, Santiago, Pinzón, Pinta, Marchena, and Wolf, in northeast Genovesa, and a small population exists in the central region (Trillmich 1984). Galápagos sea lions live on most of the islands, inhabiting both north and south parts of the Galápagos, but the largest colonies are located in the southern and central regions of the archipelago.

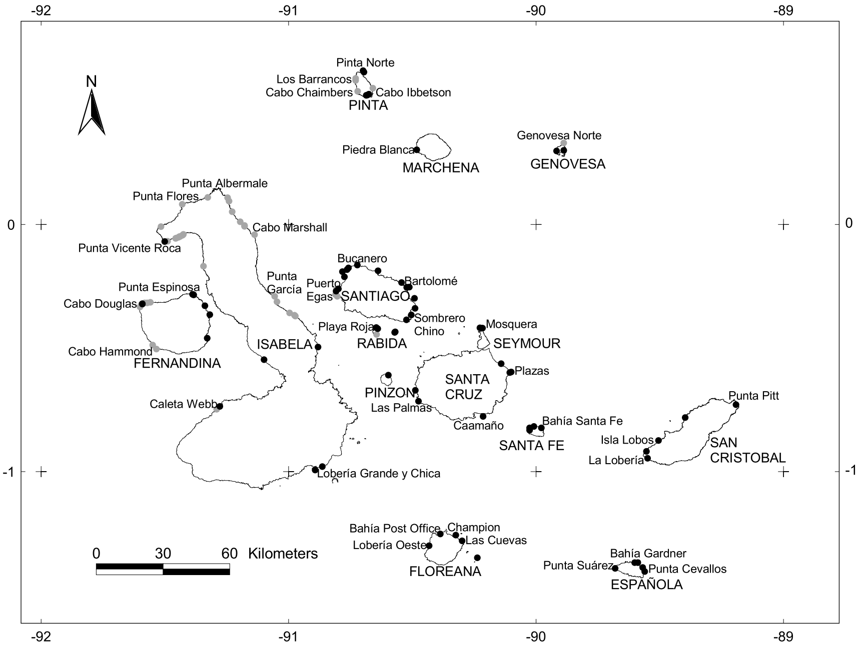


Figure 1. Map of the Galápagos Islands showing the distribution of major rookeries of *Zalophus wollebaeki* (Galápagos sea lion, black dots) and *Arctocephalus galapagoensis* (Galápagos fur seal, gray dots).

Both species are categorized as vulnerable species in the International Union for the Conservation of Nature (IUCN) Red Book of Mammals of Ecuador (Utreras et al. 2001a,b), as well as vulnerable at the global level in the IUCN, Red List of Threatened Species (Seal Specialist Group 1996a,b). Additionally, the Galápagos fur seal is listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Recent studies have demonstrated the important role of the Galápagos sea lion in the transportation of marine nutrients to the terrestrial ecosystem (Fariña et al. 2003) and as a predator in the marine environment (Okey et al. 2004). An extensive review of these studies and other conservation aspects of the two species was recently written by Salazar (2002a).

The first census of Galápagos otariids was conducted in 1977-1978, when populations of Galápagos sea lions and fur seals were found to total 40,000 and 30,000-40,000 individuals, respectively (Trillmich 1979; F. Trillmich and K. Trillmich, Dept. of Animal Behavior, Univ. of Bielefeld, unpubl. data). About two decades later, the Charles Darwin Research Station undertook a long-term monitoring and research program on Galápagos otariids. Population monitoring has been conducted since 1997on twelve Galápagos sea lion colonies located on different islands (Isla Los Lobos, El Malecon, and La Lobería on San Cristóbal Island; Santa Fe Bay on Santa Fe Island; Champion on Floreana Island; Caamaño and Plaza Sur on Santa Cruz Island; Mosquera and Seymour Norte (both located north of Baltra); and Bahía Gardner, Punta Cevallos, and Punta Suárez on Española Island), and since 2001 on three Galápagos fur seal colonies, two on Fernandina Island (Cabo Hammond and 4 km west of Punta Espinosa) and one on Santiago Island at Puerto Egas (Fig. 1). An overall pinniped census, carried out during November 2001 around the islands, covered about 97% of the coastal perimeter, missing only the smallest northern islands, Darwin and Wolf, where no more than 100 animals of both species reside. Two counting methods were used in the 2001 census: direct and distance counting.

1. Direct counting method
   Direct counting was used when landing ashore was possible and had no major safety risk. It is the most frequently used method to count pinnipeds in the Galápagos Islands. Counting started at a fixed reference point on the beach, preferably at one end of the colony. A way-point (WP)[1] was taken at the starting point and tracking was engaged using a hand-held global positioning system (GPS); geographical reference points were taken by the GPS every 10 seconds as the observers surveyed the colony. One observer searched along the coastline of the colony, including the intertidal and subtidal zones, and animals in the water were counted at least twice. In the case of fur seals, the search included grottos and accessible lava caves, and for Galápagos sea lions the nearby shrub was searched. Fixed reference points were taken at intervals to avoid double counting. One observer also looked for any signs of diseased or entangled individuals and a WP was recorded for each sighting, along with other information (e.g., age/sex category, type of affliction, and/or waste material involved). Another observer performed a complementary ordered search in the accessible coastal zone (shrub and lagoons). At the same time they collected scat samples (during the breeding season) and helped check for signs of disease or entanglement with fishing gear. If any animals entangled in fishing gear were found during monitoring, both observers, protecting themselves with leather gloves, helped the animals if the injury, weather, and accessibility conditions allowed the rescue operation. To rescue pinnipeds, observers carried a large hook net, towel, and knife.

---

[1] Way point (WP) is a geographical reference point made using a Global Positioning System (GPS), where the GPS records latitude, longitude, WP number, hour (GMT) and date.

2. Distance counting method
   In places where it was not possible to access the beach, counting was done from a boat at a distance of 2-50 meters from the coastline. In shallow areas and moderate seas, a dinghy was used at a distance of 2-8 meters from the coastline. Three people participated in distance counts: observer 1 with binoculars and counter; observer 2 with GPS and field notebook; and a dinghy driver or boat captain. A starting point was fixed on the landscape, and the entire coastline was inspected with binoculars by the first observer while the second observer recorded the number of animals in the water. Each sighting of groups or animals was registered using a WP, and the WP number, species, age/sex category, and numbers of animals were recorded in a notebook. Weather conditions such as cloudiness and sea level data were also recorded. In some cases, when it was impossible to identify a species, an unidentified species category was used. If an entangled animal was registered during the monitoring, observers proceeded according to the procedures outlined above in the direct method.

Counts made from a distance were corrected to be comparable to direct counts according to the methods of Le Boeuf et al. (1983) and Nichols and Corroy (1996). The probability of an individual animal being counted (β) in a direct count was 1. For distance counts, β values varied depending on the size and species of pinniped being counted. For distance counts of Galápagos sea lions, $\beta = 0.75$ for adult females, adult males, and those of indeterminate sex and age, and $\beta = 0.40$ for pups. For distance counts of Galápagos fur seals, $\beta = 0.50$ for adult females, adult males and those of indeterminate sex, and $\beta = 0.25$ for pups (Trillmich and Mohren 1981; Nichols and Corroy 1996; F. Trillmich and K. Trillmich, Dept. of Animal Behavior, Univ. of Bielefeld, unpubl.). Distance counts of sea lions and fur seals were divided by the appropriate β values to obtain estimates of the total number present at each site.

The mean number of individuals in colonies of both otariid species counted during the 2001 pinniped censuses are presented in Tables 1 and 2. For Galápagos sea lions 99% of the population is congregated in the islands listed in Table 1, whereas 94% of the Galápagos fur seal population was located on the islands listed in Table 2. Floreana, Santa Cruz, San Cristóbal, and Isabela islands encompassed most of the Galápagos sea lion population, with 16%, 14%, 13%, and 11%, respectively. The islands Rábida, Genovesa, and Marchena each accounted for 1% of the population. Likewise, the highest proportions of Galápagos fur seals were concentrated on Isabela and Fernandina islands, with 42% and 39%. This is complemented by looking at the average number of animals counted at the twelve regularly monitored haul-outs and rookeries of the Galápagos

Table 1. Number of breeding colonies and individuals in each colony of *Z. wollebaeki* on surveyed islands during the 2001 census of the Galápagos Islands (from Salazar 2002a).

Island	Haul-out rookeries	Individuals	% Population
Floreana	Bahía del Correo	382	
	Champion	303	
	La Lobería Oeste	35	
	Las Cuevas	43	16
Santa Cruz	Caamaño	321	
	Cerro Gallina	20	
	East Coast	24	
	Las Palmas	24	
	Plaza Norte	46	
	Plaza Sur	370	14
San Cristóbal	Cerro Brujo	90	
	Isla Lobo	282	
	La Lobería	164	
	Malecón	136	
	Punta Pitt	245	13
Isabela	East Coast	58	
	Punta Moreno	16	
	Islote Cowley	53	
	La Lobería Grande	92	
	La Lobería Pequeña	25	
	Punta Vicente Roca	22	11
Santiago	West Coast	67	
	Northeast Coast	28	
	North Coast	85	
	West Coast	62	
	Puerto Egas	73	
	Roca Cousil	16	
	Rocas Bainbridge	19	
	Rocas Beagle	94	
	Sombrero Chino	70	8

Table 1. (continued.)

Island	Haul-out rookeries	Individuals	% Population
Española	Gardner Bay	219	
	Northeast Coast	26	
	Islote Gardner	46	
	Punta Cevallos	60	
	Punta Suarez	169	8
Mosquera	Mosquera	559	7
Santa Fe	Dinamarca Bay	26	
	North Bay	30	
	Santa Fe Bay	279	
	Punta Dinamarca	23	6
Fernandina	Douglas Cape	55	
	East Coast	70	
	North Coast	4	
	Punta Espinosa	57	
	Punta Gadilan	16	
	Punta Mangle	33	5
Pinta	North Coast	63	
	South Coast	190	4
Seymour Norte	West Coast	131	2
Pinzon	Fondeadero	33	2
Rabida	Playa Roja	83	
	West Coast	15	1
Genovesa	Darwin Bay	9	
	Punta Oeste	54	1
Marchena	West Coast	39	1
Total	**68 colonies**	**5,554**	**99%**

Table 2. Number of breeding colonies and individuals in each colony for *Arctocephalus galapagoensis* on surveyed islands during the 2001 census of the Galápagos Islands (from Salazar 2002a).

Island	Haul-out rookeries	Individuals	% Population
Isabela	East Coast	233	
	North Coast	177	
	West Coast	68	
	Punta Vicente Roca	274	42
Fernandina	Douglas Cape	230	
	Hammond Cape	326	
	North Coast	107	
	West Coast	49	
	South Coast	26	39
Pinta	Cabo Chaimers	40	
	Cabo Ibeston	29	
	West Coast	36	7
Santiago	West Coast	7	
	South Coast	6	
	Puerto Egas	65	4
Rabida	South Coast	37	1
Genovesa	North Coast	7	1
Total	**43 colonies**	**1,717**	**94%**

sea lion (Fig. 2). The Mosquera colony, the only one in Mosquera Island, had the largest number of individuals (N = 559; Table 1), with an average ±SD of 528±25.81 individuals recorded during the regular 2001 monitoring (Fig. 2); followed by Bahía del Correo, Plaza Sur, and Caamaño (Table 1; Fig. 2).

The number of Galápagos fur seals counted during both the 1977-1978 and 2001 censuses are presented in Table 3. In 2001, the average colony size (number of individuals counted ±1 SD; 79.2±107.5) was lower than in both 1977 (345.5±357.4) and 1978 (395.6±469.9). High variability is also reflected in the large differences between sites in number of individuals counted (Table 3).

The results of the 2001 census yielded a total estimated population of 14,000-16,000 Galápagos sea lions (based on an actual count of 7,942 individuals), and 6,000-8,000 Galápagos fur seals (based on a count of 2,733 individuals; Salazar 2002c,d). This suggests that Galápagos pinniped populations declined significantly since the 1977-1978 surveys,

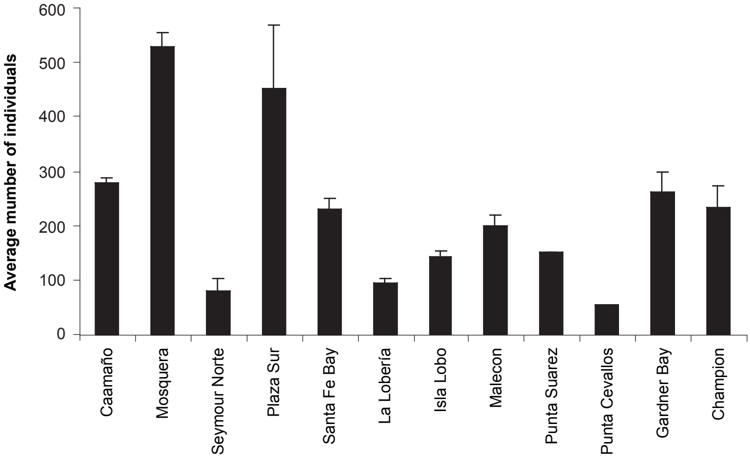


Figure 2. Average (±1 standard error) number of Galápagos sea lions counted in 12 colonies monitored by the Charles Darwin Research Station during November 2001. At Punta Suárez and Punta Cevallos colonies, the standard errors were ±0.35 and ±0.00, respectively (not shown in graph). Data from Salazar 2002a.

potentially as large as 60% for Galápagos sea lions and 80-85% for Galápagos fur seals. These declines may, in part, be due to two catastrophic El Niño events that occurred at the early 1980s and late 1990s; this is discussed in more detail later in this paper.

The survey methodologies used in the two censuses are significantly different, and there are potential biases and uncertainties in the population estimates. Therefore, percentage changes in the population and statistical comparisons of population sizes over time should be interpreted cautiously (Salazar 2002a, Bustamante et al. 2002). Unpublished population data from an expedition conducted by Le Boeuf et al. (1988) in 1988 is also being analyzed and compared with the 1977-1978 and 2001 data to further describe these declines (F. Trillmich, Dept. of Animal Behavior, Univ. of Bielefeld, pers. comm.). However, data from the two completed surveys indicate that both Galápagos pinniped populations may have declined by more than 50% in 23 years, suggesting the need for field research to confirm the current population status and trends, accompanied by precautionary conservation strategies (Salazar 2002a, Bustamante et al. 2002).

Table 3. Number of individuals of *A. galapagoensis* counted at sites in the Galápagos Islands in 1977, 1978 (F. Trillmich and K. Trillmich, Dept. of Animal Behavior, Univ. of Bielefeld, unpubl. data), and 2001 monitoring (Salazar 2002a).

Island	Site	1977	1978	2001
Baltra	Perimeter	N/A	9	48
Fernandina	Cabo Hammond	1,024	N/A	326
Floreana	Perimeter	33	N/A	1.00
Genovesa	Perimeter	N/A	298	30
Isabela	Marshal Cape	316	N/A	128
Isabela	Wolf Volcano (North)	N/A	772	124
Isabela	Wolf Volcano (East)	N/A	1,467	216
Isabela	Wolf Volcano (West)	N/A	1,116	419
Isabela	Darwin Volcano (East)	N/A	1,159	13
Isabela	Darwin Volcano (West)	N/A	167	30
Isabela	Alcedo Volcano (East)	N/A	437	115
Isabela	Alcedo Volcano (West)	N/A	0	3
Isabela	Sierra Negra Volcano (East and North)	N/A	0	0
Isabela	Cerro Azul Volcano (West)	N/A	49	100
Pinta	Perimeter	N/A	1,034	183
Marchena	Perimeter	N/A	583	15
Pinzon	Perimeter	N/A	30	12
Rabida	Perimeter	135	N/A	38
Santa Cruz	Northeast Coast	165	260	66
Santiago	James Bay-Puerto Nuevo	400	N/A	81
Santiago	Without James Bay-Puerto Nuevo	N/A	418	12
Seymour Norte	Perimeter	N/A	92	21
Santa Fe	Perimeter	N/A	0	0
San Cristobal	Perimeter	N/A	20	0
Española	Perimeter	N/A	0	0
	Average	345.5	395.6	79.2
	SD	357.4	469.0	107.5

N/A = information not recorded or not available.

Conservation and management plan

One of the primary research activities of the Charles Darwin Research Station and the Galápagos National Park Service is population monitoring of endemic marine mammals. Thus, these two institutions have implemented an ecological monitoring and conservation program for Galápagos sea lions and fur seals. The overall goal is to determine the current state and abundance of the sea lions and fur seals in the Galápagos in order to set the baseline for monitoring and evaluating the impact of fisheries bycatch mortality, natural oceanographic and atmospheric changes (e.g., El Niño), and interactions with human activities. The objectives include (a) to determine the current size, structure, and distribution of the sea lion and fur seal populations in the Galápagos; (b) to conduct health status surveys of the two pinniped populations in the Galápagos; (c) to describe inter- and intraspecific genetic relationships; (d) to develop and train personnel in simple pinniped capture and rescue techniques (Salazar 2002b, 2003b); (e) to conduct ethological studies of pinniped social organization (F. Trillmich and J. Wolf, Dept. of Animal Behavior, Univ. of Bielefeld, pers. comm.); and (f) to provide information on the location of entangled or hooked sea lions and fur seals, including information on interactions with alien species. Another monitoring program activity currently under way is the establishment of a project of Sighting Logs through a bi-institutional effort (Charles Darwin Foundation and the Galápagos National Park Service) to improve the compilation of information from observers and users of the Galápagos Marine Reserve. The recorded sightings include marine mammal sightings (pinnipeds, whales, dolphins, and porpoises), entangled animals, fishery activities, and general observations of scuba-dive guides (e.g., sharks, rays, sea turtles).

Through the long-term research and monitoring program, researchers investigate the population, health status, and effects of human activities on the Galápagos sea lion and fur seal, with the goal of conserving biological diversity in the Galápagos through the protection and management of these vulnerable species and their habitats. The results will inform environmental management planners of the Galápagos National Park Service and the management authorities of the Galápagos National Park and Marine Reserve, and raise greater awareness among local students, teachers, residents, fishermen, and naturalist guides about conservation needs.

In 2001, research was undertaken to make taxonomic comparisons between Galápagos and California sea lion skulls and teeth. Approximately 200 sea lion skulls in the collection of the Charles Darwin Foundation Museum were measured (D. Aurioles-Gamboa, CICIMAR-INP, La Paz, Mexico, pers. comm.). This taxonomic investigation supported the listing of the Galápagos sea lion and the California sea lion as separate species in support of Rice (1998). In addition, two interdisciplinary expeditions were conducted in the Galápagos Islands in February 2002 and March

2003, with special emphasis on the feeding ecology, health status, genetics, and rescue training techniques of Galápagos fur seals and sea lions (Salazar 2002b, 2003b; Charles Darwin Foundation for the Galápagos Islands 2002).

Natural events

El Niño events

Classic studies and documentation of the negative effects of El Niños on pinniped populations, particularly sea lions from the Galápagos Islands, were conducted by Trillmich and Limberger (1985) and Trillmich and Dellinger (1991). The two strongest El Niño events that negatively affected pinniped populations in the Galápagos Islands during the last 30 years occurred during 1982-1983 and 1997-1998. The 1982-1983 El Niño caused a drastic reduction in the number of Galápagos fur seals and sea lions. For fur seals, there was almost total depletion of the four youngest year classes (1980-1983). The mortality rate of pups born in 1982 was 100% by five months of age, while there was an 89% (21 individuals) decrease in the number of pups born in 1983 when compared to average number of pups (N = 195) existing during the years (1979-1981) previous to the 1982-1983 El Niño event. For adult females and non-territorial males, mortality rates were about 30%, but were nearly 100% for large territorial males (Trillmich and Limberger 1985, Trillmich and Dellinger 1991, Gerber and Hilborn 2001). Foraging trips for females were three times longer and the trip duration variance increased tremendously due to the deterioration of food resources and prey composition changes. As a result, mortality of pups and dependent juveniles was high because of starvation (abandonment of pups by females) as well as the minimal transfer of low quality milk from females (Trillmich and Limberger 1985, Trillmich and Dellinger 1991). After the 1982-1983 El Niño, Galápagos fur seals recovered slowly, and redistributed to habitats and islands with better environmental conditions.

Galápagos sea lions also experienced high mortality in 1982, with 100% mortality of pups that year and more than a 50% decline in the number of juveniles. Likewise, in 1983, pup production was 30% less than in previous years on most islands, with high variability from colony to colony (from 3% on Santiago Island to 65% on Santa Fe Island), while adult mortality was greater than juvenile and pup mortality in 1982. After the El Niño period, sea lion pup production returned to normal in 1984, but it was lower in 1985. The adult population decreased during the El Niño, and it was suggested that the mortality of adult animals, mainly territorial males, was relatively high (Trillmich and Limberger 1985, Trillmich and Dellinger 1991). As for Galápagos fur seals, this event promoted local redistribution of sea lions and the population slowly recovered (Trillmich and Dellinger 1991, Gerber and Hilborn 2001). During the 1997-1998 El

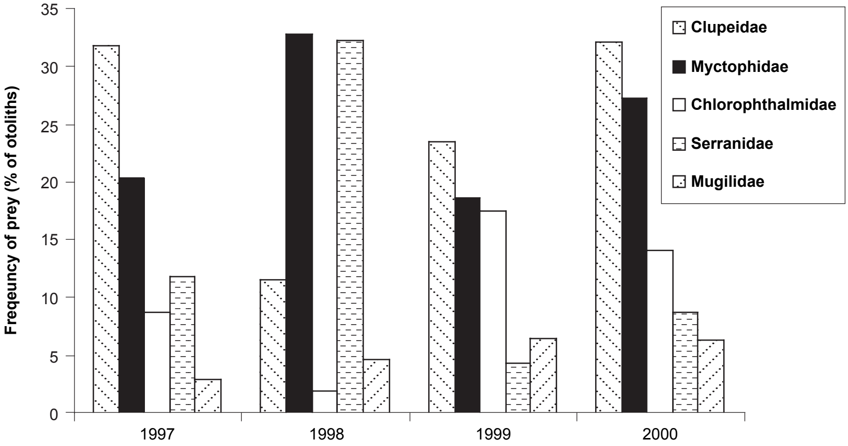


Figure 3. Frequency of occurrence of prey items in Galápagos sea lion scat (*Zalophus wollebaeki*) collected in 1997-2000, based on fish otolith identification. The 1997-1998 El Niño was recorded from December 1997 to June 1998. Data from Salazar and Bustamante (2003); and Salazar (2002a).

Niño, a 50% decline was reported on the Galápagos sea lion population (twelve colonies monitored), of which 35% was due to natural mortality and 15% was linked to migration and movement to other areas (Salazar and Bustamante 2003). The age classes most affected were pups and adult territorial males, with the 1997-1998 pup year-class having a survival rate of only about 10%. In subsequent years (1998-1999, 1999-2000, and 2000-2001), pup production was lower, with a maximum of 50% of the pup population recorded before the 1997-1998 El Niño event (Salazar and Bustamante 2003).

Abundance and composition of prey changes during El Niño events, evidenced by changes in the diet of Galápagos pinnipeds, are shown in Fig. 3. Before the 1997-1998 El Niño and during normal conditions, sardines and pilchards (Clupeidae: *Sardinops sagax sagax*, *Opisthonema berlangai*, *Opisthonema libertate*); lanternfishes (Myctophidae: *Diogenicthys laternatus*, *Loweina laurae*, *Triphoturus oculeus*); creole fish and groupers —“bacalaos” (Serranidae: *Paranthias colonus, Paralabrax albomaculatus, Mycteroperca olfax*); Chlorophthalmidae fishes (related to the presence of cold waters); and mullets (Mugilidae: *Mugil cephalus* and *M. galapagensis*) had frequencies of occurrence of 32.5%, 21%, 12%, 9%, and 3% in sea lion feces, respectively (Fig. 3). On the other hand, during both the 1997-1998 El Niño and 1998, there was a shift in diet composition to Myctophidae (33%) and Serranidae (32%); and away from Clupeidae (12%), mullets (5%), and Chlorophthalmidae (2%) (Salazar and Bustamante 2003). Thus the frequency of occurrence of its main prey, sardines, before the 1997-1998 El Niño, was much reduced during the event, and switched to species that might be reflecting probably a lower nutritional and energetic value (Salazar and Bustamante 2003).

Studies performed during the 1982-1983 El Niño highlighted that the Galápagos fur seal was seriously affected by the lack of food resources as evidenced by starved, emaciated, and dead animals (Trillmich and Limberger 1985). When the El Niño event is absent, the Galápagos fur seal diet is primarily composed of lanternfish and members of the Bathylagidae, with frequencies of occurrence in the range of 42-81% and 5-57% respectively. Secondary prey items include Clupeidae or sardines, Carangidae, and Chlorophthalmidae fishes (Trillmich and Dellinger 1991, Dellinger and Trillmich 1999). After the1982-1983 El Niño when lanternfish were still scarce, sardines were an unusual prey for the fur seal, with frequencies of occurrence ranging only from 0.2 to 6%, (Trillmich and Dellinger 1991). Apparently, during the 1997-1998 El Niño, Galápagos fur seals were less affected than Galápagos sea lions since pups observed in monitored colonies appeared to be healthier (S. Salazar, pers. obs.)

Hence, El Niño events are associated with acute or severe nutritional stress from bottom-up forces. Galápagos otariids have had to adapt to the periodic stresses in order to survive on these islands. In general, otariid species, with marked polygyny and metapopulation dynamics, are vulnerable to such catastrophic events, which can cause depletion and severe oscillations in population size, in some cases close to extinction, but with a slow recovering across long periods of time (Gerber and Hilborn 2001). In addition to the effects of El Niños, density-dependent factors controlling population growth may play a major role in the population size of otariids. At this level, intraspecific competition, mainly during a scarcity of prey, may cause loss of energy (exploitative competition) for conversion into pups and loss of time (interference competition) invested in foraging (Schoener 1973). Increased energy expenditures during El Niños were reflected in longer and less frequent foraging trips by females, compounded by the added energetic costs of pregnancy and lactation (Trillmich and Limberger 1985, Trillmich and Dellinger 1991).

Diseases

Among potential diseases, the canine distemper virus (CDV) poses the greatest threat to the otariid populations inhabiting the Galápagos Islands. CDV outbreaks have been detected among domestic dog (*Canis familiaris*) populations living in urbanized areas (e.g., Puerto Ayora, Santa Cruz Island) close to major sea lions colonies. During the CDV outbreak of early 2001, 569 cases were recorded in dogs, of which 275 died from the disease and 294 were euthanized (Salazar et al. 2001). The Center for Rehabilitation of Seals of Holland conducted an immunological study on sea lions from different colonies and islands in May 2001, but no antibodies against the canine distemper virus were reported. They recommended that all dogs on the islands be vaccinated with the trivalent vaccine, which protects against the CDV, hepatitis B, and parvovirus, to mitigate the risk of transmission to sea lion populations (Salazar et al. 2001). Outbreaks of CDV, phocine distemper virus (PDV), and other viral infections (morbillivirus) in Europe have caused mortalities of harbor (*Phoca vitulina*), gray (*Halichoerus grypus*), and Baikal seals (*Phoca siberica*) (Osterhaus et al. 1988; Dietz et al. 1989; Osterhaus et al. 1989, 1990; Visser et al. 1991). Environmental contamination has been potentially linked as a cause of immunosuppression of seals, enhancing the susceptibility of these pinnipeds to viral diseases (Ross et al. 1995).

Surveys of sea lions and fur seals on the Galápagos Islands conducted in 2002 and 2003 revealed a number of diseases and parasites, none of which appear to be imminent threats to the populations (Parás et al. 2002, Charles Darwin Foundation for the Galápagos Islands 2004). Between 60 and 100% of the sea lion pups surveyed had an eye infection or conjunctivitis associated with a bacillococcus bacteria and potentially a new species of ocular parasite (*Philophthalmus zalophi*) (Dailey et al. 2005). While there was no immunological response to brucellosis, Galápagos sea lions were susceptible to nine strains of the bacterium *Leptospira*, and Galápagos fur seals were susceptible to two strains. Ectoparasites such as lice (*Antarctophthirius microchir*) and nasal mites (*Orthohalarachne diminuata*) were also identified in various individuals (Salazar 2002b, 2003b).

Anthropogenic impacts

Oil spills and pollution

The threat of oil spills and pollution poses a significant threat to the marine ecosystem of the Galápagos Islands. One recent oil spill, from the tanker *Jessica*, occurred in January 2001 at the entrance to Bahía Naufragio, San Cristóbal Island. The oil tanker released 60% of its total cargo (300 and 600 t of bunker fuel and diesel, respectively) during an emergency-response operation. Galápagos sea lions were one of the priority species in the monitoring and contingency plan for impacted fauna of the Charles Darwin Research Station and Galápagos National Park, since some colonies were relatively close to the oil spill (Salazar 2003a). A survey to count oiled animals was conducted along the beaches of different islands (Fig. 1) affected during the first two weeks (17-31 January 2001) following the spill. About 79 oiled Galápagos sea lions were recorded around San Cristóbal (n = 24), Santa Fe (n = 43), Isabela (n = 3), and Floreana islands (n = 9).The degree of oiling was estimated on 73 rescued animals, of which 27 were severely affected (>50% of body), 12 were moderately affected (<10%), and 34 lightly oiled. Approximately half of these animals required washing and other treatments, with one fatality and a high incidence of conjunctivitis and burns (Salazar 2003a). In the year following the oil spill, no significant decreases in the Galápagos sea lion population were observed in any colony.

In early July 2002, a second oil spill took place in the Galápagos Islands. On this occasion, a tanker (BAE/*Taurus*) transporting fuel sank and spilled 2,000 gallons of diesel fuel off the coast of Puerto Villamil, Isabela Island. Fortunately, no sign of fuel was found on the beaches and marine animals, including sea lions, inhabiting the area, due primarily to the effort of the Galápagos National Park Service and Charles Darwin Foundation, who set up barriers of absorbent material

In addition to oil spills, minor oil leaks, and fuel releases from small tankers, fishing boats, and tourist vessels, mainly in the major urbanized areas (Santa Cruz and San Cristóbal), represent pollution sources and pathways of chronic exposure not only for sea lions but also for all the marine fauna of the islands. At present, it is unclear what the impacts of the oil spills and other minor spills are on otariids. Similarly unknown are the effects of persistent organochlorine pollutants (POPs) such as polychlorinated biphenyls (PCBs), polychlorinated dibenzo-*para*-dioxins (PCDDs), dichlorodiphenyltrichloroethanes (DDTs), and polybrominated diphenyl ethers (PBDEs), as well as polycyclic aromatic hydrocarbons (PAHs), antifouling paints used on boats, and other organochlorine pesticides, herbicides, fungicides, and fertilizers on the health of Galápagos sea lions and fur seals. Under experimental conditions, Ross et al. (1995, 1996) reported impairments to the immunological systems of captive harbor seals exposed to contaminated food obtained from areas polluted by POPs, but it is not known if this has affected pinnipeds in the Galápagos.

Direct anthropogenic interactions

Anthropogenic injuries to sea lions are caused by entanglement with nets, nylon, ropes, fishhooks in the snout, and cuts from outboard motor propellers (Charles Darwin Foundation for the Galápagos Islands 2000, Salazar 2002a). While there is evidence of delphinid mortality due to incidental take in longline, gillnet, and tuna purse-seine fisheries (Perrin et al. 1994, Palacios and Salazar 2002), little is known about fishery interactions involving Galápagos pinnipeds. Between 1995 and 2003, a total of 251 Galápagos sea lions were found entangled in fishing gear or other human artifacts. Most entanglements involved refuse from fisheries (134 of 251, or 54%), while the remainder (117 of 251, or 47%) may have been related to tourism (Fig. 4; Salazar 2002a). The most affected age classes are the juveniles (60%), followed by adults (35%); the categories less affected are the pups (5%). It is evident that hooks, nylon, plastic, and ropes are the artifacts of most concern that need to be addressed. Increases in illegal fishing, as well as current fishing methods (e.g., longlines), may

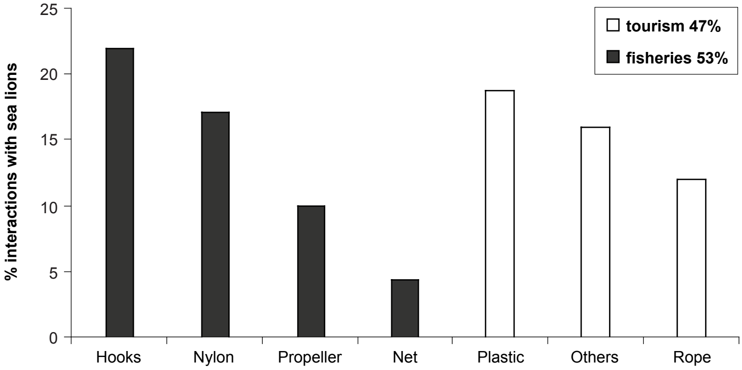


Figure 4. **Percent frequency of interaction between Galápagos sea lions and objects related to both fisheries and tourism. The chart represents field data collected through sighting logs and weekly records by marine observers and nature guide rangers, 1995-2003.**

represent potential threats to pinniped populations in the Galápagos Islands (Charles Darwin Foundation for the Galápagos Islands 2001), but currently no studies are under way to address them.

Sealing and hunting

Historically, Galápagos fur seals were hunted by commercial whalers in the early 1800s, and later by commercial sealers. It is estimated that during the period 1816 to 1933 about 22,000 animals were killed, nearly causing the extinction of fur seals on the islands by the early twentieth century (Jefferson et al. 1993, Reeves et al. 2002). In 1934, the Ecuadorian government prohibited commercial hunting of fur seals; this prohibition has been enforced since 1959, when most of the Galápagos Islands were declared a national park (Reeves et al. 2002).

In July 2001, fifteen subadult and adult Galápagos sea lions, four females and eleven males ranging from 4 to 12 years old, were illegally killed on San Cristóbal Island, near La Lobería (Salazar 2001, Salazar and Edgar 2001). This illegal hunt may be linked with the Asian black market for aphrodisiac products, since all male reproductive organs were removed by the hunters (Salazar 2001, Salazar and Edgar 2001). A reward of $4,000 was offered by the Ecuadorian Environment Ministry for information leading to the arrest and conviction of the perpetrators (Salazar and Edgar 2001).

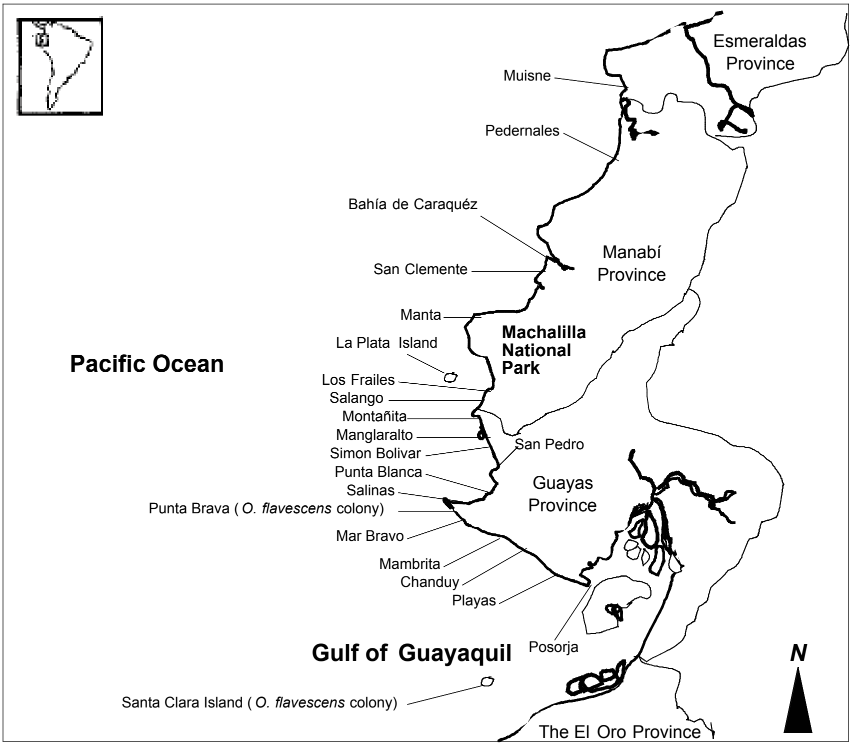


Figure 5. Map of the Ecuadorian mainland coast indicating the sites where otariid species have been recorded from 1989 to 2002, including the colonies of *Otaria flavescens* at Santa Clara Island and Punta Brava.

Pinniped species in the Ecuadorian coastal zone

Along the Ecuadorian continental coast, there are no haul-out sites or rookeries or reproductive colonies of pinnipeds, nor is it common to find sea lions as permanent residents. In the last two decades, however, there have been several observations of otariids in isolated non-reproductive colonies in Ecuador (Fig. 5). Ortiz (1980) was the first to observe and document a Galápagos sea lion on the continental coast at Bahía de Caráquez (00°37S, 80°26W). Nowak (1986) indicated that a small breeding colony was present on La Plata Island (01°16S, 81°04W), located at the Machalilla National Park and 30 km off the coast of Ecuador (Fig. 5). However, subsequent trips to the island found evidence of only a few individuals (~3 animals), and no suggestion of a reproductive colony (Curry 1993, Carvajal 1996). Moreover, it has yet to be confirmed if these individuals were Galápagos or California sea lions. Palacios et al. (1997) noted the presence of Galápagos sea lions on the central coast of Ecuador (n = 3) and Colombia (n = 5), confirmed by individual sightings of young animals, and suggesting that these individual could have been moved from La Plata Island, but originated from the Galápagos Islands.

Another species regularly observed is the South American sea lion (*O. flavescens*) with 13 sightings confirmed by identification of live animals, carcasses, or skulls between 1973 and 1994 (Félix et al. 1994). Two individuals from these sightings were previously recorded in Pinta (00º35N, 90º50W) and Santa Cruz (00º40S, 90º20W) islands, Galápagos Islands (Wellington and de Vries 1976, Merlen 1993). Moreover, several male skulls of this species were recorded at various locations in the Galápagos, but no live animals were seen (Merlen 1995). All of these records are probably isolated sightings, but permanent or semi-permanent groups may inhabit a marine wildlife refuge on Santa Clara Island on the southwest Ecuadorian coastline, where approximately 10 animals were recorded (Calle and Suarez 2003). Similarly, another 12-30 male South American sea lions were observed on Punta Brava, Salinas (2º12S, 81º00W) on the Ecuadorian coast (Fig. 5; Félix 2002). These observations were highly correlated with El Niño events along the southeastern Pacific coast (e.g., Peru and Ecuador). It is likely that most of the individuals sighted in Ecuador were resident animals moving from the Peruvian coast where the El Niño event negatively affected productivity and prey availability for this species.

In addition, ten live Galápagos fur seals were sighted on the Ecuadorian coast between 1991 and 1997 (Félix et al. 2001). The identity of these individuals was confirmed by morphological and mtDNA analyses (Félix et al. 2001). Galápagos fur seals have also been recorded on the coast of Colombia (Capella et al. 2002) and Mexico (D. Aurioles-Gamboa, CICIMAR-INP, La Paz, Mexico, pers. comm.), and their presence on the continent may be simply vagrant behavior or related to oceanographic and climatic conditions.

Merlen (1995) reported the presence of a different kind of fur seal, possibly a Juan Fernandez (*A. philippii*) or Guadalupe fur seal (*A. townsendi*), on the southwest side of San Cristóbal, Galápagos Islands. Unfortunately, this animal was not seen again. The South American fur seal (*A. australis*) was observed for the first time on the Ecuadorian coast by Félix (1996), and again in 2003 by a naturalist guide on Punta Suárez, Española Island, Galápagos, where it spent about three weeks. A definitive confirmation that this was indeed *A. australis* has not occurred, and additional studies have not been carried out to support this range extension. Capella et al. (2002) documented the regular appearance of 34 individual otariid pinnipeds along the Pacific coast of Colombia, including the South American sea lion, the Galápagos sea lion, and the Galápagos fur seal, from 1970 to 2001. They also suggested that these sightings were linked with oceanographic conditions (e.g. El Niño), ocean dynamics, and vagrant behavior of juvenile individuals.

Along the Ecuadorian coast, there are no marine mammal rescue centers or specialized stranding response teams. However, marine mammal monitoring in this area, including the rescue of sea lions, has been undertaken by volunteers and members (most of them biology students from the University of Guayaquil) of the Ecuadorian Foundation for the Study of Marine Mammal (Fundacion Ecuatoriana para el Estudio de Mamiferos Marinos, or FEMM) since the late 1980s. This nongovernmental organization has carried out environmental education for coastal human communities and special marine mammal seminars/courses at universities to initiate and enhance the research, conservation, and protection of marine mammals in Ecuador. Recently, the first marine mammal museum and education center was established in Salinas, Santa Elena Peninsula, and it reflects the cumulative work and dedicated efforts of FEMM personnel (Ben Haase, FEMM, Guayaquil, Ecuador, 2004, pers. comm.).

Conclusion

The Galápagos Islands and Ecuador provide opportunities to pursue studies on population dynamics and trends, probability of extinction, vagrant behavior, energetic and feeding ecology, impact of natural events (e.g., diseases), and effects of anthropogenic activities (e.g., fishery interaction) on pinniped species. To protect these unique and endemic species, conservation efforts and research must continue in order to insure their existence in these tropical areas.

The environmental management plan of the Galápagos Marine Reserve, led by the Galápagos National Park Service and the Charles Darwin Foundation, have incorporated sea lions as priority species to conserve and monitor, but local measures and strategies should be enhanced and expanded to mitigate human actions (illegal hunting) and fishery activities that could jeopardize these marine mammals. Decision-making from local authorities and the federal government (Ministry of Environment) should consider regulation of fisheries to avoid interactions in sensitive areas (e.g., no-take zones) where major populations of pinnipeds are present. In addition, domestic dogs on the Galápagos Islands should be vaccinated against viral pathogens to avoid horizontal transmission of diseases to pinnipeds. Incidental catch by fisheries, entanglement in marine debris, and the potential threat of organic contaminants on pinniped populations residing in the Galápagos Archipelago are also important conservation and research arenas.

In the long term, special attention should be directed toward understanding the effects of El Niño events, which have resulted in dramatic population declines of Galápagos otariid pinnipeds and may play an important role in promoting genetic variability through inter-island movements. The frequency and intensity of El Niños may be linked to global climate change. Cumulative and synergistic impacts of anthropogenic and natural factors should be addressed in the conservation and research monitoring plan for Galápagos otariids.

Acknowledgments

The authors warmly thank L.W. Fritz and S. Keller for their valuable suggestions and editorial reviewing of this manuscript, as well as for the opportunity to make this contribution to the proceedings volume. We also thank two anonymous reviewers for their important insights and recommendations to improve this manuscript. The first author greatly appreciated the travel grant provided by the Alaska Sea Grant College Program, U.S. Department of Commerce, NOAA, and particularly wants to thank Sherri Pristash for her efforts so that I could attend and participate in the 22nd Wakefield Fisheries Symposium—Sea Lions of the World: Conservation and Research in the 21st Century. The second author thanks the Galápagos National Park Service for permits and collaboration, the volunteers of the Sea Lion Project of the Charles Darwin Foundation, as well as funds to support the 2001 census and population survey (USAID, Karl Meyer Foundation and GEF). Thanks also to the local tourism operators, especially Metropolitan Touring (ETICA), Quazar Nautica, SubAqua, and Scuba Iguana, for their collaboration on many field trips.

References

Aurioles-Gamboa, D., S. Salazar, I. Contreras, and L. Barnes. (unpublished). Dental characters among various sea lion populations of the genus *Zalophus* (Carnivora, Otariidae): Taxonomic and evolutionary implications.

Bustamante, R.H., G.M. Branch, R. Bensted-Smith, and G.J. Edgar. 2002. The status of and threats to marine biodiversity. In: R. Bensted-Smith (ed.), A Biodiversity vision for the Galápagos Islands. Charles Darwin Foundation and World Wildlife Fund, Puerto Ayora, Santa Cruz, Galápagos, pp. 80-95. www.darwinfoundation.org. (Accessed Dec. 2005.)

Calle, M., and H. Suárez. 2003. Estado poblacional de las aves marinas residente del Refugio de Vida Silvestre-Isla Santa Clara para los meses de Diciembre 2002 y Julio 2003. EDC, Ministerio del Ambiente, Guayaquil, Ecuador. (In Spanish.)

Capella, J.J., L. Florez-Gonzalez, P. Falk-Fernandez, and D.M. Palacios. 2002. Regular appearance of otariid pinnipeds along the Colombian Pacific coast. Aquat. Mammal. 28:67-72.

Carvajal, R.1996. Lobos marinos en la Isla de la Plata (*Zalophus californianus*; provincia de Manabí). FEMM, El Observador Informativo 8(1):1-3. (In Spanish.)

Charles Darwin Foundation for the Galápagos Islands. 2000. Annual Report 1999, Projections. Quito, Ecuador. 84 pp. www.darwinfoundation.org. (Accessed Dec. 2005.)

Charles Darwin Foundation for the Galápagos Islands. 2001. Sea lion monitoring and conservation. Department of Marine Reserve and Conservation, Charles Darwin Research Station, Puerto Ayora, Santa Cruz, Galápagos, Ecuador. www.darwinfoundation.org. (Accessed Dec. 2005.)

Charles Darwin Foundation for the Galápagos Islands. 2002. Annual Report 2001. Puerto Ayora, Santa Cruz Island, Galápagos, Ecuador. 39 pp. www.darwinfoundation.org. (Accessed Dec. 2005.)

Charles Darwin Foundation for the Galápagos Islands. 2004. Annual Report 2003. Puerto Ayora, Santa Cruz, Galápagos, Ecuador. 30 pp. www.darwinfoundation.org. (Accessed Dec. 2005.)

Curry, R.L.1993. Update from Isla de la Plata. Noticias de Galápagos 52:24-25.

Dailey, M., R. Ellin, and A. Parás. 2005. First report of parasites from pinnipeds in the Galápagos Islands, Ecuador, with a description of a new species of *Philophthalmus* (Digenea: Philophthalmidae). J. Parasitol. 91(3):614-617.

Dellinger, T., and F. Trillmich. 1999. Fish prey of the sympatric Galápagos fur seals and sea lions: Seasonal variation and niche separation. Can. J. Zool. 77:1204-1216.

Dietz, R., M.P. Heide-Jorgensen, and T. Harkonen. 1989. Mass deaths of harbor seals (*Phoca vitulina*) in Europe. Ambio 18:258-264.

Fariña, J.M., S. Salazar, P. Wallem, J. Witman, and J.S. Ellis. 2003. Nutrient exchanges between marine and terrestrial ecosystems: The case of the Galápagos sea lion (*Zalophus wollebaeki*). J. Anim. Ecol. 72:873-887.

Félix, F. 1996. Primer registro del lobo fino Sudamericano (*Arctocephalus australis*) en Ecuador. In: Resúmenes, 7ª Reunión de Trabajo y 1er Congreso de la Sociedad Latinoamericana de Especialistas en Mamíferos Acuáticos de América del Sur, 22-25 de Octubre 1996. Viña del Mar, Chile. (In Spanish.)

Félix, F. 2002. Una colonia de lobos marinos sudamericanos (*Otaria flavescens*) en Salinas, Ecuador. *Acta Oceanográfica del Pacífico* 11(1):327-331. (In Spanish.)

Félix, F., B. Haase, J. Samaniego, and J. Oechsle. 1994. New evidence of the presence of the South American sea lion *Otaria flavescens* (Carnivora: Pinnipedia) in Ecuadorian waters. Estudios Oceanológicos13:85-88.

Félix, F., G. Lento, J. Davis, B. Haase, and D. Chiluiza. 2001. El lobo fino de Galápagos *Arctocephalus galapagoensis* en la costa continental de Ecuador, primeros registros confirmados a traves de análisis morfólogicos y genéticos. Estudios Oceanológicos 20:63-68. (In Spanish.)

Gerber, L.H., and R. Hilborn. 2001. Catastrophic events and recovery from low densities in populations of otariids: Implications for risk of extinction. Mamm. Rev. 31(2):131-150.

Jefferson, T.A., S. Leatherwood, and M.A. Webber. 1993. FAO species identification guide: Marine mammals of the world. FAO, Rome. 320 pp.

Le Boeuf, B., D. Aurioles, R. Condit, C. Fox, R. Gisiner, R. Romero, and F. Sinsel. 1983. Size and distribution of the California sea lion population in Mexico. Proceedings of the California Academy of Sciences 43(7):77-85.

Le Boeuf, B.J., D.P. Costa, S.D. Feldkamp, F. Trillmich, A.C. Huntley, J. Reiter, H. Vargas, and R. Davis. 1988. Report of an expedition to the Galápagos Islands, 11 April to 27 May 1988 aboard the *Mystique*. Unpubl. report available from the University of California, Santa Cruz. 31 pp.

Limberger, D., F. Trillmich, H. Biebach, and R.D. Stevenson. 1986. Temperature regulation and microhabitat choice by free-ranging Galápagos fur seal pups (*Arctocephalus galapagoensis*). Oecologia 69:53-59.

Merlen, G. 1993. Flotsam and jetsam. Noticias de Galápagos 52:4-5.

Merlen, G. 1995. A field guide to the marine mammals of the Galápagos. Instituto Nacional de Pesca, Guayaquil, Ecuador.

Nichols, J.D., and M.J. Corroy. 1996. Techniques for estimating abundance and species richness. In: D.E. Wilson, F. Russell Cole, J.D. Nichols, R. Rudran, and M.S. Foster (eds.), Measuring and monitoring biological diversity: Standard methods for mammals. Vol. 10. Smithsonian Institution Press, Washington, D.C., pp 177-202.

Nowak, B. 1986. Isla de la Plata and the Galápagos. Noticias de Galápagos 48:17. (In Spanish.)

Okey, T., A. St. Banks, A.F. Born, R. Bustamante, M. Calvopiña, G. Edgar, E. Espinoza, J.M. Fariña, V. Francisco, L.E. Garske, S. Salazar, S. Shepherd, V. Toral, and P. Wallem. 2004. A balanced trophic model of a Galápagos subtidal rocky reef for evaluating marine conservation strategies. Ecol. Model. 172:383-401.

Ortiz, F. 1980. Un registro de mamífero nuevo para el Ecuador continental. Museo Ecuatoriano de Ciencias Naturales 2(2):51-56. (In Spanish.)

Osterhaus, A.D.M.E., J. Groen, P. de Vries, F.G.C.M. UytdeHaag, B. Klingeborn, and R. Zarnke. 1988. Canine distemper virus in seals. Nature 335:403-404.

Osterhaus, A.D.M.E., J. Groen, F.G.C.M. UytdeHaag, I.K.G. Visser, M.W.G. van de Bildt, A. Bergman, and B. Klingeborn. 1989. Distemper virus in Baikal seals. Nature 338:209-210.

Osterhaus, A.D.M.E., J. Groen, H.E.M. Spijkers, H.W.J. Broeders, F.G.C.M. UytdeHaag, P. de Vries, J.S. Teppema, I.K.G. Visser, M.W.G. van de Bildt, and E.J. Vedder. 1990. Mass mortality in seals caused by a newly discovered morbillivirus. Vet. Microbiol. 23:343-350.

Palacios, D.M., and S. Salazar. 2002. Cetaceos. In: E. Danulat and G.J. Edgar (eds.), Reserva Marina de Galápagos, Linea Base de la Biodiversidad. Fundacion Charles Darwin/Servicio Parque Nacional Galápagos, Santa Cruz, Galápagos, Ecuador. Cap. 16, pp. 291-304. (In Spanish.)

Palacios, D. M., F. Félix, L. Florez-González, J.J. Capella, D. Chiluiza, and B. Haase. 1997. Sightings of Galápagos sea lions (*Zalophus californianus wollebaeki*) on the coasts of Colombia and Ecuador. Mammalia 61(1):114-116.

Páras, A., D.M. Brousset, S. Salazar, and D. Aurioles. 2002. Field anesthesia of two species of pinnipeds found in the Colon Archipelago or Galápagos, (*Arctocephalus galapagoensis* and *Zalophus wollebaeki*). In: American Association of Zoo Veterinarians: Proceedings of the Annual Meeting. Milwaukee, Wisconsin, October 2002.

Perrin, W.F., G.P. Donovan, and J. Barlow. 1994. Report of the workshop on mortality of cetacean species in passive fishing nets and traps. In: W.F. Perrin, G.P. Donovan and J. Barlow (eds.), Gillnets and cetacean. Int. Whaling Comm. Rep. Comm. Spec. Issue 15:1-71.

Reeves, R.R., B.S. Stewart, P.J. Clapham, and J.A. Powell. 2002. Guide to the marine mammals of the world. National Audubon Society, New York. 527 pp.

Rice, D.W. 1998. Marine mammals of the world: Systematics and distribution. Society for Marine Mammalogy Special Publication 4. 231 pp.

Ross, P.S., R.L. De Swart, and R.F. Addison.1996. Contaminant-induced immunotoxicity in harbour seals: Wildlife at risk? Toxicology 112:157-169.

Ross, P.S., R.L. De Swart, P.J.H. Reijnders, H.V. Loveren, J.G. Vos, and A.D.M.E. Osterhaus. 1995. Contaminant-related suppression of delayed-type hypersensitivity and antibody responses in harbor seals fed herring from the Baltic Sea. Environ. Health Perspect. 103:162-167.

Salazar, S. 2001. Auscultación y estudio de cadáveres de lobos marinos encontrados en "La Lobería" –Isla San Cristóbal. Informe Técnico. Estación Científica Charles Darwin, Departamento de Investigación y Conservación Marina. Santa Cruz, Galápagos, Ecuador. 5 pp. (In Spanish.)

Salazar, S. 2002a. Galápagos sea lion and fur seal. In: E. Danulat and G.J. Edgar (eds.), Reserva Marina de Galápagos, Linea Base de la Biodiversidad. Fundacion Charles Darwin/Servicio Parque Nacional Galápagos, Santa Cruz, Galápagos, Ecuador, Cap. 15, pp. 267-290. (In Spanish.)

Salazar, S. 2002b. Preliminary report: Health status, genetic and rescue techniques of the Galápagos pinnipeds. Charles Darwin Foundation. Technical report February 2002, presented to the Galápagos National Park Service and participant organizations, Santa Cruz, Galápagos, Ecuador. 13 pp. (In Spanish and English.)

Salazar, S. 2002c. Estado poblacional de los pinnípedos en las islas Galápagos. In: Resúmenes 10ª RT y 4º Congreso SOLAMAC, 14-19 de octubre 2002, Valdivia, Chile. 47 pp.

Salazar, S. 2002d. Preliminary report of pinniped census in the Galápagos Islands, November 2001. Informe técnico-Noviembre 2001 presentado a SPNG, FCD and Karl Meyer Foundation, Santa Cruz, Galápagos, Ecuador. 12 pp. (In Spanish.)

Salazar, S. 2003a. Impacts of the *Jessica* oil spill on sea lions (*Zalophus wollebaeki*) populations. Mar. Pollut. Bull. 47:313-318.

Salazar, S. 2003b. Preliminary report: Health status, genetic and rescue techniques of the Galápagos pinnipeds. Charles Darwin Foundation. Technical report March 2003, presented to Charles Darwin Foundation, Galápagos National Park Service and participant organizations, Santa Cruz, Galápagos, Ecuador. 13 pp. (In Spanish and English.)

Salazar, S., and R.H. Bustamante. 2003. Effects of the 1997-98 El Niño on population size and diet of the Galápagos sea lions (*Zalophus wollebaeki*). Noticias de Galápagos 62:40-45.

Salazar, S., and G. Edgar. 2001. Galápagos sea lion massacre. Mar. Pollut. Bull. 42:705.

Salazar S., M. Cruz, and D. Cruz. 2001. Canine distemper in the Galápagos Islands: Possible consequences and prevention plan. Charles Darwin Foundation–Galápagos National Park Service. Technical report February 2001, presented to Agriculture Ministry (CESA), Santa Cruz, Galápagos, Ecuador. 10 pp.

Schoener, T.W. 1973. Population growth regulated by intraspecific competition for energy or time: Some simple representations. Theor. Popul. Biol. 4:56-84.

Seal Specialist Group. 1996a. *Zalophus wollebaeki*. In: IUCN 2004. 2004 IUCN Red List of Threatened Species. www.redlist.org. (Accessed 7 October 2005.)

Seal Specialist Group. 1996b. *Arctocephalus galapagoensis*. In: IUCN 2004. 2004 IUCN Red List of Threatened Species. www.redlist.org. (Accessed 7 October 2005.)

Trillmich, F.1979. Galápagos sea lion and fur seal. Noticias de Galápagos 29:8-14.

Trillmich, F. 1984. The natural history of the Galápagos fur seal (*Arctocephalus galapagoensis*, Heller 1904). In*:* R. Perry (ed.), Key environments: Galápagos. Pergamon Press, Oxford, UK, pp. 215-223.

Trillmich, F., and T. Dellinger.1991.The effects of El Niño on Galápagos pinnipeds. In: F. Trillmich and K.A. Ono (eds.), Pinnipeds and El Niño: Responses to environmental stress. Springer-Verlag, Berlin, pp. 66-74.

Trillmich, F., and D. Limberger. 1985. Drastic effects of El Niño on Galápagos pinnipeds. Oecologia 67:19-22.

Trillmich, F., and W. Mohren. 1981. Effects of the lunar cycle on the Galápagos fur seal. Oecologia (Berlin) 48:85-92.

Utreras, V., D. Tirira, and S. Salazar. 2001a. The Galápagos sea lion (*Zalophus wollebaeki*). In: D. Tirira (ed.), The red book of the mammals of Ecuador. Simbioe, Ecociencia, Environmental Ministry, and IUCN, Quito, pp. 66-67. (In Spanish.)

Utreras, V., D. Tirira, and S. Salazar. 2001b. The Galápagos fur seal (*Arctocephalus galapagoensis*). In: D. Tirira (ed.), The red book of the mammals of Ecuador. Simbioe, Ecociencia, Environmental Ministry, and IUCN, Quito, pp. 64-65. (In Spanish.)

Visser, I.K.G., J.S. Teppema, and A.D.M.E. Osterhaus. 1991. Virus infections of seals and other pinnipeds. Rev. Med. Microbiol. 2:1-9.

Wellington, G.M., and T. de Vries. 1976. The South American sea lion (*Otaria byronia*) in Galápagos Islands. J. Mammal. 57:166-167.

Uncertain Management or Management of Uncertainty: Steller Sea Lion—a Case Study

Robert J. Small
Alaska Department of Fish and Game, Juneau, Alaska

Douglas P. DeMaster
NOAA Fisheries, Alaska Fisheries Science Center, Seattle, Washington

Abstract

The abundance of Steller sea lions (sea lions) declined ~15% per year during the 1980s in the Bering Sea, Aleutian Islands, and Gulf of Alaska regions, resulting in a threatened listing under the Endangered Species Act (ESA) in 1990. Numerous factors may have contributed to the decline, and there has been substantial uncertainty regarding the relative impact of these factors when management actions were implemented to promote recovery. One key hypothesis for the continued decline in the 1990s (~5%/year) has been a reduction in sea lion prey biomass and quality caused by either commercial fishing or an "oceanographic regime shift" resulting in substantial changes in the abundance or availability of dominant prey species, which may have subsequently resulted in nutritional stress on the sea lion population. Following the 1997 ESA endangered listing of the western population and the determination that competition with commercial groundfish fisheries in Alaska was likely, additional fishery management restrictions were implemented. Counts of sea lions in 2002 and 2004 indicate the decline of sea lions may have begun to cease. The evidence for nutritional stress, especially post-1990, is somewhat contradictory and equivocal which contributes to continued uncertainty. Given the ESA's mandate to U.S. federal regulatory agencies to manage in a strongly precautionary manner, greater uncertainty can be translated to mean more precautionary management. To address ongoing uncertainty about causal factors and the efficacy of conservation actions, we believe that a research strategy with four primary components should be pursued: (1) population monitoring and fundamental sea lion ecological research, (2) fishery interaction studies designed to test the localized depletion hypothesis, (3) determining the mechanism by which changes in prey biomass or nutritional quality of the prey species may result in chronic nutritional stress that results in decreased sea lion survival and reproduction, and (4) adaptive management experiments to assess the impact of fisheries on the sea lion prey field and subsequently sea lion demography. In addition, recently suggested modifications to conservation policy should be pursued: (a) establishing a specific quantitative standard for risk of extinction (under the ESA), (b) defining jeopardy and adverse modification of critical habitat (under the ESA) in terms of risk of extinction, and (c) establishing a quantitative standard for ecosystem protection in developing recovery strategies for ESA listed species. Implementation of these research and conservation policy recommendations could substantially decrease uncertainty and increase the probability of effective conservation of sea lions.

Introduction

The abundance of Steller sea lions (sea lions) declined at an annual rate of ~15% during the 1980s in the Bering Sea and Aleutian Islands (BSAI) and Gulf of Alaska (GOA) regions, with substantial spatial and temporal differences in the decline across their extensive geographic range. Although important life history and population assessment research was conducted on sea lions during the 1980s, knowledge of the functional relationships that had caused the overall abundance to decline by ~80% by 1990 was scant (Braham et al. 1980; Loughlin et al. 1984, 1992; Trites and Larkin 1996; Merrick et al. 1997; NMFS 2001). Numerous factors have been considered as contributing causes of the decline, including: incidental mortality in fisheries, pollution and contaminants, harassment and illegal shooting, commercial harvests of pups, Alaska Native subsistence harvests, disease, predation, and reduced prey biomass and quality due to oceanographic changes (i.e., regime shifts) and indirect competition for prey with commercial fisheries resulting in nutritional stress (Fritz et al. 1995, Loughlin and York 2000, NMFS 2000, NMFS 2001, Trites and Donnelly 2003, Springer et al. 2003).

Evidence of decreased juvenile survival, based on mark-resight and modeling analyses, and a reduction in pregnancy and lactation rates of adult females between the 1970s and 1980s indicated that nutritional stress could be one contributing cause of the decline (Calkins and Goodwin 1988, York 1994, Loughlin 1998, Sease and Merrick 1997, Trites and Donnelly 2003). Although the functional mechanism by which nutritional stress could reduce survival and reproduction was unknown, the basic premise was a “bottom up” effect due to reduced prey biomass or availability and/or nutritional quality of the prey. Such nutritional stress would have occurred during the period when commercial fisheries expanded in the BSAI and GOA regions, and followed a substantial "regime shift" in the late 1970s (Fritz et al. 1995, Calkins et al. 1998, Benson and Trites 2002). Both fisheries and the effect of regime shifts can potentially reduce sea lion prey biomass and quality, and both received substantial attention as the primary factors that were contributing to the continued sea lion decline (NMFS 2001); however, little consideration was given to the cumulative or synergistic effects of these two factors.

Substantial uncertainty, associated with the potential causes of the severe decline that occurred during the 1980s, remained when sea lions of U.S. waters were listed as threatened under the Endangered Species Act (ESA) in 1990. Numerous conservation measures were implemented following the 1990 listing, including a prohibition on intentional killing (except for subsistence taking by Alaska Natives), a limit on incidental take in fisheries, increased monitoring of the subsistence harvest, reduced disturbance, and modified fishery management regulations. The Steller Sea Lion Recovery Team was formed in 1990 by the National Marine Fisheries Service, with the primary purpose of writing a recovery plan that outlined specific actions to promote recovery. Due to the substantial uncertainty regarding the causes of the sea lion decline, a large proportion of the recovery recommendations called for additional research.

Critical habitat for Steller sea lions was designated under the ESA in 1993 (58 FR 45269), based primarily on a combination of satellite telemetry data from adult female sea lions, visual observations of sea lions at sea in locations assumed to represent common foraging areas, and the distribution of groundfish (i.e., sea lion prey) catches in the Bering Sea/Gulf of Alaska and waters around the Aleutian Islands. Critical habitat, which included areas around both rookeries and major haul-outs and the additional three aquatic foraging areas, represented the spatial landscape from which federal actions would be evaluated under ESA Section 7 consultations. For most fisheries actions, the action agency (sustainable fisheries divisions with Regional Offices of NOAA Fisheries) and the consulting agency (protected resources divisions with Regional Offices of NOAA Fisheries) are both part of the same agency; i.e., NOAA Fisheries. If a proposed federal action is determined, through informal consultation, to be likely to adversely affect sea lions or their critical habitat, then the action is evaluated through a formal ESA Section 7 consultation under the ESA. The consulting agency conducts the formal consultation, which results in the preparation of a biological opinion. In that biological opinion, the consulting agency must make a decision as to whether the proposed action would "jeopardize" the continued existence of the ESA listed species, or result in the destruction or adverse modification of its critical habitat. The definition of "jeopardize" under the ESA is "jeopardize the continued existence of means to engage in an action that reasonably would be expected, directly or indirectly, to reduce appreciably the likelihood of both the survival and recovery of a listed species in the wild by reducing the reproduction, numbers, or distribution of that species." (50 CFR 402.01). The definition of destruction or adverse modification of critical habit under the ESA is ". . . a direct or indirect alteration that appreciably diminishes the value of critical habitat for both the survival and recovery of a listed species." (50 CFR 402.01).

In the mid-1990s, researchers found genetic differences between sea lions on either side of 144ºW (near Cape Suckling, Alaska) (Bickham et al. 1996, Loughlin 1997). Also, sea lion abundance in the BSAI and GOA (west of Cape Suckling) regions continued to decline in the 1990s, whereas abundance in Southeast Alaska and farther south was stable or increasing. In 1997, the Steller sea lion was reclassified into two distinct population segments (50 CFR 24345). The western distinct population segment was changed to endangered due to the overall magnitude (>80%) and continuous nature of the decline, and the eastern distinct population segment was maintained as threatened due to uncertainty in recovery, especially in the southern portion of the range.

The working hypothesis regarding sea lion interactions with the groundfish fishery in Alaska was that the fishery could adversely impact the ability of sea lions to forage in the GOA and BSAI by reducing the availability of prey (Fritz et al. 1995). Based on locations obtained through satellite transmitters attached to sea lions (Merrick and Loughlin 1997, Loughlin et al. 2003), it was determined that most foraging by sea lions was likely to occur near (<20 nautical miles) haul-outs and rookeries. Under the assumption that "localized depletion" of sea lion prey biomass and quality due to fisheries resulted in nutritional stress, and subsequently reduced survival and reproduction of sea lions, additional fisheries regulations were implemented in the 1990s. The primary intent of those regulations was to more evenly distribute the catch in time and space, thus reducing the potential for localized depletion (Fritz et al. 1995). In a retrospective analysis, Hennen (2006) found a significant, positive correlation between several metrics of fishing activity and the sea lion decline prior to 1991. No such relationship was found using data collected after 1991. Hennen interpreted his findings as consistent with an interpretation that management measures were effective in moderating the localized effects of fishing activity on sea lions.

In 2000, a formal ESA Section 7 consultation on the fishery management plans for the BSAI and GOA resulted in a biological opinion that determined groundfish fisheries for Pacific cod and pollock jeopardized the continued existence of the western distinct population segment of sea lions, and adversely modified its critical habitat. As required by the ESA, whenever a jeopardy determination is made, the 2000 biological opinion included a reasonable and prudent alternative that consisted of management measures to mitigate the impacts of the groundfish fisheries for pollock, cod, and Atka mackerel in the Bering Sea, Aleutian Islands, and Gulf of Alaska. Those measures included an adaptive management experiment, with a series of large areas either open or closed to fisheries (Rusin 2002). The primary objectives of the proposed adaptive management experiment were to mitigate potential adverse impacts of the groundfish fishery on the western distinct population segment of sea lions in the areas closed to fishing, while also allowing NOAA Fisheries to assess the effectiveness of the management measures and determine whether further measures were necessary.

However, the adaptive management experiment was not implemented, due in part to the anticipated adverse economic impacts to the groundfish fishery and concerns regarding the feasibility of the experimental design relative to sea lion ecology (NMFS 2001, Bowen et al. 2001). A Congressional appropriations bill provided a one-year time period for the North Pacific Fishery Management Council and NOAA Fisheries to craft an alternative suite of fishery management regulations that would remove jeopardy and adverse modification of critical habitat. The intent of Congress was that NOAA Fisheries would implement alternate regulations that minimized the economic impacts to the fishing industry while also accounting for the substantial uncertainty in both the knowledge of sea lion ecology and the impact of fisheries on the sea lion prey field. Ambiguity in the ESA definition of jeopardy (i.e., “reasonably would be expected,” “reduce appreciably the likelihood”) contributed additional uncertainty at the policy level. The combined scientific and policy uncertainty generated extensive discussion and debate about developing a suite of fishery management regulations that would remove jeopardy and adverse modification of critical habitat. In 2001, NOAA Fisheries consulted on a revised set of management regulations, and released a biological opinion (NMFS 2001) that evaluated the potential for jeopardy or adverse modification of critical habitat under those regulations. The agency determined that the suite of management measures, if implemented, were not likely to result in jeopardy or adverse modification of critical habitat (Rusin 2002). The regulations were implemented without a large-scale adaptive management experiment, although several small-scale experiments were proposed to test the localized depletion hypothesis. In addition, Congress appropriated more than a tenfold increase in funding for sea lion research in fiscal year 2001, specifically to address thirteen areas of uncertainty. The results of this greatly enhanced research program are now starting to be reported in the published scientific literature.

Current status

Data similar to those collected during the 1970-1980s were not available from the 1990s, and thus a direct comparison to assess whether the level of nutritional stress has changed was not possible (M. Castellini, University of Alaska Fairbanks, unpubl.). Research on nutritional stress in the 1990s relied on indirect methods, including comparisons between the western and eastern distinct populations, which could be problematic (e.g., Davis et al. 2006; B.S. Fadely, NMFS NMML, unpubl.; L.A. Hoopes, Texas A&M University, unpubl.) The majority of research has been conducted on adult females and their pups during the summer period, and results indicate little or no evidence of nutritional stress during the 1990s and beyond (Trites and Donnelly 2003). Overall, the evidence for nutritional stress in all age classes and all seasons post 1990 is less than there was in the 1980s, and the evidence reported in the post 1990 period is limited; e.g., decreased reproduction (Holmes and York 2003). Several other issues contribute to continued uncertainty about whether nutritional stress persisted as a threat to the recovery of sea lions in the 1990s. Specifically, the adult females with pups studied on rookeries could represent animals that survived the impact of nutritional stress, whereas those females that were unable to complete gestation due to nutritional stress may have remained at sea and did not return to the rookeries. As noted by the NRC (2003), "This attendance behavior is a critical limitation in monitoring pup production rates and female condition. Essentially, only those females healthy enough to produce pups arrive at rookeries." In addition, other cohorts that were not well studied, especially recently weaned juveniles, may have been more susceptible to the impacts of nutritional stress. At the ecosystem level, if the sea lion population has now begun to stabilize at a reduced carrying capacity, nutritional stress will likely be less pronounced compared to the periods of dramatic population declines, assuming the relative influence of food availability on population regulation has remained similar.

In addition to a general lack of compelling evidence for the nutritional stress hypothesis in the post-1990 period, several publications have suggested that top-down forcing (i.e., predation) may be an important factor in understanding the past, as well as the current, dynamics of sea lions (Springer et al. 2003, Williams et al. 2004). In particular, the publication by Springer et al. (2003) speculated that predation by killer whales is the most likely cause of the rapid decline of the western sea lion population in the 1980s and the continued decline in the 1990s. However, the Springer et al. (2003) paper has generated considerable controversy, and several recent publications contend that the available data do not support the assumptions and hypotheses within Springer et al. (DeMaster et al. 2006, Trites et al. 2006, Mizroch and Rice 2006). Subsequently, research efforts to further understand the importance of predation on the western distinct population segment of sea lions have been undertaken; unfortunately, results from these studies are not yet available.

Counts of sea lions in 2002 and 2004 increased relative to counts obtained during 2000. However, three additional biennial counts are required to statistically confirm the decline has stopped and that the western population was increasing at ~5% per biennium as indicated by the 2002 and 2004 counts (NMFS 2000, DeMaster unpubl.). Results from the sea lion research program, which expanded in the later 1990s and again in 2001, have substantially increased the knowledge of sea lion ecology and improved the understanding of how various factors may affect the population. Yet, although some factors are now considered relatively minor threats (NRC 2003), substantial uncertainty persists concerning the suite of factors that may be impeding recovery, and the cumulative and synergistic effects among these factors remain largely unknown (Loughlin and York 2000).

Linking research priorities and conservation measures

Thus, although the most recent counts of sea lions do not indicate a continued decline of the western distinct population segment, substantial uncertainty persists on what factors are impeding recovery and what management measures will be most effective in promoting recovery. Certainly, population monitoring and fundamental sea lion ecological research must continue, including studies of population abundance and trend, age-specific vital rates, foraging ecology, diet, essential habitat, environmental monitoring (e.g., regime shifts), and improved estimates of the abundance, diet, and movement patterns of transient killer whales. Beyond such sea lion monitoring research, however, a more explicit link between research priorities and management measures is required to reduce the uncertainty associated with the factors impeding recovery and to determine which management measures to implement. Specifically, research that has a direct bearing on jeopardy or adverse modification of critical habitat findings and the effectiveness of conservation measures should receive the highest priority, as recommended by Bowen et al. (2001). We believe a primary link would be to further examine how both commercial fisheries and the variability in oceanographic conditions affect the seasonal distribution and abundance of the sea lion prey field, and how such changes affect sea lion population dynamics. Below, we present some specifics of this approach.

Fishery management measures have been implemented based on the assumption that fisheries may jeopardize the continued existence of the western distinct population segment of sea lions and may adversely modify critical habitat through a local reduction in prey biomass and quality. Thus, research studies designed to determine if fisheries indeed deplete or disturb the sea lion prey field, to the extent that foraging success is reduced, need to be completed. Specifically, "fishery interaction" studies designed to assess prey biomass before, during, and after fishing in a treatment area with comparisons to prey biomass in an unfished control area should continue (Loughlin and Mattson 1998, Wilson et al. 2003, Conners et al. 2004), and need to be expanded. Such studies must be conducted at spatial and temporal scales relevant to both foraging sea lions and current operational fisheries to assess the magnitude and duration of changes in the prey field, both with and without the influence of fisheries, with an experimental design that reduces potential biases and alternative interpretations. Several years, and possibly decades, of research may be required to account for natural variability in prey biomass and distribution. In addition to field research studies, models should be developed that integrate sea lion foraging parameters and reproductive energetics within a spatially explicit demographic model to identify the types of perturbations to the prey field that negatively impact sea lion fitness. Additional modeling is also needed to assess the impact of single-species fisheries management on ecosystem carrying capacity (Goodman et al. 2002, Pikitch et al. 2004).

Another research priority is to determine the mechanism by which changes in prey biomass and quality may result in chronic nutritional stress (Trites and Donnelly 2003) that subsequently decreases sea lion survival and reproduction. As recommended by Bowen et al. (2001), research examining the physiological response of sea lions to changes in prey biomass and quality must ultimately provide insights as to how such changes affect sea lion demography in order for the results to be applied toward sea lion recovery and conservation. Further, understanding the demographic effect of changes in prey and the mechanism of nutritional stress is important because sea lion populations may respond to changes in more than one factor (e.g., regime shifts, fisheries, interspecific competition) in the same manner.

Two extensive reviews of sea lion interactions with fisheries have recommended an adaptive management approach to examine the hypothesized mechanisms of a negative influence of fisheries on sea lions (Bowen et al. 2001, NRC 2003). We believe such an adaptive management approach is required to examine how a potential reduction in prey biomass and quality could lead to physiological responses by sea lions that directly (e.g., reduced fecundity) or indirectly (e.g., increased mortality from predators due to increased foraging) reduces their population growth, both in the short-term and possibly over the long-term that could result in a lower carrying capacity. An experiment under such an adaptive management approach should be at a finer spatial scale than proposed in the 2000 biological opinion, and should integrate the objectives of the fishery interaction studies mentioned above with the monitoring of a suite of sea lion demographic and behavioral response parameters. Such a complex experiment has not been attempted previously in marine ecosystems, and prior to initiating such an experiment several important questions must be thoroughly addressed.

First, are such experiments necessary? Boyd (1995) recommended that individually based models should be developed to explore whether or not the impact of localized depletion can be sufficiently assessed prior to experiments. Fishery interaction studies could determine that fisheries do not cause significant short-term reductions in prey biomass. Whether such studies can determine the potential long-term impact of fisheries on the prey field needs to be addressed. Second, are such experiments feasible? The challenge to develop a robust experimental design for the experiments is tremendous (Punt and Fay 2006, Bowen et al. 2001), especially due to the spatial and temporal scale that would be required to account for the movement of sea lions and their prey, and the inherent variability in the marine ecosystem. Critical to a successful and informative experiment will be selecting the suite of variables to measure for both the prey field (e.g., species composition, biomass, age structure) and sea lions (e.g., foraging effort, body condition) and determining how they will be interpreted. Finally, the ESA has restrictions on the type of experimental treatments that may negatively impact a listed species, and such restrictions will need to be met in developing the experimental design.

As stated by Goodman (2005), "Mechanisms are needed to deal rationally with the uncertainties about causes of population declines and uncertainties about eventual effectiveness of planned conservation measures." Uncertainty would most likely be reduced resulting in a more robust conservation strategy with the continued, and refined, implementation of the four research components outlined above: (1) population monitoring and fundamental sea lion ecological research, (2) fishery interaction studies designed to test the localized depletion hypothesis, (3) determining the mechanism by which changes in prey biomass and quality may result in chronic nutritional stress that results in decreased sea lion survival and reproduction, and (4) adaptive management experiments to assess the impact of fisheries on the sea lion prey field and subsequently sea lion demography. Such a strategy should increase the likelihood that conservation measures are implemented, maintained, or modified such that they can be effective without unnecessary burden on commercial fisheries. Without such a strategy, there will be a much lower likelihood of gaining additional insights on how different threats may influence sea lion population dynamics. In addition, the opportunity to distinguish between the effects of human activities versus those that may occur naturally could be greatly diminished.

Conservation policy

Opportunities also exist to reduce the uncertainty inherent in conservation policy, which would further enhance the effectiveness of the sea lion conservation strategy. Goodman (2005) described the need to develop more explicit policy standards, which could result in reduced litigation and more consistent implementation of conservation policies. Below we briefly discuss three specific policy modifications outlined by Goodman (2005) that are relevant to sea lion conservation.

First, the current ESA definitions of endangered ("in danger of extinction throughout all or a significant portion of its range") and threatened ("likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range") species imply a time horizon and level of probability. The lack of a more specific standard associated with these definitions results in substantial uncertainty as to when species should be listed or delisted. For example, the western distinct population segment of sea lions was listed as endangered when its abundance of adults was ~40,000, yet the abundance of the discrete population of Cook Inlet beluga whales had declined over several years to ~350 animals when the decision by NOAA Fisheries, which was upheld by an Appeals Court judge, was made that they were not threatened with extinction. Modifying the ESA definitions of endangered and threatened to include a specific standard for extinction, for example a 1% probability of becoming extinct in 100 years (see DeMaster et al. 2004), would reduce uncertainty and increase consistency in listing decisions.

The second policy modification needed is to employ the extinction standard used in ESA listings into ESA Section 7 consultations. Specifically, determining whether an action would result in jeopardy or adverse modification of critical habitat would be linked to a change in the risk of extinction. Further, a decision rule that quantitatively accounts for uncertainty, associated with both the action (e.g., fisheries) and the listed species, should be developed to assess whether the standard has been met. For example, if a proposal to substantially modify fishery operations (i.e., the action) resulted in a formal ESA Section 7 consultation, the knowledge and associated uncertainty of how the fishery could influence the sea lion prey field and subsequently affect sea lion demography would be examined and assessed relative to the extinction standard.

Third, uncertainty could be reduced by establishing a quantitative standard for the ecosystem protection provision of the Magnuson-Stevens Fishery Conservation and Management Act and the joint U.S. Fish and Wildlife Service–NOAA Fisheries policy on ecosystem considerations in developing recovery strategies for ESA listed species. Acknowledging that uncertainty and indeterminacy are fundamental characteristics of our knowledge of ecosystems, long-term monitoring of biological and climate indices is needed to improve the understanding of how natural oceanic and climate variability affect the dynamic behavior and biological composition of ecosystems. As our understanding of ecosystem dynamics improve through such monitoring, one example of how a quantitative standard for ecosystem protection could be applied to sea lions would be in assessing the potential impact of managing fisheries at the single-species level. Certainly, substantial challenges exist when undertaking fisheries management at the ecosystem level (Pikitch et al. 2004). However, data and modeling approaches exist to assess the impact of single-species fisheries management on ecosystem carrying capacity (Goodman et al. 2002).

In summary, the dramatic decline of Steller sea lions in the BSAI and GOA regions over the last 25 years has resulted in an immense research and management effort designed to promote the species' recovery. Due to limited baseline information on the ecology of sea lions and their marine ecosystem, combined with the inherent complexity and variability of both, substantial uncertainty has persisted in the development, implementation, and justification of conservation strategies. Since ESA listing of sea lions in 1990, required decisions are based on the best available data with the burden of proof favoring protection and recovery of the sea lion population. Without clear evidence that commercial fisheries do not adversely affect sea lions or their critical habitat, restrictive fishery management actions will be necessary. We have outlined four components of a robust research strategy that would substantially reduce uncertainty. In addition, we encourage management agencies to pursue recently suggested modifications to conservation policy; in particular, the development of more explicit quantitative policy standards for ESA listing should increase consistency in the implementation of conservation efforts and reduce the potential for litigation. Implementation of these research and policy recommendations could substantially increase the probability of effective conservation: precautionary actions needed for the recovery for the endangered sea lion and minimal unnecessary burden on commercial fisheries.

Acknowledgments

We thank the Steller Sea Lion Recovery Team for their numerous discussions on the diverse issues involved in determining how best to promote the recovery of sea lions. Two anonymous reviewers, Shane Capron, Lloyd Lowry, and Tim Ragen provided comments that improved earlier versions of this manuscript.

References

Benson, A.J., and A.W. Trites. 2002. Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. Fish Fish. 3:95-113.

Bickham, J.W., J.C. Patton, and T.R. Loughlin. 1996. High variability for control-region sequences in a marine mammal: Implications for conservation and biogeography of Steller sea lions (*Eumetopias jubatus*). J. Mammal. 77:95-108.

Bowen, W.D., H. Harwood, D. Goodman, and G.L. Swartzman. 2001. Review of the November 2000 Biological Opinion and Incidental Take Statement with respect to the western stock of the Steller sea lion. Final Report to the North Pacific Fishery Management Council, May, 2001. 19 pp.

Boyd, I.L. 1995. Steller sea lion research. National Marine Mammal Laboratory, Seattle, pp. 1-90.

Braham, H.W., R.D. Everitt, and D.J. Rugh. 1980. Northern sea lion decline in the eastern Aleutian Islands. J. Wildl. Manag. 44:25-33.

Calkins, D.G., and E. Goodwin. 1988. Investigation of the declining sea lion population in the Gulf of Alaska. Unpubl. Rep., Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518. 76 pp.

Calkins, D.G., E.F. Becker, and K.W. Pitcher. 1998. Reduced body size of female Steller sea lions from a declining population in the Gulf of Alaska. Mar. Mamm. Sci. 14:232-244.

Conners, M.E., P. Munro, and S. Neidetcher. 2004. Pacific cod pot studies 2002-2003. AFSC Processed Rep. 2004-04, NOAA, NMFS Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115. 64 pp.

Davis, R.W., E.A.A. Brandon, D.G. Calkins, and T.R. Loughlin. 2006. Female attendance and neonatal pup growth in Steller sea lions (*Eumetopias jubatus*). In: A.W. Trites, S.W. Atkinson, D.P. DeMaster, L.W. Fritz, T.S. Gelatt, L.D. Rea, and K.M. Wynne (eds.), Sea lions of the world. Alaska Sea Grant College Program, University of Alaska Fairbanks.

DeMaster, D.P., A.W. Trites, P. Clapham, S. Mizroch, P. Wade, R.J. Small, and J. Verhoef. 2006. The sequential megafaunal collapse hypothesis: Testing with existing data. Prog. Oceanogr.

DeMaster, D., R. Angliss, J. Cochrane, P. Mace, R. Merrick, M. Miller, S. Rumsey, B. Taylor, G. Thompson, and R. Waples. 2004. Recommendations to NOAA Fisheries: ESA listing criteria by the Quantitative Working Group, 10 June 2004. NOAA Tech. Memo. NMFS-F/SPO-67. 85 pp.

Fritz, L.W., R.C. Ferrero, and R.J. Berg. 1995. The threatened status of Steller sea lions, *Eumetopias jubatus*, under the Endangered Species Act: Effects on Alaska groundfish fisheries. Mar. Fish. Rev. 57:14-27.

Goodman, D. 2005. Adapting regulatory protection to cope with future change. In: J.E. Reynolds III, W.F. Perrin, R.R. Reeves, S. Montgomery, and T.J. Ragen (eds.), Marine mammal research: Conservation beyond crisis. Johns Hopkins University Press, Baltimore, pp. 165-176.

Goodman, D., M. Mangel, G. Parkes, T. Quinn, V. Restrepo, T. Smith, and K. Stokes. 2002. Scientific review of the harvest strategy currently used in the BSAI and GOA groundfish fishery management plans. North Pacific Fishery Management Council, 605 West 4th Ave., Suite 306, Anchorage, AK 99501.

Hennen, D.R. 2006. Associations between the Steller sea ion decline and the Gulf of Alaska and Bering Sea commercial fisheries. Ecol. Appl. 16.

Holmes, E., and A.E. York. 2003. Using age structure to detect impacts on threatened populations: A case study using Steller sea lions. Conserv. Biol. 17:1794-1806.

Loughlin, T.R. 1997. Using the phylogeographic method to identify Steller sea lion stocks. In: A.E. Dizon, S.J. Chivers, and W.F. Perrin (eds.), Molecular genetics of marine mammals. Society for Marine Mammalogy Spec. Publ. 3:159-171.

Loughlin, T.R. 1998. The Steller sea lion: A declining species. Biosphere Conservation 1(2):91-98.

Loughlin, T., and T. Mattson. 1998. Panel recommendations from an experimental design workshop on testing the efficacy of Steller sea lion no-trawl fishery exclusion zones in Alaska, 6-7 May 1997. NOAA, NMFS, Alaska Fisheries Science Center, Seattle. 32 pp.

Loughlin, T.R., and A.E. York. 2000. An accounting of the sources of Steller sea lion, *Eumetopias jubatus*, mortality. Mar. Fish. Rev. 62(4):40-45.

Loughlin, T.R., D.J. Rugh, and C.H. Fiscus. 1984. Northern sea lion distribution and abundance: 1956-80. J. Wildl. Manag. 48:729-740.

Loughlin, T.R., A.S. Perlov, and V.A. Vladimirov. 1992. Range-wide survey and estimation of total number of Steller sea lions in 1989. Mar. Mamm. Sci. 8:220-239.

Loughlin, T.R., J.T. Sterling, R.L. Merrick, J.L. Sease, and A.E. York. 2003. Diving behavior of immature Steller sea lions (*Eumetopias jubatus*). Fish. Bull. U.S. 101(3):566-582.

Merrick, R.L., and T.R. Loughlin. 1997. Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. Can. J. Zool. 75:776-786.

Merrick, R.L., M.K. Chumbley, and G.V. Byrd. 1997. Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: A potential relationship. Can. J. Fish. Aquat. Sci. 54(6):1342-1348.

Mizroch, S.A., and D.W. Rice. 2006. Have north pacific killer whales switched prey species in response to depletion of the great whale populations? Mar. Ecol. Prog. Ser.

NMFS. 2000. Section 7 consultation on the authorization of the Bering Sea and Aleutian Islands groundfish fishery under the BSAI FMP and the authorization of the Gulf of Alaska groundfish fishery under the GOA FMP. NOAA Fisheries, Office of Protected Resources, Nov. 30, 2000.

NMFS. 2001. Steller Sea Lion Protection Measures Final Supplemental Environmental Impact Statement. Implemented under the Fishery Management Plans for the Groundfish of the GOA and the Groundfish of the BSAI. 2001. NMFS, Alaska Region, P.O. Box 21668, Juneau, AK 99801.

NRC. 2003. Decline of the Steller sea lion in Alaskan waters; untangling food webs and fishing nets. National Research Council, National Academy Press, Washington, D.C. 184 pp.

Pikitch, E.K., C. Santora, E.A. Babcock, A. Bakun, R. Bonfil, D.O. Conover, P. Dayton, P. Doukakis, D. Fluharty, B. Heneman, E.D. Houde, J. Link, P.A. Livingston, M. Mangel, M.K. McAllister, J. Pope, and K.J. Sainsbury. 2004. Ecosystem-based fisheries management. Science 305:346-347.

Punt, A.E., and G. Fay. 2006. Can experimental manipulation be used to determine the cause of the decline of the western stock of Steller sea lions (*Eumetopias jubatus*)? In: A.W. Trites, S.K. Atkinson, D.P. DeMaster, L.W. Fritz, T.S. Gelatt, L.D. Rea, and K.M. Wynne (eds.), Sea lions of the world. Alaska Sea Grant College Program, University of Alaska Fairbanks.

Rusin, J.D. 2002. Management of the western Alaska Steller sea lion, *Eumetopias jubatus*, under the Endangered Species Act: Evolution of interagency consultation and impacts on Alaska groundfish fisheries. Master's thesis, University of Washington. 117 pp.

Sease, J.L., and R.L. Merrick. 1997. Status and population trends of Steller sea lions. In: G. Stone, J. Goebel, and S. Webster (eds.), Pinniped populations, eastern North Pacific: Status, trends and issues. A symposium of the 127th Annual Meeting of the American Fisheries Society. New England Aquarium, Conservation Department, Central Wharf, Boston, MA 02110, pp. 22-30.

Springer, A.M., J.A. Estes, G.B. van Vliet, T.M. Williams, D.F. Doak, E.M. Danner, K.A. Forney, and B. Pfister. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? PNAS 100:12223-12228.

Trites, A.W., and C.P. Donnelly. 2003. The decline of Steller sea lions in Alaska: A review of the nutritional stress hypothesis. Mamm. Rev. 33:3-28.

Trites, A.W., and P.A. Larkin. 1996. Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: How many were there? Aquat. Mamm. 22:153-166.

Trites, A.W., V.B. Deecke, E.J. Gregr, J.K.B. Ford, and P.F. Olesiuk. 2006. Killer whales, whaling and sequential megafaunal collapse in the North Pacific: A comparative analysis of the dynamics of marine mammals in Alaska and British Columbia following commercial whaling. Mar. Mamm. Sci. 22.

Williams, T.M., J.A. Estes, D.F. Doak, and A.M. Springer. 2004. Killer appetites: Assessing the role of predators in ecological communities. Ecology 85:3373-3384.

Wilson, C.D., A.B. Hollowed, M. Shima, P. Walline, and S. Stienessen. 2003. Interactions between commercial fishing and walleye pollock. Alaska Fishery Research Bulletin 10(1):61-77.

York, A. 1994. The population dynamics of the northern sea lions, 1975-85. Mar. Mamm. Sci. 10:38-51.

Avoidance of Artificial Stimuli by the Steller Sea Lion

Kohji Iida, Tae-Geon Park, Tohru Mukai, and Shoji Kotani
Hokkaido University, Graduate School of Fisheries Sciences, Hakodate, Hokkaido, Japan

Abstract

Every winter, hundreds of Steller sea lions (*Eumetopias jubatus*) visit the coast of Hokkaido, northern Japan. Their foraging behavior destroys fishing gear, which is a serious problem. In order to find a solution that allows the coexistence of both Steller sea lions and fishing activities, attempts have been made to control their behavior using acoustical and optical stimuli. This study examined methods of repelling Steller sea lions from fishery gear using aerial and underwater sounds and flashing lights. In this study, we (1) observed and analyzed the relationship between the calls and the behavior of Steller sea lions; (2) searched for effective stimuli for repelling Steller sea lions; (3) developed a displacing system that generates artificial stimuli to repel Steller sea lions using sounds and lights; and (4) tested the displacing system.

Experiments were conducted at a Steller sea lion haul-out located on the west coast of Hokkaido, on the Sea of Japan. Steller sea lions were exposed to acoustical and optical stimuli consisting of repeated intermittent sounds with or without flashing lights. This system was controlled from the edge of a cliff, and the reactions of Steller sea lions were monitored using a video camera and microphone.

Most of the Steller sea lions responded to the stimuli by vocalizing toward the source, while moving away and jumping in the water. The most effective stimuli for repelling Steller sea lions were aerial sounds, underwater sounds, and flashing lights in that order.

Introduction

Every winter, a few hundred Steller sea lions (*Eumetopias jubatus*) from Sakhalin and the northern Kuril Islands visit the coast of Hokkaido, northern Japan (Davies 1958, Scheffer 1958, Peterson and Bartholomew 1967,

Figure 1. Steller sea lions hauled out on reefs near Cape Ofuyu in Hokkaido, Japan.

Schusterman 1981, King 1983, Loughlin et al. 1984). They land on reefs in coastal areas with steep cliffs, and forage for food from these bases (Fig. 1). There are also many active coastal fisheries along this coast, including set net and gillnet fisheries that catch cod, pollock, and greenlings. However, fisheries resources around this area have been decreasing for decades.

The areas of Steller sea lion and fishery activity overlap. Steller sea lions not only forage for food in the fishing grounds, but also break nets while foraging. The estimated damage to the fisheries due to Steller sea lions exceeds US $10 million annually. In order to reduce fishery damage by Steller sea lions, while allowing their coexistence in coastal waters, we tested methods to repel Steller sea lions from fishing gear using acoustical and optical stimuli.

Steller sea lions have very good hearing, and can identify the noise emitted by hunting boats (Moore and Schusterman 1976, Schusterman 1981, Richardson et al. 1995, Akamatsu et al. 1996, Kastak and Schusterman 1998, Schusterman et al. 2000). In order to drive Steller sea lions away from fishing gear, a displacing system that emits sounds and lights was developed. Prior to the field experiments, reactions of captive Steller sea lions in an aquarium to sound and light stimuli were observed.

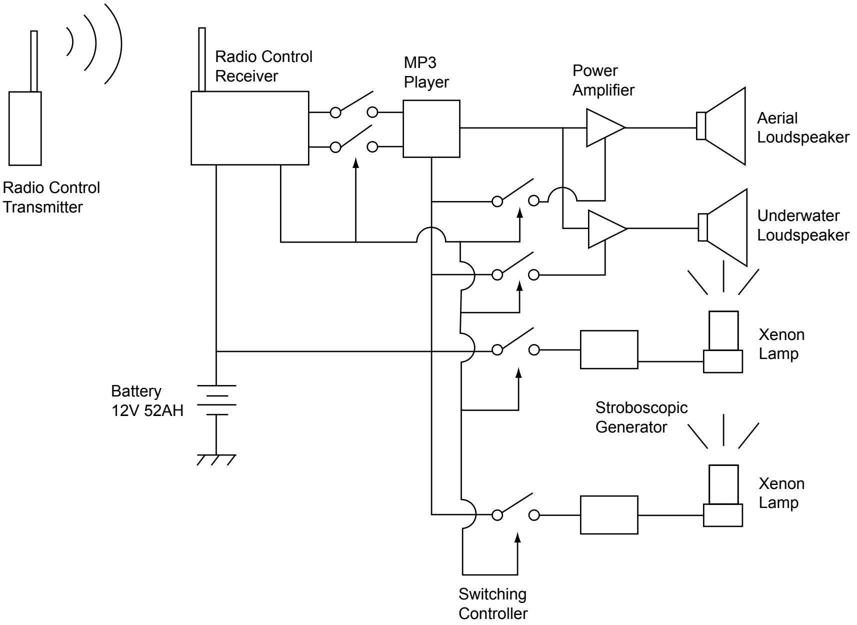


Figure 2. Remote controlled displacing aerial and underwater sounds and flashing stroboscopic light generators.

Reactions of wild Steller sea lions to the displacing system were investigated.

Materials and methods

Displacing sound generator and characteristics of the sound

The system was intended to control the behavior of animals using multiple stimuli, combining aerial and underwater sounds and a flashing stroboscopic light. It was designed to emit high-intensity sounds audible to the animals over a wide frequency range, while not damaging either the operators or the animals, or affecting the environment. Loudness of the sound is the same level as the sea lion's roar, and the sound stimuli are emitted intermittently. The sound generator consisted of a sound source, an amplifier, an antenna, an underwater loudspeaker, and a remote control system (Fig. 2). The sounds used consisted of engine noises generated by a fishing boat, the sounds of explosions generated by firecrackers, and digitally synthesized sounds. The emitted sound was audible and had a major component at frequencies less than 1,000 Hz. A 30 W amplifier was

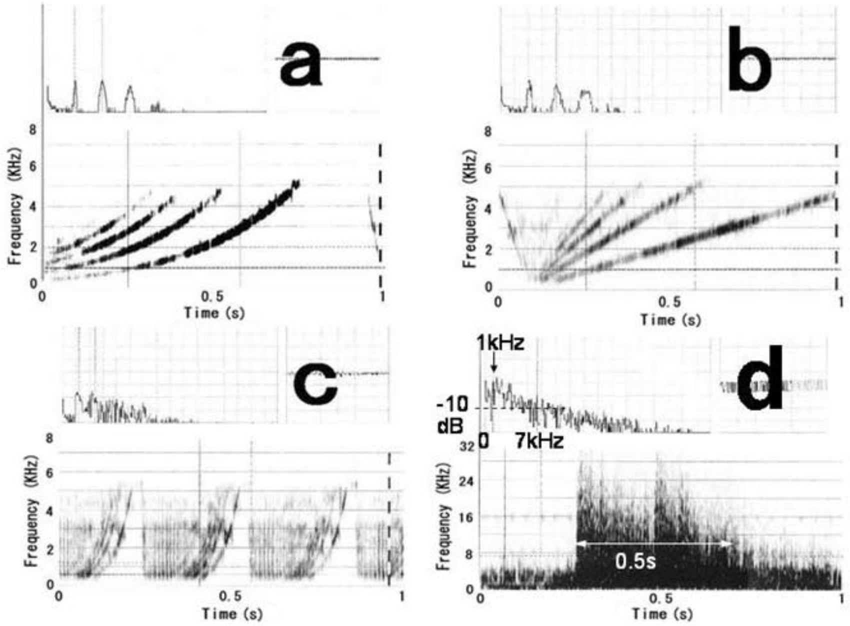


Figure 3. Sonograms of artificial sound stimuli used for displacing Steller sea lions: (a) logarithmic frequency sweep sound, (b) linear frequency sweep sound, (c) successive logarithmic frequency sweep sound, and (d) hammering sound.

used to obtain a sufficiently high sound pressure within a range of 100 m. The digitally synthesized displacing sounds included three types of chirp sound that swept the frequency range from 100 to 1,000 Hz, which included the frequencies audible to Steller sea lions. The waveforms, frequency spectra, and sonograms are shown in Fig. 3a,b,c.

Displacing light generator and characteristics of the flashing light

A flashing stroboscopic light was tried as a stimulus for displacing Steller sea lions. A dispelling light generator was designed as shown in Fig. 4. A xenon lamp was used as the light source in order to obtain an intense light covering a wide area. The xenon lamp was flashed intermittently so as not to decrease its dispelling effects. Since the energy consumption of the battery depended on the frequency of flashes, one emission consisted of 30 flashes at 1 second intervals. A single emission requires a power of 235 Joules (470 μF, 1,000 V), thus the lamp could emit 9,700 flashes when using a 65AH battery.

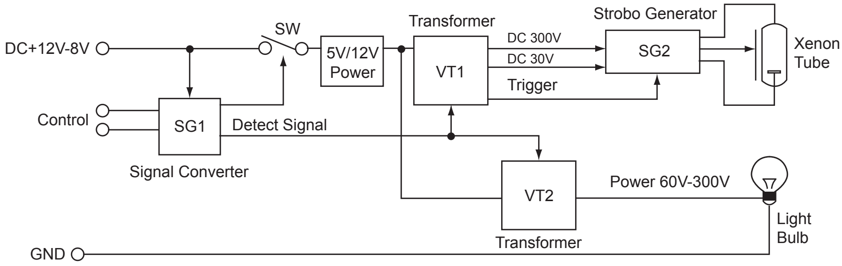


Figure 4. Block diagram of displacing light generator.

Observations of the reactions of captive Steller sea lions to artificial stimuli

Prior to the experiment to displace wild Steller sea lions by artificial stimuli, the reactions of captive Steller sea lions to the artificial sounds and lights were observed on three animals kept at Muroran Aquarium. The reactions of animals were observed using a video camera and the artificial sound was analyzed using a sonograph. A video camera and microphone were placed outside the cage facing the pool, and the behavior of the Steller sea lions was recorded using a videocassette recorder (VCR) placed in a shed 30 m from the pool. The artificial stimuli consisted of hammering sounds and a flashing stroboscopic light. Hammering sounds were played in the pool for a few hours, while the light was flashed intermittently 50 times at a frequency of 1 to 3 times per minute. A sonogram of the hammering sound is shown in Fig. 3d.

Observing the avoidance behavior of wild Steller sea lions in response to displacing sounds and flashing lights

In order to observe the avoidance behavior of wild Steller sea lions in response to the displacing sound and flashing light, experiments using a sound generator and a xenon lamp were conducted in the early spring of 2003 and 2004 on a reef near Cape Ofuyu, where wild Steller sea lions land.

A sound generator and xenon lamp were placed on the reef facing the Steller sea lion haul-out, and these were operated by radio remote control from a cliff 300 m from the reef (Fig. 5). In order to monitor the reaction to the stimuli at close range, a video camera and microphone were placed on the reef and continuous recordings with a VCR were made. An underwater loudspeaker was submerged near the reef at a depth of 3 m. An antenna for receiving radio control signals was built on the reef. An antenna for transmitting the radio control signals and a video camera

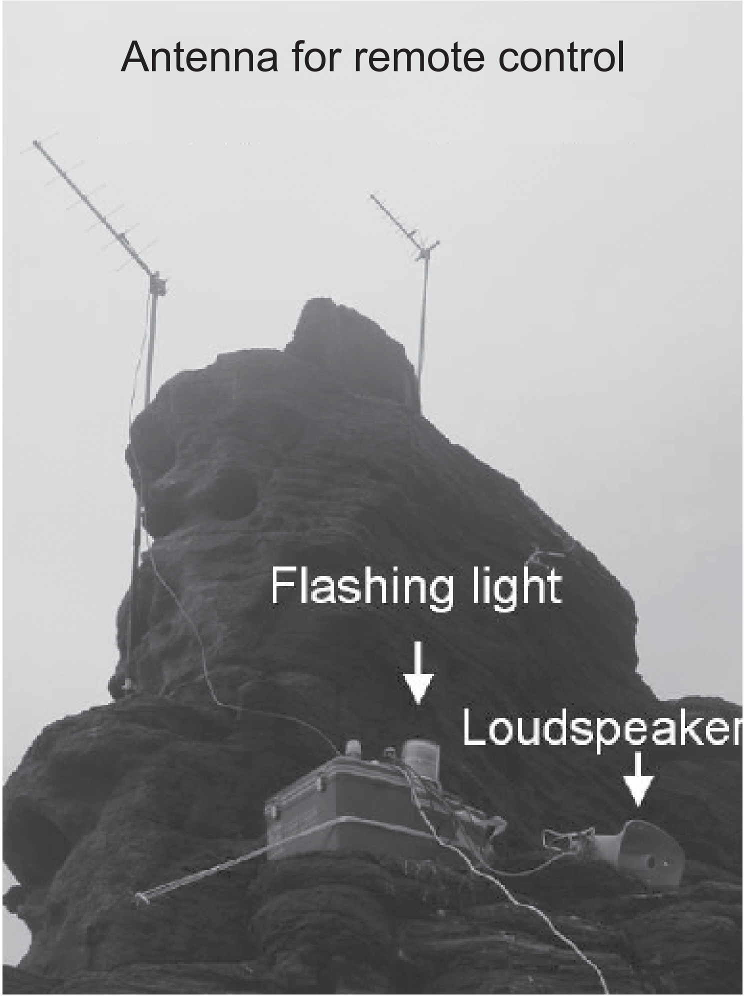


Figure 5. **Displacing system placed on the top of the reef. The system was operated by radio remote control from a cliff 300 m from the reef.**

equipped with a telephoto lens were placed on the cliff to observe the entire reef area, and the behavior of Steller sea lions was recorded using another VCR.

Results

Acoustical behavior and the reaction of captive Steller sea lions to sound and light

Ordinarily, the captive Steller sea lions wake around sunrise, are active in the pool during the day, and sleep in the pool after sunset. They enter the water or holding room in cold weather and bask at poolside in warm weather. They rest after meals and increase their roaring before a meal, as they have been conditioned to the behavior of their keepers.

The relationship between calls and behavior were investigated by analyzing the calls emitted in response to sound stimuli. The calls of the three captive Steller sea lions were classified into three categories: “acknowledge calls,” “communication calls,” and “wheedling calls” (Evance 1966, Park et al. 2006). The acoustic characteristics of these sounds are shown in Table 1.

The adult pair of sea lions conducted a roaring duet to request food that increased until they were fed. Moreover, their three-year-old male pup, which was kept in a small pool 50 m from the main pool, frequently roared with them from sunrise until the morning meal. In response to a single artificial hammering sound, they initially showed an aversive reaction, with roaring. With successive hammering sounds, they showed avoidance behavior, moving away from the sound source. According to the sonogram (Fig. 3d), the hammering sound lasted for 0.5 s and had a peak frequency at 1 kHz with a band width about 7 kHz at –10 dB.

In response to a flashing xenon lamp, the Steller sea lions showed an “acknowledge reaction,” in which they stared at the light source, and an “aversive reaction,” in which they roared briefly. Generally, they noticed the onset of the stimulus and stared at the lamp, but they soon lost interest in successive light flashes (Fig. 6). Moreover, they ignored all light stimuli at night.

Avoidance of the displacing sound and light stimuli by wild Steller sea lions

Reaction to the stroboscopic light

Three experiments in which wild Steller sea lions were exposed to lights from a xenon lamp were conducted in April 2003. Flashing lights were emitted for 30 minutes at a frequency of 80 times per second. While the Steller sea lions showed an acknowledge reaction in 2 trials, the light was ignored in the another two trials (upper rows in Table 2).

Table 1. Acoustic characteristics of calls made by captive Steller sea lions for each sound category (Park et al. 2006).

				Dominant F1 (Hz)			Fundamental F0 (Hz)			Duration T (s)			Density PRR (Hz)		
Sex	Age	Weight (kg)	Call category	N	Ave.	S.D.	N	Ave.	S.D.	N	Ave.	S.D.	N	Ave.	S.D.
Male	23	>850	Communication	62	372	2.56	62	35	0.32	62	1.63	0.04	62	39	0.84
			Wheedling	72	357	4.30	72	26	0.71	72	1.57	0.09	72	33	0.86
Female	18	250	Communication	98	469	4.74	98	53	0.49	98	1.78	0.05	98	56	0.44
			Acknowledge	78	472	3.70	78	54	0.35	78	1.14	0.04	78	53	0.33
			Threat	26	406	10.21	26	28	1.82	26	1.03	0.09	26	53	1.74
Male pup	4	150	Communication	30	626	4.33	30	76	3.06	30	1.50	0.08	30	97	1.61

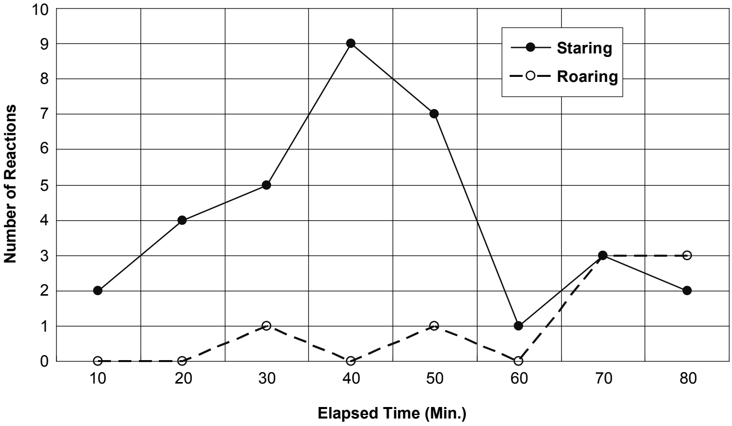


Figure 6. Changes in reactions to flashing lights for captive Steller sea lions. An acknowledge reaction (staring) and an aversive reaction (roaring) were observed.

Reaction to an aerial displacing sound

Displacing experiments using aerial sounds were conducted at Cape Ofuyu three times in April 2003, and once in March 2004. The sound stimuli consisted of a single chirp sound and successive chirp sounds that repeated the single chirp sound for 1-2 minutes. Figure 7 shows the avoidance behavior of wild Steller sea lions to the aerial displacing sound. Wild Steller sea lions near the sound source showed (a) an acknowledge reaction to the single chirp sound, (b) escaping behavior consisting of moving away from the source, and last (c,d) diving into the water in response to successive chirp sounds. In addition, a duet reaction to the sound stimuli, a searching reaction for the sound source, and an aversion reaction to the sound source were observed (middle rows in Table 2).

Generally, wild Steller sea lions appeared cautious when exposed to novel artificial stimuli, such as chirp sounds. Animals near the sound source abruptly initiated avoidance behavior. When combined with a flashing light, the effect was compounded. In 2003, 2 of 5 landed animals dove into the water, and 26 of 37 landed animals did the same in 2004.

Reaction to an underwater displacing sound

A displacing experiment using underwater sound was conducted at Cape Ofuyu in April 2003. A displacing sound was emitted by an underwater loudspeaker at a depth of 3 m. In 28 trials, wild Steller sea lions showed avoidance behavior in response to the sound, including 9 "landing reactions" in which swimming animals abruptly landed on the reef, 5

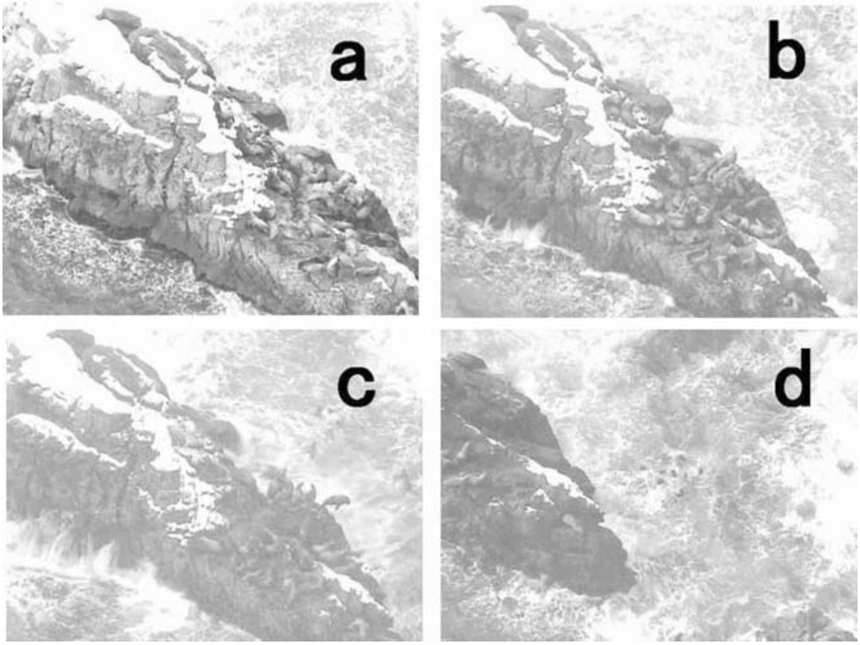


Figure 7. **Escaping behavior to the aerial displacing sound for wild Steller sea lions on the reef. Sea lions near the sound source showed (a) an acknowledge reaction to the single chirp sound, (b) escaping behavior consisting of moving away from the source, and lastly (c,d) diving into the water in response to successive chirp sounds.**

"swimming reactions" in which animals in the water swam to escape the sound source, and 10 "diving reactions" in which floating animals dove into the water abruptly (lower rows in Table 2). These results showed that animals both diving and swimming on the surface with their head submerged could hear the underwater sound. The degree of avoidance behavior appeared to be higher in the "landing reaction" than in the "swimming reaction," whereas the "diving reaction" was thought to be a scouting behavior.

Discussion

Detecting wild Steller sea lions by call analysis

As the dominant frequency of the call of Steller sea lions ranges from 200 to 500 Hz (frequencies that propagate well on the sea surface) and the intensity of the call is high (Thomas and Kuechle 1982), it is possible to

Table 2. **Reactions of groups of Steller sea lions at Cape Ofuyu to 149 experimental attempts to displace them using flashing lights (n = 4), aerial sounds (n = 92), underwater sound (n = 28) and a combination of aerial and underwater sounds (n = 25). Documented avoidance behaviors included vocalizing (negative), staring at the source, searching for the source, searching and aversion (duet), moving away from the source (escape), jumping into the water, jumping onto land, and diving.**

		Steller sea lion behavioral reactions							
Stimuli	Date	Negative	Stare	Search	Duet	Escape	Jump	Land	Dive
Flashing light	2003.4.13		2						
	2003.4.14	1							
	2003.4.15	1							
Aerial sound	2003.4.13	5	8	1	5	1	1		
	2003.4.14		1	1	1	2	1		
	2003.4.15	7	3	12	6				
	2004.3.10	0	2	6		3	26		
Underwater sound	2003.4.13	1				3		4	5
	2003.4.14	3				2			
	2003.4.15							5	5
Combination	2003.4.[a]	3	3	9	7	2	1		

[a] 3 days total.

detect the calls of animals up to a few hundred meters away. Therefore, by monitoring the sounds around reefs and analyzing the frequency spectra of the sounds, it was possible to anticipate the appearance of wild Steller sea lions. The accuracy of detection could be improved with the use of multiple band pass filters that only pass the harmonics of the Steller sea lion calls.

Acoustical behavior of Steller sea lions

The relationship between the call and the behavior of captive Steller sea lions in an aquarium was easy to observe. By contrast, a variety of behavioral patterns, including communication among families and groups, foraging behavior, and quarrelling, were observed in wild Steller sea lions. By analyzing the calls using a microphone placed where wild Steller sea lions landed, it was possible to distinguish males from females and juveniles from adults (K. Iida et al., Hokkaido University, 2004, pers. comm.).

Avoidance of artificial stimuli by Steller sea lions

Direct avoidance was greatest with the aerial sound and increased with a flashing light, especially at twilight and night. Underwater sound was less effective at triggering avoidance because the sea lions do not hear as well underwater. Therefore, a signal that can be detected from a distance should be used. Multiple stimuli combining sound and light were useful. The main obstacle to applying this method in practice is the "adaptation effect," which is often observed with displacing systems for wild animals, such as crows and wild boars. Adaptation typically follows initial avoidance when the possible threat posed by an artificial stimulus does not eventuate. Therefore, any artificial stimuli used to repel wild Steller sea lions from fishing facilities should be reinforced by association with a tangible threat.

Problems with the practical application of a displacing system for wild Steller sea lions

Our results showed that artificial stimuli involving both aerial and underwater sounds associated with punishment were effective for displacing wild Steller sea lions from the vicinity of fishing gear. Any practical displacing system should include a detecting system to predict their landing and a displacing system with a punishment, to teach them to avoid the stimuli after landing, as shown in Fig. 8.

We recommend that a sanctuary for wild Steller sea lions be established in the coastal area, to which they can be led by avoidance of the displacing systems. In addition, as the Steller sea lions that migrate to the coast of Hokkaido every winter are from the same populations in the north, a system based on learning will improve the avoidance effect, thereby decreasing damage to the fisheries.

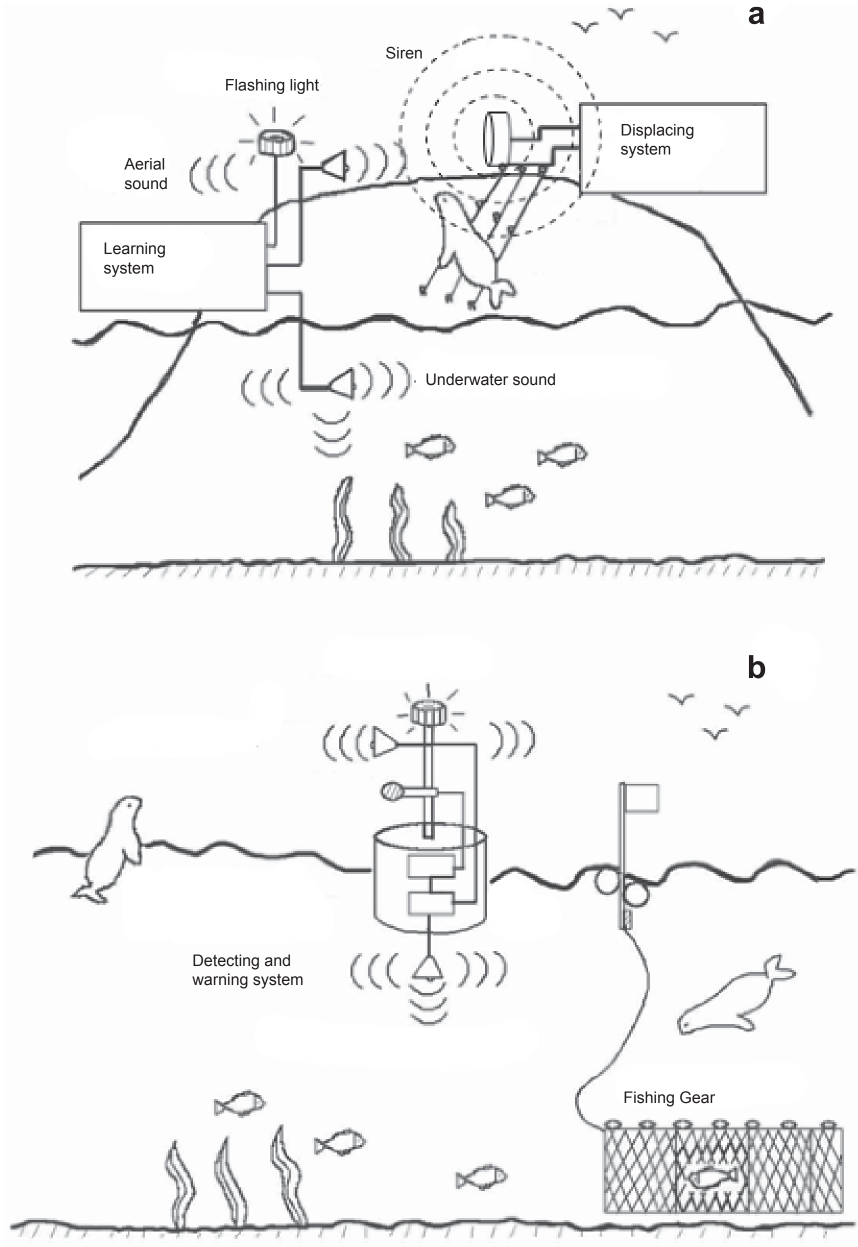


Figure 8. Concept of practical use of artificial stimuli for displacing wild Steller sea lions from the vicinity of fishing gear. The system includes (a) a learning and displacing system, and (b) a detecting and warning system, placed near fishing gear.

Acknowledgments

The authors thank Emeritus Professor Haruo Ogi of Hokkaido University, who motivated us to begin this research. We also thank Dr. Donhyug Kang, Dr. Kyounghoon Lee, and Mr. Takuma Takayama for their assistance with the experiments and data analysis. This research was partially supported by the Department of Fisheries and Forestry, Hokkaido Government.

References

Akamatsu, T., K. Nakamura, H. Nitto, and M. Watabe. 1996. Effects of underwater sounds on escape behavior of Steller sea lions. Fish. Sci. 62(4):503-510.

Davies, J.L. 1958. The Pinnipedia: An essay in zoogeography. Geogr. Rev. 48:1817-1832.

Evance, W.E. 1966. Vocalization among marine mammals. In: W.N. Tavolga (ed.), Marine bio-acoustics. Pergamon Press, London, pp.159-186.

Kastak, D., and R.J. Schusterman, 1998. Low-frequency amphibious hearing in pinnipeds: Methods, measurements, noise, and ecology. J. Acoust. Soc. Am. 103:2216-2228.

King, J.E. 1983. Seals of the world. Oxford University Press, Oxford. 240 pp.

Loughlin, T.R., D.J. Rugh, and C.H. Fiscus. 1984. Northern sea lion distribution and abundance: 1956-80. J. Wildl. Manag. 48:719-740.

Moore, P.W.B., and R.J. Schusterman. 1976. Discrimination of pure-tone intensities by the California sea lion. J. Acoust. Soc. Am. 60:1405-1407.

Park, T.G., K. Iida, and T. Mukai. 2006. Characteristics of vocalizations in Steller sea lions. In: A.W. Trites, S.K. Atkinson, D.P. DeMaster, L.W. Fritz, T.S. Gelatt, L.D. Rea, and K.M. Wynne (eds.), Sea lions of the world. Alaska Sea Grant College Program, University of Alaska Fairbanks.

Peterson, R.S., and G.A. Bartholomew. 1967. The natural history and behavior of the California sea lion. American Society of Mammalogy Special Publication No.1.

Richardson, W.J., C.R. Greene Jr., C.I. Malme, and D.H. Thomson.1995. Marine mammals and noise. Academic Press, San Diego.

Scheffer, V.B. 1958. Seals, sea lions, and walruses. A review of the Pinnipedia. Stanford University Press, Palo Alto, California. 179 pp.

Schusterman, R.J. 1981. Steller sea lion, *Eumetopias jubatus*. In: S.H. Ridgway and R.J. Harrison (eds.), Handbook of marine mammals. Vol. 1. Walrus, sea lions, fur seals and sea otters. Academic Press, New York, pp. 119-141.

Schusterman, R.J., D. Kastak, D.H. Levenson, C.J. Reichmuth, and E.L. Southall. 2000. Why pinnipeds don't echolocate. J. Acoust. Soc. Am. 107:2256-2264.

Thomas, J.A., and V.B. Kuechle. 1982. Quantitative analysis of Weddell seal (*Leptonychotes weddelli*) underwater vocalizations at McMurdo Sound, Antarctica. J. Acoust. Soc. Am. 72(6):1730-1738.

Characteristics of Vocalizations in Steller Sea Lions

Tae-Geon Park, Kohji Iida, and Tohru Mukai
Hokkaido University, Graduate School of Fisheries Sciences, Hakodate, Hokkaido, Japan

Abstract

We investigated the acoustics of Steller sea lion (*Eumetopias jubatus*) calls in wild individuals hauled out on shore reefs off the west coast of Hokkaido, northern Japan, and in captive sea lions at an aquarium using video camera observations. Steller sea lion calls were classified as “communication,” “threat,” “wheedling,” and “acknowledge” according to associated behaviors. Classified calls were analyzed by means of sonograms for formant frequency (F_1), sound duration (T), and pitch pattern. All sounds emitted by males were lower in formant frequency than those of females, while sounds made by wild animals were lower than those of captive animals. Sounds by males were also longer in duration than those by females, while those made by wild animals were shorter than those by captive ones. Pitch of “communication” calls was a long flat pattern type, “threat” was a short descending type, and “wheedling” was a short ascending type for wild animals and a short wave-like type for the captives. The characteristics of pitch patterns of wild and captive animals suggest that the calls of Steller sea lions are for communication.

Introduction

Steller sea lions are distributed along the North Pacific coast and into the Okhotsk and Bering seas. Between 300 and 500 Steller sea lions migrate annually from the Kamchatka Peninsula and Kuril Islands to the western coast of Hokkaido in northern Japan from November to April (Davies 1958, Scheffer 1958, Peterson and Bartholomew 1967, Schusterman 1981, King 1983, Loughlin et al. 1984). In the long distance migration from the Okhotsk Sea to Hokkaido, roaring sounds of sea lions may have an important role in navigation and communicating with each other. The damage caused by Steller sea lions to the fishing industry of Hokkaido has resulted in studies of migration and breeding areas. However, a study on vocal communication and the acoustic characteristics of calls has not been previously done.

Materials and methods

Data acquisition

The experiments were carried out with Steller sea lions at the Muroran Municipal Aquarium, and with wild sea lions at a winter haul-out on reefs near Cape Ofuyu along the western coast of Hokkaido, northern Japan.

Three captive Steller sea lions (a 3- and a 23-year-old male, and an 18-year-old female) were recorded day and night with video cameras (TC-D5M, Sony, Japan) set atop a fence surrounding a swimming pool at the aquarium (November 1-30, 2001). The entire pool area was recorded from approximately 20 m, which did not affect the sea lions' behaviors. Roaring sounds were recorded simultaneously using a microphone built into the video camera.

Calls and behaviors of 42-66 wild sea lions that migrated to the haul-out near Cape Ofuyu were recorded for five days (April 12-16, 2003). The video camera and a microphone recorded behaviors and vocalizations of the sea lions from sunrise to sunset.

The calls of captive and wild Steller sea lions were analyzed using an oscilloscope, FFT analyzer, and digital sonograph (Kay model DSP Sona-Graph 5500), and were compared with their behaviors recorded on videotape.

We catalogued 185 calls from three captive sea lions in 2001, and 303 calls from wild sea lions in 2003.

Classification of calls

According to activities observed in captive Steller sea lions, each individual had specific calls that corresponded to specific behaviors. These included "communication" calls emitted to communicate with other sea lions, "threat" calls emitted to fight for or defend territory, "wheedling" calls emitted during socialization or when eating prey, and "acknowledge" calls emitted in response to other sea lions (Fig. 1). These specific calls were also used to distinguish vocalizations of wild sea lions. Unfortunately, it was difficult to accurately classify the activities of wild individuals due to various environmental factors. In particular, the large numbers of sea lions at the haul-out made it almost impossible to identify individuals, as was done for captive sea lions. The characteristics of calls were classified based on the above four call types related to behaviors of captive sea lions. Three types of calls were classified (communication, threat, and wheedling) and examined in relation to the behaviors of the wild sea lions.

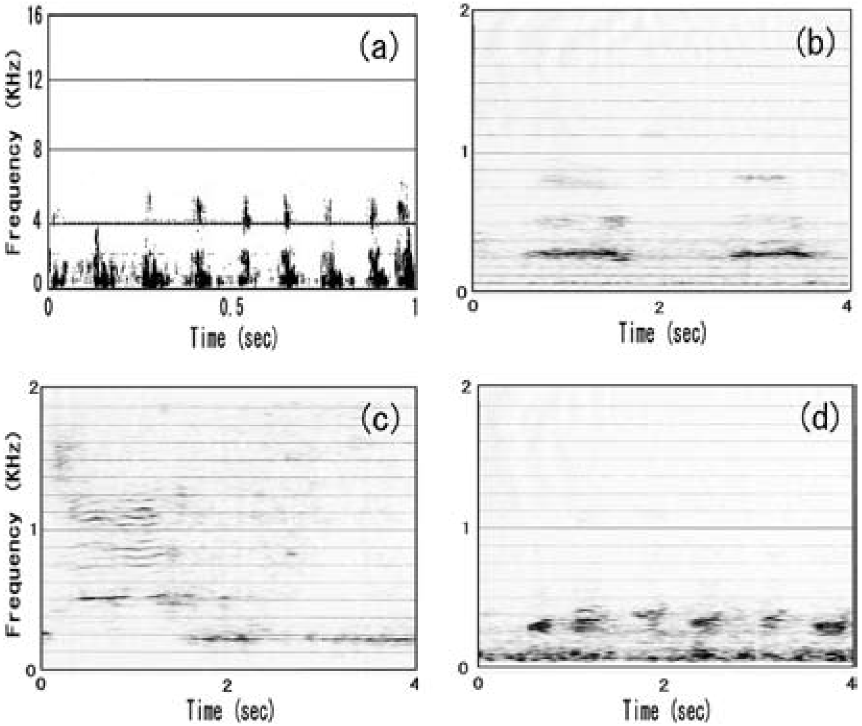


Figure 1. Vocalization classification by Steller sea lion behaviors: (a) "wheedling" sound in captive male, (b) "communication" sound in wild male, (c) "acknowledge" sound in captive female, and (d) "threat" sound in wild male.

We analyzed and classified the acoustical characteristics for wild (three types) and captive sea lions (four types) according to formant frequency (F_1), sound duration (T), and pitch pattern of the vocalizations.

Results

Formant frequency (F_1)

The F_1 of "communication," "wheedling," and "threat" calls for females was generally higher than those for males (Fig. 2). The F_1 of the "communication" sound of females was higher than that of males for both wild and captive sea lions. The F_1 of "wheedling" and "threat" sounds of wild females were higher than those of wild males. The F_1 of wild sea lions was lower than that of captive ones. The F_1s of the "threat" sound for males and females were similar.

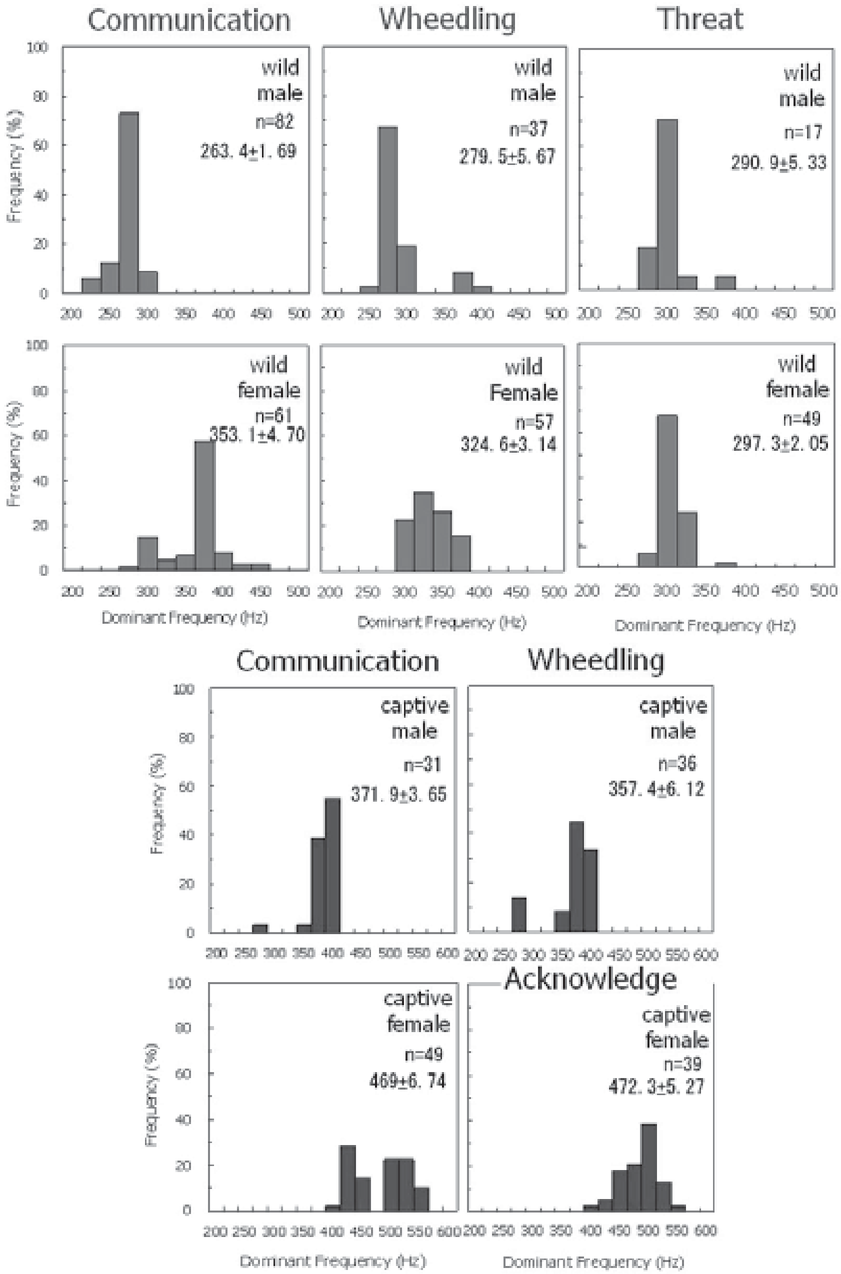


Figure 2. Comparison of formant frequency between males and females for wild and captive Steller sea lions.

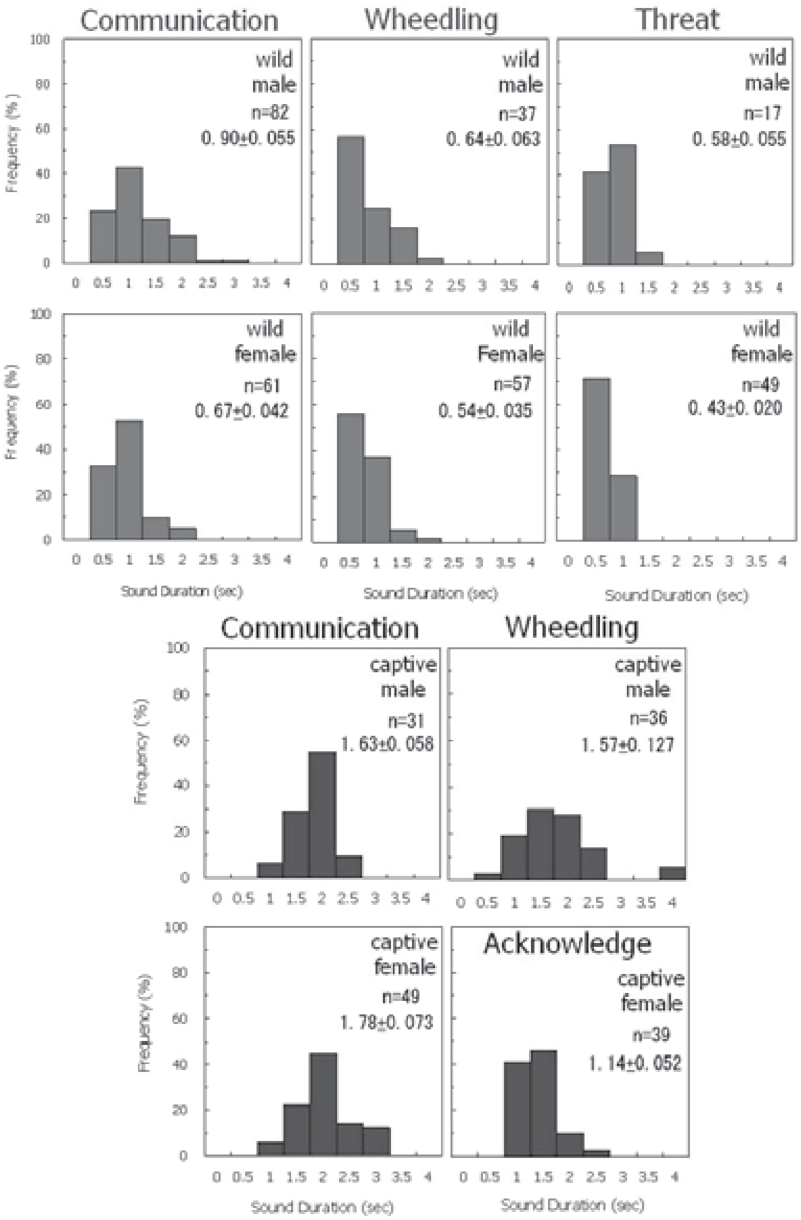


Figure 3. Comparison of sound duration between males and females for wild and captive Steller sea lions.

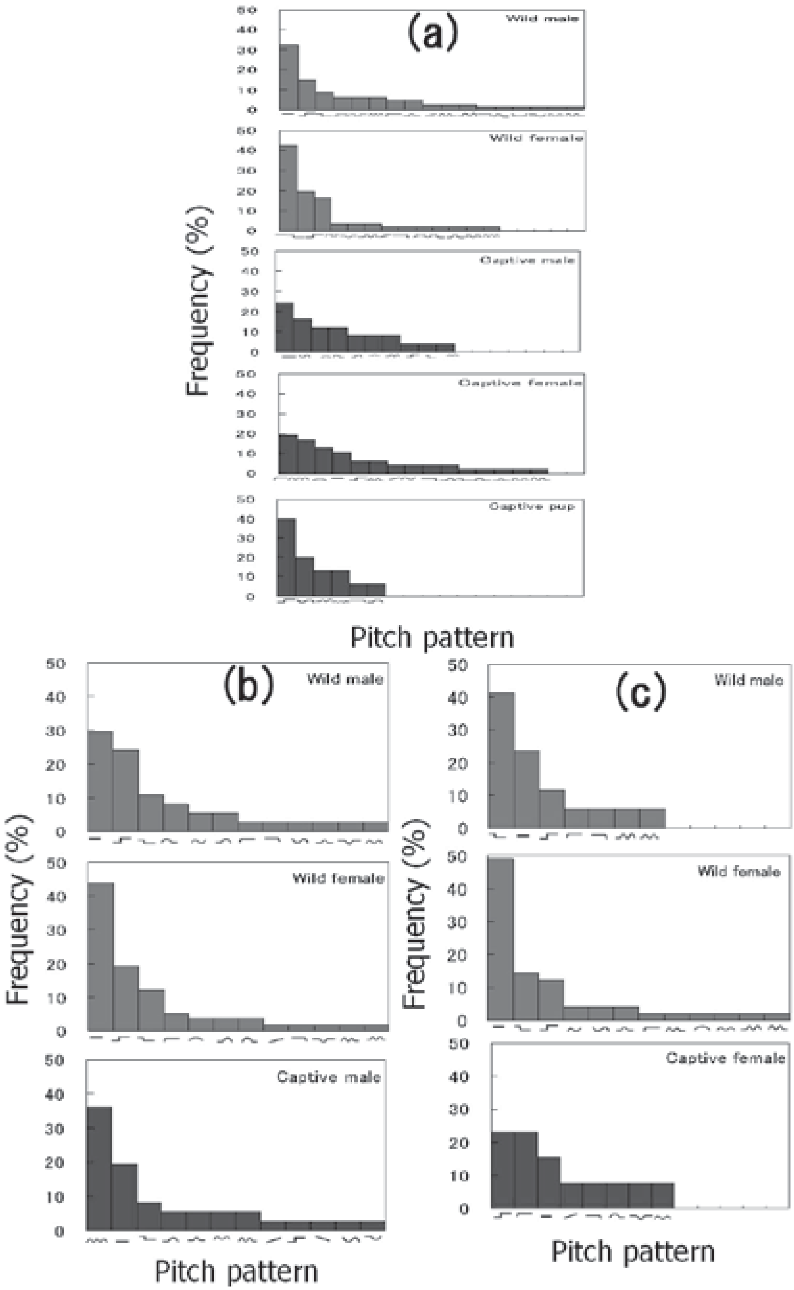
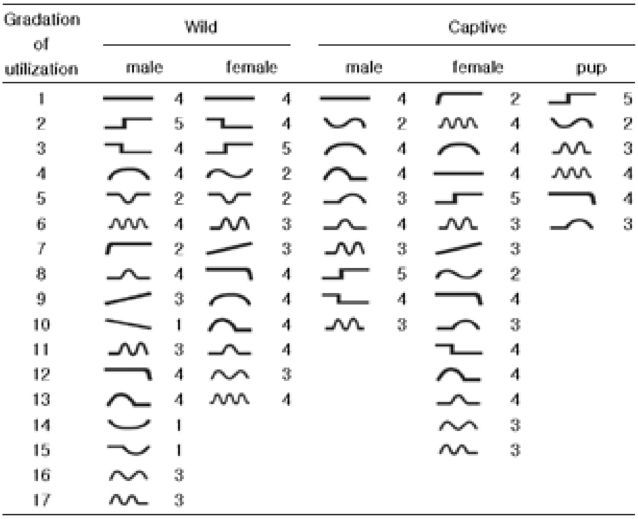


Figure 4. Pitch pattern distributions of (a) "communication" sound, (b) "wheedling" sound, and (c) "threat" sound, for Steller sea lions.

Table 1. Pitch pattern distributions of "communication" sound for Steller sea lions. The number is a frequency that the Steller sea lions used.



Gradation of utilization	Wild				Captive					
	male		female		male		female		pup	
1		4		4		4		2		5
2		5		4		2		4		2
3		4		5		4		4		3
4		4		2		4		4		4
5		2		2		3		5		4
6		4		3		4		3		3
7		2		3		3		3		
8		4		4		5		2		
9		3		4		4		4		
10		1		4		3		3		
11		3		4				4		
12		4		3				4		
13		4		4				4		
14		1						3		
15		1						3		
16		3								
17		3								

Sound duration (T)

Figure 3 shows the sound durations of classified call types of wild and captive Steller sea lions. The histograms for the wild individuals show sound durations of both males and females were shorter for threat sounds than for wheedling sounds, which were shorter in turn than communication sounds. Additionally, sound duration of the calls of captive lions was longer than those of the wild ones.

Common feature of pitch patterns

Figure 4a shows pitch pattern of "communication" for captive sea lions and wild ones. The frequency distribution of pitch patterns of "wheedling" and "threat" sounds for captive sea lions and wild ones were similar (Figs. 4b and 4c).

Table 1 shows the common features of pitch patterns in the order of frequency of "communication" sound for both wild and captive sea lions based on Fig. 4a (Dreher 1961). The numbers of pitch pattern types used in the "communication" calls were 17 for wild males, 13 for the wild females, 10 for a captive male, 15 for a captive female, and 6 for the captive juvenile.

The main pitch pattern of "communication" was the "long flat" type. The number 5 means it was a more common feature of pitch patterns,

Table 2. Pitch pattern distributions of "wheedling" sound for Steller sea lions. The number is a frequency that the Steller sea lions used.

Gradation of utilization	Wild				Captive	
	male		female		male	
1		3		3		1
2		3		3		3
3		3		3		3
4		2		2		3
5		1		1		2
6		3		3		2
7		2		2		2
8		2		2		2
9		2		2		3
10		2		2		1
11		2		2		2
12		2		1		1

and the number 1 means it was a less common feature. Common features are indicative of animals that share the same environment; few common features of males and females implies they use different environments.

In the common feature of pitch pattern for the captive juvenile, 3 out of 6 types showed features in common. It can be considered as the result of learning "communication" sound from their parents in the same group. The reason that there were only a few pitch patterns was likely because juveniles are in the middle of learning.

Table 2 shows 12 pitch patterns of "wheedling" for captive male Steller sea lions and wild male and female sea lions. The primary pattern of "wheedling" was short and ascending for the wild sea lions and a short waveform for the captive male. The captive male and wild Steller sea lions had a relatively high degree of common features for "wheedling."

For pitch patterns used in the "threat" sound of Steller sea lions, the wild males showed 7 types, the wild females 12 types, and captive female 8 types (Table 3). The main pattern was short and descending for the wild animals. The common characteristic was low for "threat" and high for "wheedling."

Discussion

The English language has 26 letters of which some are repeatedly used more than other letters (Shannon 1948, Witten 1990). Information coding can be studied by analyzing the frequency of use of letters (Shannon

Table 3. Pitch pattern distributions of "threat" sound for Steller sea lions. The number is a frequency that the Steller sea lions used.

Gradation of utilization	Wild				Captive	
	male		female		female	
1		2		3		3
2		3		2		3
3		3		3		3
4		3		1		1
5		2		1		2
6		2		1		1
7		1		3		1
8				1		2
9				1		
10				2		
11				2		
12				1		

1948, Cherry 1978). Plotting the frequency of occurrence on a log-probability plot is one means of uncovering the relationship between information theory and language (Dreher and Evans 1964). Therefore, the calls of sea lions could be inferred to hold valuable information if the occurrence frequency of call types falls on the line in a log probability plot (Fig. 5).

Pitch pattern arrangement graphs of the three call types were used to confirm whether the calls that were classified by their activities had meanings of information exchange with each other. The graphs plotted pitch pattern frequency against the logarithm of probability (where the number of their calls was converted to 1,000). They showed that the pitch patterns used by each Steller sea lion fell on a straight line for "communication," which suggests that "communication" has a meaning of information interchange among individuals. "Wheedling" and "threat" sounds also have a meaning of information interchange (Fig. 6).

It can be concluded that calls can be identified between males, females, and juveniles based on the characteristics of calls. The results showed sea lions may have the ability to find their offspring using vocalizations, as northern fur seals do (Takemura et al. 1983, Riedman 1990, Insley 1992). Moreover, the calls of sea lions appear to be used to exchange information, as echolocation does for whales (Watkins and Schevill 1977). Thus it can be concluded that the calls of sea lions are important to maintain their groups, and may even play a role in facilitating sea lion navigation.

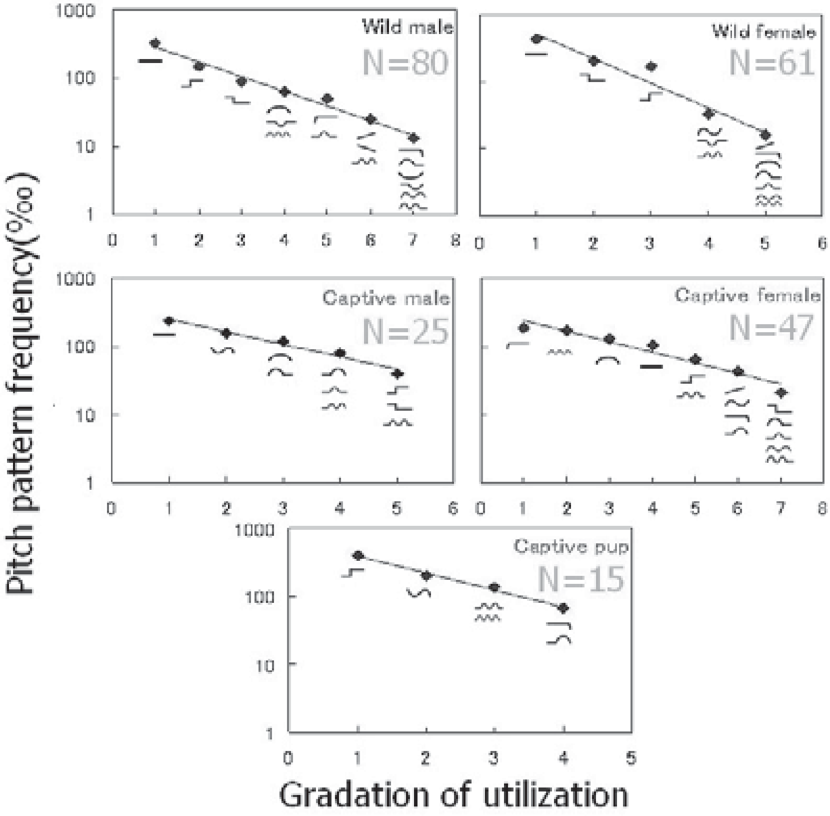


Figure 5. Pitch pattern frequency relative to pattern types of "communication" sound for Steller sea lions.

Acknowledgments

The authors thank Emeritus Professor Haruo Ogi of Hokkaido University, who motivated us to begin this research. We also thank Dr. Donhyug Kang, Dr. Myounghee Kang, Dr. Kyounghoon Lee, Mr. Takuma Takayama, and Mr. Shoji Kotani for their assistance with the experiments and in collecting material. We wish to thank the Muroran Municipal Aquarium for providing captive Steller sea lions.

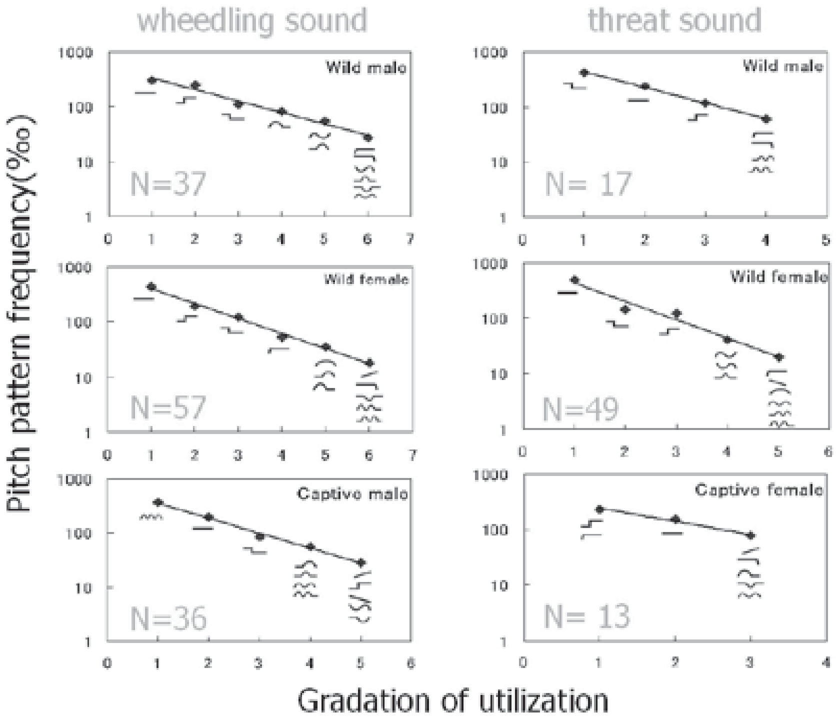


Figure 6. Pitch pattern frequency relative to pattern types of "wheedling" sound and "threat" sound for Steller sea lions.

References

Cherry, C. 1978. On human communication. 3rd edn. MIT Press.

Davies, J.L. 1958. The Pinnipedia: An essay in zoogeography. Geogr. Rev. 48:1817-1832.

Dreher, J.J. 1961. Linguistic considerations of porpoise sounds. J. Acoust. Soc. Amer. 33:1799-1800.

Dreher, J.J., and W.E. Evans 1964. Cetacean communication. Marine Bio Acoustics, Academic Press, pp. 373-393.

Insley, S.J. 1992. Mother-offspring separation and acoustic stereotypy: A comparison of call morphology in two species of pinnipeds. Behaviour 120:103-121.

King, J.E. 1983. Seals of the world. Oxford University Press, Oxford. 240 pp.

Loughlin, T.R., D.J. Rugh, and C.H. Fiscus. 1984. Northern sea lion distribution and abundance: 1956-80. J. Wildl. Manag. 48:719-740.

Peterson, R.S., and G.A. Bartholomew 1967. The natural history and behavior of the California sea lion. Amer. Soc. Mamm. Special Publ. No. 1.

Riedman, M. 1990. The pinnipeds: Seals and sea lions. University of California, Berkeley.

Scheffer, V.B. 1958. Seals, sea lions, and walruses: A review of the Pinnipedia. Stanford University Press, Palo Alto, California. 179 pp.

Schusterman, R.J. 1981. Steller sea lion, *Eumetopias jubatus* (Schreber 1776). In: S.H. Ridgway and R.J. Harrison (eds.), Handbook of marine mammals. Vol. 1. Walrus, sea lions, fur seals and sea otters. Academic Press, New York, pp. 119-141.

Shannon, C.E. 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27:379-423, 623-656.

Takemura, A., K. Yoshida, and N. Baba. 1983. Distinction of individual northern fur seal pups, *Callorhinus ursinus*, through their call. Bull. Fac. Fish. Nagasaki Univ. 54:29-34.

Watkins, W.A., and W.E. Schevill. 1977. Sperm whale codas. J. Acoust. Soc. Amer. 62(6):1485-1490.

Witten, H. 1990. Source models for natural language text. Int. J. Man-Machine Studies 32:545-579.

Organochlorines in Walleye Pollock from the Bering Sea and Southeastern Alaska

Ron Heintz
NOAA Fisheries, Alaska Fisheries Science Center, Auke Bay Laboratory, Juneau, Alaska

Margaret M. Krahn and G.M. Ylitalo
NOAA Fisheries, Northwest Fisheries Science Center, Environmental Conservation Division, Seattle, Washington

Frank Morado
NOAA Fisheries, Alaska Fisheries Science Center, Resource Assessment and Conservation Engineering Division, Seattle, Washington

Abstract

The ubiquitous distribution and toxicity of organochlorines in high latitude food webs has been suggested as one factor in preventing the recovery of the western Steller sea lion stock. However, there are few data describing the bio-availability of these contaminants in the sub-arctic Bering Sea and Gulf of Alaska. We measured concentrations of dioxin-like and other selected polychlorinated biphenyls (PCBs), DDTs, and hexachlorobenzene (HCB) in a prey species of Steller sea lions (walleye pollock) that is distributed throughout the range of these marine mammals, to test the hypothesis that contaminant loads in western stock food webs would be higher than those of the eastern stock. More than 110 fish were collected from six regions: western Bering Sea, western Aleutians, eastern Aleutians, Pribilof Islands, northern Bering Sea, and southeastern Alaska. Organochlorine levels were found to correlate with fish age and size ($r^2 > 0.390$), but were uncorrelated with lipid content. Pollock from southeastern Alaska were significantly more contaminated than Bering Sea pollock ($P < 0.01$) with length-corrected concentrations of 5.00 ng per g wet weight, 4.93 ng per g, and 1.15 ng per g for total PCBs ($\sum$PCBs), total DDTs ($\sum$DDTs), and HCB, respectively. Aerial transport and precipitation likely account for the relatively high levels of contamination in southeastern Alaska. Eastern stock sea lion populations have been increasing while apparently consuming prey with higher organochlorine loads. Consequently, presence of organochlorines in high latitude food webs does not appear to be a major factor inhibiting the recovery of the western sea lion stock.

Introduction

The toxic effects of organochlorines have been proposed as one of the causes for the decline of the western stock of Steller sea lions and its failure to recover. Steller sea lions populations from Cape Yakutaga westward through the Aleutian Islands (Western stock) have been declining rapidly since the 1980s. In contrast, Steller sea lion populations in British Columbia and southeastern Alaska have been slowly increasing during the same period. Included among the organochlorines are the polychlorinated biphenyls (PCBs), hexachlorobenzene (HCB), and many pesticides including the dichlorodiphenytrichloroethanes (DDTs). The high volatility of these compounds allows them to be carried into the upper atmosphere at low latitudes and transported to colder northern latitudes where they condense and precipitate back to the earth's surface (AMAP 1998). Organochlorines are lipophilic and are therefore readily entrained in food webs, where they can be concentrated in the lipid-rich tissues of apex predators such as Steller sea lions. Although there are programs in place for monitoring organochlorine levels and trends in Arctic regions, much less effort has been directed at the subarctic Bering Sea and northern Gulf of Alaska, an area where populations of Steller sea lions and other apex predators have been declining over the last 20 years (Springer et al. 2003). Few Steller sea lion samples are available for contaminant analysis, because of the logistical difficulty associated with the capture and biopsy of individuals in this extremely remote region. In addition, captive animals are few which precludes controlled exposure studies.

Steller sea lions primarily acquire organochlorines through ingestion, so one way to understand the risk imparted by organochlorines to Steller sea lions is to evaluate their potential exposure by examining their prey in different parts of the sea lion range. Such an analysis depends on sampling a prey item that is ubiquitously distributed throughout the sea lion range; thus the confounding effects of trophic level, ecology, and lipid content can be minimized. Fortunately, walleye pollock (*Theragra chalcogramma*) are a frequently encountered prey item (Merrick and Calkins 1996, Calkins 1998, Womble and Sigler 2006). Estimates of the frequency of pollock in juvenile Steller sea lion scats range from 75% in the western Aleutians to 85% in southeastern Alaska.

Previous reports have measured organochlorines in walleye pollock, but these data shed little light on the relationship of organochlorine ex-

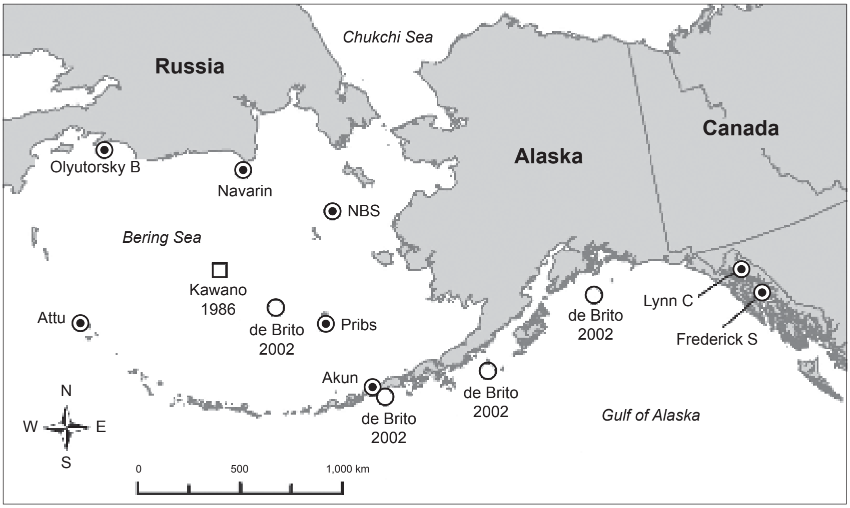


Figure 1. Sampling locations for pollock used in this study and those sampled by Kawano et al. (1986) and de Brito et al. (2002).

posure to declining populations of pollock predators, such as Steller sea lions. The first observation (Kawano et al. 1986) measured DDT, PCB, HCB, and chlordane levels in the whole bodies of three pollock collected from the mid-shelf of the Bering sea in 1982 (Fig. 1). In 1992, de Brito et al. (1992) estimated concentrations of these same compounds in the livers of 29 pollock collected from three locations in the Bering Sea and three in the Gulf of Alaska (Fig. 1). All of these samples were collected from the region in which apex predator populations are declining, but there are no comparable data from areas where predator populations are stable. Furthermore, time trends in organochlorine levels cannot be determined from these limited data sets because different tissues were used. Beckmen (2001) describes a third set of pollock analyzed for these compounds, but the specific sampling locations are not described.

The objective of this report is to understand spatial variation of organochlorines in a prey species of Steller sea lions. We present data describing the concentrations of 15 PCB congeners, five DDTs, and HCB in the tissues of walleye pollock collected from the Bering sea and southeastern Alaska, collected opportunistically in 2002 and 2003. In particular, we tested the hypothesis that the availability of organochlorines to apex predators from the Bering Sea is the same as that in southeastern Alaska by using the levels of these organochlorines in pollock as an index to their availability in local food webs. In addition we examine the relative concentrations of individual PCB congeners in pollock samples to determine if the PCB composition in the food webs varies among different geographic regions.

Methods

Sample collection and preparation

Walleye pollock samples were collected in the Bering Sea and southeastern Alaska in 2002 and 2003. In some cases, samples from locations relatively near each other were pooled to make collections representative of a region. Locations sampled during the summer and fall of 2002 included Frederick Sound in southeastern Alaska, Attu Island in the western Aleutian Islands, and Akun Island in the eastern Aleutians, a series of points along a transect between St. Lawrence and St. Matthew islands in the northern Bering Sea, Cape Navarin, and Olyutorsky Bay on the western shore of the Bering Sea. In February 2003 pollock were collected during the commercial fishery near the Priblilof Islands. Additional samples were collected from Lynn Canal in southeastern Alaska during April 2003 and added to the Frederick Sound samples to represent southeastern Alaska. Each of these sites is located on Fig. 1. Sampling dates, specific locations, and fish sizes are listed in Table 1. Samples chosen for processing were representative of the size range available at those sites during collection, with the exception of the Russian sites where size of the fish was limited by the logistics of transport back to the United States.

After collection, samples were immediately frozen and shipped as soon as possible to the NOAA Auke Bay Laboratory for preparation. Otoliths were removed and whole fish were cut in small pieces and homogenized in a commercial meat grinder. The resulting paste was spread over a 25 by 45 cm cutting board and two 5 gram samples were composited from randomly selected aliquots. One of the samples was kept for lipid extraction and the other was shipped frozen to the NOAA Montlake Laboratory in Seattle for organochlorine analysis. Samples for organochlorine analysis were stored in certified jars with Teflon lined lids. All homogenized samples were topped with nitrogen and stored at –80ºC prior to analysis. Temperature of the homogenates never exceeded 0ºC during processing. All grinding and sampling equipment was washed with hot soapy water between samples and rinsed with hexane between sets of samples from different locations. Ages of fish were determined from the otoliths at NOAA's ageing laboratory in Seattle, Washington, by two independent readers. Their age estimates agreed 90% of the time.

Organochlorine analysis by HPLC/PDA

Whole body homogenate samples of pollock were analyzed for selected organochlorines, including dioxin-like polychlorinated biphenyls (PCBs)

Table 1. Location names and sample information for walleye pollock collected for organochlorine analysis.

Region	Location	Latitude	Longitude	Collection date	Sample size	Average length (mm)	Average weight (g)	Average age (years)
SEAK	Lynn Canal	58°30'N	134°48'W	08-Apr-03	10	306.0 (73.4)	300.0 (323.4)	3.2 (1.8)
SEAK	Frederick Sound	58°21'N	134°08'W	03-Apr-02	10	489.0 (92.7)	1159.2 (744.1)	7.5 (1.0)
WAI	Attu Is.	52°48'N	172°24'E	21-Jun-02	12	456.7 (28.8)	627.1 (185.2)	4.6 (1.5)
EAI	Akun Is.	54°24'N	165°30'W	19-May-02	15	475.3 (28.8)	752.6 (132.6)	6.4 (1.1)
PRIBS	Pribilof Is.	56°44'N	170°21'W	26-Feb-03	15	443.3 (47.6)	583.3 (162.3)	6.1 (1.2)
NBS	Northern Bering Sea	60°57'N	171°31'W	28-Sep-02	27	353. (154.9)	537.2 (448.1)	5.1 (4.0)
WBS	Cape Navarin	61°35'N	178°36'E	1-Oct-02	15	124.8 (79.5)	37.6 (61.7)	0.6 (1.1)
WBS	Olyutorsky Bay	59°30'N	167°03'E	22-Sep-02	7	227.6 (20.4)	122.4 (29.5)	1.8 (0.4)

EAI = eastern Aleutian Islands, NBS = northern Bering Sea, PRIBS = Pribilof Islands, SEAK = southeastern Alaska, WAI = western Aleutian Islands, WBS = western Bering Sea. Numbers in parentheses represent 1 standard deviation.

and DDTs, by a high-performance liquid chromatography photodiode array (HPLC/PDA) method (Krahn et al. 1994). Briefly, whole fish homogenate (1.7-3.0 g), hexane/pentane (1:1 v/v), sodium sulfate (5 g), and a surrogate standard were homogenized and separated from interfering compounds (e.g., lipids, aromatic compounds) on a gravity flow cleanup column that contained neutral, basic, and acidic silica gels eluted with hexane/methylene chloride (1:1 v/v). Eight dioxin-like congeners (PCBs 77, 105, 118, 126, 156, 157, 169, 189) were resolved from other selected PCBs (PCBs 99/101/149, 110, 128, 138, 153, 170/194, and 180) and six additional organochlorines [*o,p′*-DDD, *p,p′*-DDD, *p,p′*-DDE, *o,p′*-DDT, *p,p′*-DDT, hexachlorobenzene (HCB)] by HPLC on two Cosmosil PYE analytical columns, connected in series and cooled to 16ºC. The congeners were measured by an ultraviolet (UV) photodiode array detector and were identified by comparing their UV spectra (200-310 nm) and retention times to those of reference standards in a library. The analyte purity was confirmed by comparing spectra within a peak to the apex spectrum.

Summed PCB (∑PCB) concentrations were calculated using the following formula: ∑PCBs = ∑concentrations of 15 PCBs listed above (based on individual response factor) + ∑concentrations of other PCB congeners (calculated by summing areas of peaks identified as PCBs and using an average PCB response factor). Summed DDT (∑DDTs) concentrations were calculated by summing the concentrations of five DDTs (*o,p′*-DDD, *p,p′*-DDD, *p,p′*-DDE, *o,p′*-DDT, *p,p′*-DDT).

Lipid extraction

Lipid was extracted using a modification of Folch's method (1957) outlined by Christie (1989) using a Dionex Accelerated Solvent Extractor (ASE) 200. Approximately 1 g of wet homogenate was mixed with a drying agent (Hydromatrix) and masticating agent (sand) and loaded into ASE cells. Samples were extracted using a 2:1 (v:v) chloroform:methanol solvent at 1,200 psi and 120ºC. Following extraction, the filtrate was washed to remove the coextractables with a 0.88% KCl solution followed by a solution of 1:1 (v:v) methanol:deionized water, both in a volume equal to 25% of the extract volume. Excess solvent was evaporated to reduce the sample volume to 1 ml. Percent lipid was calculated gravimetrically.

Quality assurance

During lipid extraction, quality assurance samples were extracted with each batch of 17 samples and these included (1) a blank, (2) a replicate sample consisting of a second aliquot of homogenate of one of the samples in the batch, and (3) a reference sample of herring homogenate, which had been previously characterized for lipid content. Accuracy of the estimate for the reference sample, repeatability, and method cleanliness were required to meet laboratory criteria or the batch was re-extracted.

To monitor the accuracy of our HPLC/PDA method, a National Institute of Standards and Technology (NIST) Standard Reference Material (blue mussel SRM1974b or fish homogenate SRM1946) was analyzed with each sample set and results met laboratory criteria (Wise et al. 1993). Approximately 10% of fish homogenate samples were analyzed in duplicate to measure precision of the method, and the laboratory quality assurance criteria were met for all analytes detected in these samples. Method blanks also met laboratory criteria.

Statistical analysis

Sample collections varied in average fish size and age (Table 1), suggesting the presence of important covariates with location in the analysis of the sample collections. Consequently, statistical analysis began by understanding how age, size, and lipid content related to the observed organochlorine concentrations. The observed concentrations of $\sum$PCBs, $\sum$DDTs, and HCB were plotted against length, age, and lipid content (percent wet weight) for the entire data set and the resulting relationship evaluated by linear regression. Observations below detection limit were set to zero. In addition, the relationships between the covariates were also examined by linear regression.

Spatial variation in organochlorine content was examined by ordinal logistic regression with region as a factor and age as a covariate. Logistic regression was used because organochlorine concentrations in different regions were not normally distributed and had heterogeneous variances. Ordinal logistic regression requires categorical response variables, so the organochlorine contents of all specimens were sorted and assigned to deciles. Consequently, the regression examined the frequency distribution of deciles within each region, while accounting for differences in age. When assigning deciles to observations of $\sum$DDTs, 32 of the 111 samples were found to have undetectable DDT levels; these were removed from the analysis. Finally, ANCOVA was used to calculate least square mean organochlorine contents for fish from each region using age as a covariate. These values were not tested, but are used here to report representative age-normalized values for contaminant load in different regions. In the event that an interaction between age and region was found to influence organochlorine levels, the slopes of the age and organochlorine relationships between regions were compared using Student's *t* test.

Compositional differences in the organochlorines found in fish from different geographical regions were examined by a combination of ANCOVA and multivariate analysis of covariance (MANCOVA). The observed concentrations of PCB congeners found to be above the detection limit in at least two fish from each region were examined individually by ANCOVA with region as the main factor and age as the covariate. Prior to analysis, the concentrations were transformed by dividing each congener's concentration by the observed $\sum$PCBs to generate relative con-

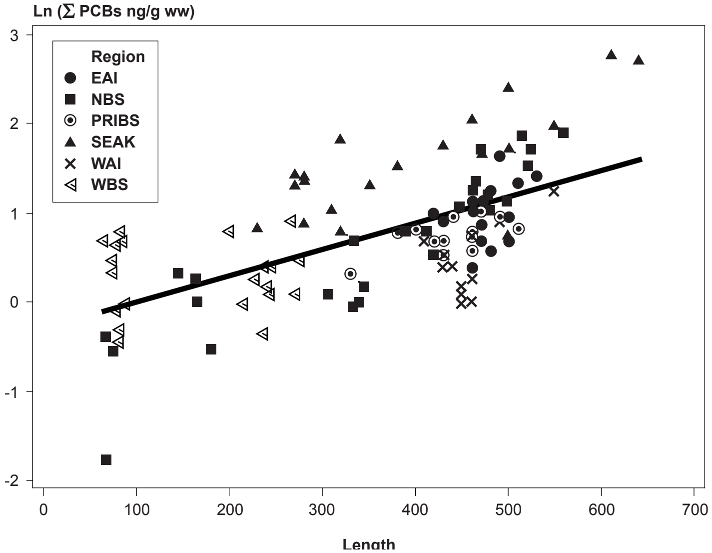


Figure 2. Relationship between natural log of ∑PCBs (ng per g wet weight) and length (mm) for pollock in the Bering Sea and southeastern Alaska. The line depicts the regressed fit for all samples. Abbreviations: EAI = eastern Aleutian Islands, NBS = northern Bering Sea, PRIBS = Pribilof Islands, SEAK = southeastern Alaska, WAI = western Aleutian Islands, WBS = western Bering Sea.

centrations. In addition, the entire group of congeners was subsequently examined together by MANCOVA to test the hypothesis that the relative concentrations of the congeners varied among regions.

Results

Relationships between covariates and organochlorine concentrations

There were strong relationships between the organochlorine content of pollock and their lengths. Average values (±1 s.d.) for ∑PCBs ranged from 1.40±0.55 to 5.79±4.00 ng per g wet weight in samples from western Bering Sea and southeastern Alaska, respectively (Table 2). Coincidently, these two collections represent those with the smallest and largest pollock, respectively (Table 1). The linear regression between the ∑PCBs and length for all of the fish sampled was significant ($P < 0.0005$, $r^2 = 0.252$). However, a scatter plot of the relationship indicated an exponential curve was better at describing this relationship (Fig. 2). This was confirmed by

Table 2. Observed average lipid content and organochlorine concentrations in walleye pollock from different locations. Only those congeners are shown for which concentrations were above detection limits.

			PCB congener ng per g							
Region	Location	% Lipid	101	110	118	138	153	∑PCB ng per g	∑DDT ng/g	HCB ng/g
SEAK	Lynn Canal	2.18 (0.68)	1.78 (0.77)	0.05 (0.11)	0.382 (0.34)	0.24 (0.33)	0.82 (0.64)	4.28 (2.65)	3.80 (3.34)	0.89 (0.28)
SEAK	Frederick Sound	4.02 (1.71)	1.53 (0.91)	0.24 (0.18)	0.80 (0.51)	0.44 (0.62)	1.54 (0.84)	7.30 (4.61)	8.36 (6.81)	1.62 (0.54)
WAI	Attu Is.	2.48 (1.33)	0.65 (0.28)	0.03 (0.09)	0.05 (0.12)	0.37 (0.16)	0.82 (0.27)	1.70 (0.74)	1.33 (0.63)	0.30 (0.41)
EAI	Akun Is.	3.55 (1.03)	1.17 (0.40)	0.07 (0.19)	0.35 (0.38)	0.31 (0.19)	0.90 (0.26)	2.88 (0.98)	1.65 (0.58)	1.37 (0.40)
PRIBS	Pribilof Is.	3.72 (1.65)	1.18 (0.28)	0.06 (0.11)	0.10 (0.11)	0.08 (0.11)	0.61 (0.11)	2.17 (0.38)	0.89 (0.22)	1.47 (0.41)
NBS	Northern Bering Sea	4.16 (2.29)	1.18 (1.30)	0.12 (0.15)	0.11 (0.15)	0.13 (0.22)	0.38 (0.35)	2.54 (1.85)	0.81 (0.98)	1.09 (0.46)
WBS	Cape Navarin	5.56 (1.34)	1.12 (0.56)	0.06 (0.11)	nd	nd	0.07 (0.15)	1.35 (0.53)	nd	0.92 (0.18)
WBS	Olyutorsky Bay	5.25 (1.68)	1.26 (0.76)	n.d	nd	nd	0.15 (0.16)	1.50 (0.63)	nd	0.76 (0.21)

EAI = eastern Aleutian Islands, NBS = northern Bering Sea, PRIBS = Pribilof Islands, SEAK = southeastern Alaska, WAI = western Aleutian Islands, WBS = western Bering Sea.
All concentrations are expressed as ng compound per g wet weight. Numbers in parentheses represent 1 standard deviation.
nd = analytes were not detected.

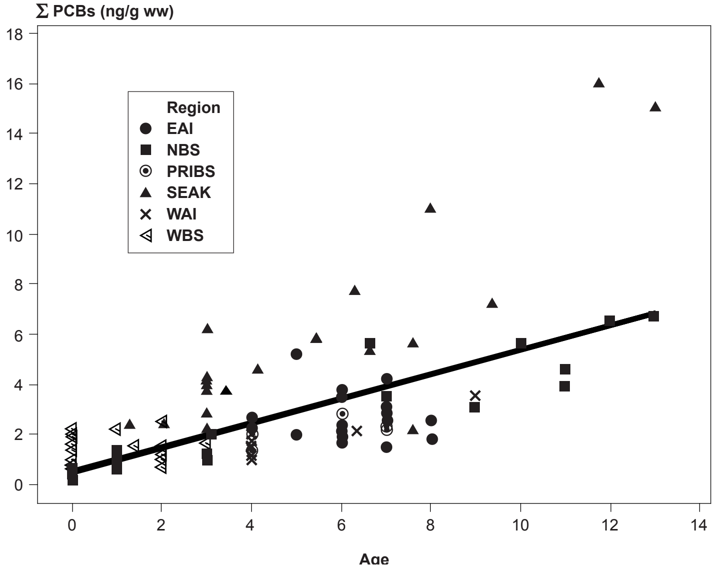


Figure 3. Relationship between ∑PCBs (ng per g wet weight) and age of walleye pollock collected from the Bering Sea and southeastern Alaska. Line depicts regression fit for all samples. Abbreviations are the same as those in Fig. 2.

regressing the natural logarithm of ∑PCBs against length ($P < 0.005$, $r^2 = 0.398$). Similarly, the concentrations of ∑DDTs varied with fish size, ranging from non-detectable to 6.08±5.72 ng per g wet weight for fish from the western Bering Sea and southeastern Alaska, respectively. While the regressed relationships between fish length and the natural logarithms of ∑DDTs and HCB were also significant ($P < 0.0005$), they were weakly correlated ($r^2 < 0.140$).

Age was directly related to contaminant load (Fig. 3). There was a linear relationship between age and ∑PCBs ($P < 0.0005$, $r^2 = 0.392$). Similarly, the relationships between age and ∑DDTs and HCB did not require transformation to natural logarithms ($P < 0.0005$, $0.140 < r^2 < 0.250$). This was consistent with the observed relationships between contaminant loads and size; as fish age they grow. The difference in the shapes of the relationships between age and length with organochlorine levels resulted from the asymptotic relationship between age and length in the pollock (Fig. 4). As pollock age, their contaminant levels apparently increase, but their growth rates level off resulting in a nonlinear relationship between size and contaminant level.

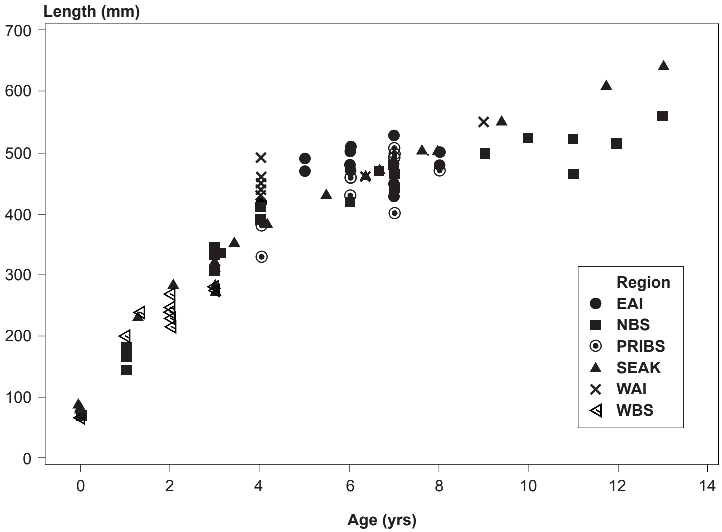


Figure 4. Relationship between age and length for walleye pollock collected from the Bering Sea and southeastern Alaska.

The lipid content, expressed as a percentage of wet mass, was unrelated to organochlorine level in pollock. Linear regression between ∑PCBs and the percent lipid content was not significant ($P = 0.854$, $r^2 = 0.0$). Inspection of a scatter plot revealed little indication of any relationship between lipid content and ∑PCBs (Fig. 5). Similarly, there was no relationship between lipid content and ∑DDTs ($P = 0.724$, $r^2 = 0.0$). However, there was a weakly correlated relationship between lipid and HCB ($P < 0.0005$, $r^2 = 0.189$). The general lack of relationship between percentage lipid and organochlorine content was consistent with a lack of relationship between lipid content and size of the pollock ($P = 0.071$, $r^2 = 0.021$), which has been previously described (Anthony et al. 2000, Vollenweider 2005).

Spatial variation in organochlorine concentrations

Ordinal logistic regression of the ∑PCBs levels in pollock from different regions indicated a significant elevation in the availability of ∑PCBs to pollock in southeastern Alaska. There was a significant interaction between age and region on ∑PCB level ($\chi^2 = 14.8$, $P = 0.011$) indicating that pollock in different regions acquire ∑PCBs at different rates with respect to time. Removing the northern Bering Sea collection from the regression resulted in no interaction ($\chi^2 = 7.81$, $P = 0.099$) and a significant difference among regions ($\chi^2 = 14.00$, $P = 0.007$). Age-corrected estimates of

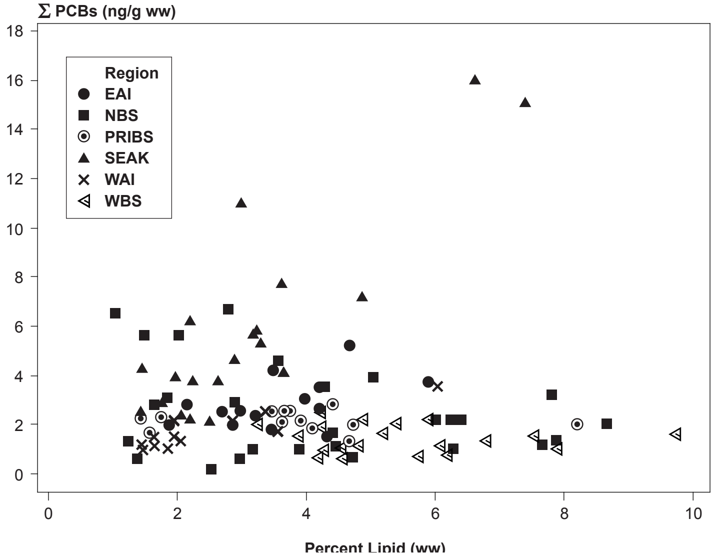


Figure 5. Relationship between ∑PCBs (ng per g wet weight) and lipid content (% wet weight) of pollock collected from the Bering Sea and southeastern Alaska. No relationship was detected by regression. Abbreviations are the same as those in Fig. 2.

the mean ∑PCBs, derived by ANCOVA (Fig. 6) indicated pollock from southeastern Alaska had greater ∑PCBs than those from the western Aleutians and western Bering Sea. Pollock, aged 4.6 years, averaged 5.0 ng ∑PCBs per g wet weight while those from the western Aleutian Islands and western Bering Sea averaged less than 1.7 ng ∑PCBs per g wet weight (Table 2). Pollock from the eastern Aleutians and Pribilofs averaged 3.3 and 2.0 ng per g, respectively. Heterogeneous variances and interactions prevent direct comparison of these means, but comparison of the slopes relating age and ∑PCBs for pollock from southeastern Alaska and northern Bering Sea indicated that pollock from southeastern Alaska acquire PCBs at nearly two and one-half times the rate of those in the northern Bering Sea and western Aleutians ($t > 14.0$, $P < 0.0005$). However, there was no difference in the slopes relating age and ∑PCBs for pollock from the northern Bering Sea and western Aleutians ($t = 1.71$, $P = 0.115$) (Fig. 3). Other comparisons of slopes were not made due to the narrowness of the age ranges in collections from the remaining regions (Table 1).

DDT content of pollock depended on the region in which fish were collected ($\chi^2 = 28.83$, $P < 0.0005$). There was no interaction between region and age on DDT content ($\chi^2 = 3.76$, $P = 0.440$). Pollock from southeastern

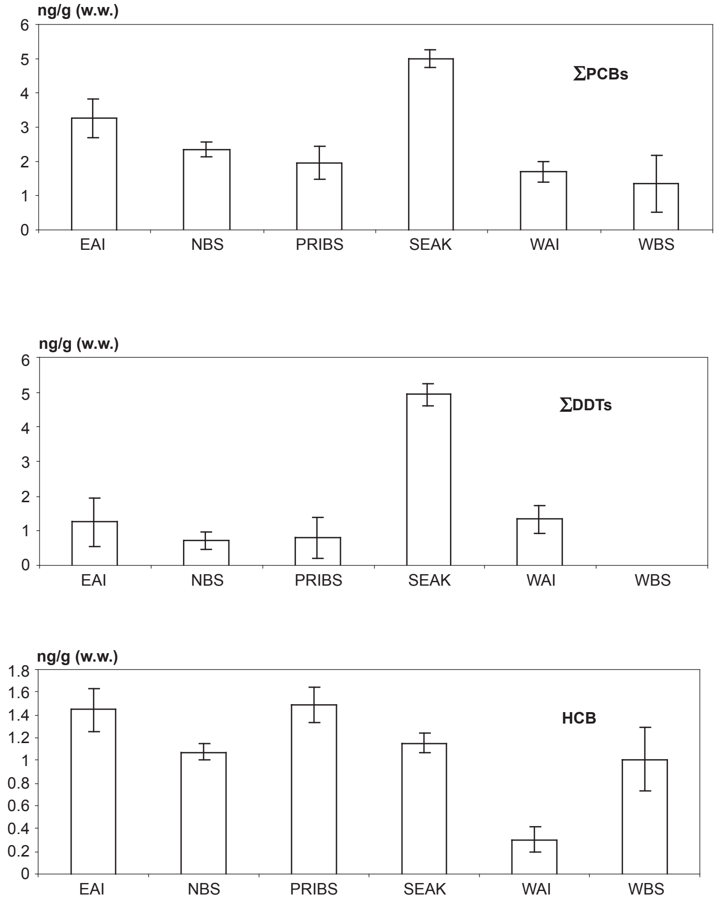


Figure 6. Age adjusted organochlorine (OC) concentrations (ng OC per g wet weight) (± 1 s.e.) in pollock collected from different locations in the Bering Sea and southeastern Alaska. Top panel: ∑PCBs, middle: ∑DDTs, and lower: HCB. Abbreviations are the same as those in Fig. 2.

Alaska had the greatest DDT concentrations with age 4.6 pollock averaging 4.9 ng ∑DDTs per g wet weight in contrast to those from the western Aleutians, eastern Aleutians, Pribilofs, and northern Bering Sea, which averaged less than 1.33 ng ∑DDTs per g wet. No DDTs were detected in tissues of fish from the western Bering Sea (Table 2) (Fig. 6).

HCB content also varied regionally ($\chi^2 = 14.30$, $P = 0.014$). No interaction between age and region was observed for HCB content ($\chi^2 = 8.06$,

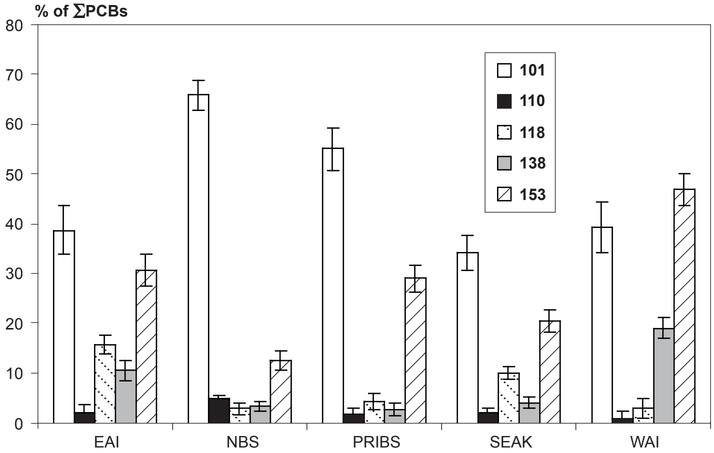


Figure 7. Relative concentrations of selected PCB congeners (age adjusted by ANCOVA) in tissues of pollock from different regions in the Bering Sea and southeastern Alaska.

$P = 0.153$). The regional differences arose from the relatively low levels of HCB observed among pollock from the western Aleutians (Table 2) (Fig. 6). Age 4.6 pollock from the western Aleutians averaged 0.30 ng HCB per g wet weight, in contrast to those from the other regions, whose HCB levels exceeded 1.01 ng HCB per g wet weight.

Spatial variation in composition

The generally low levels of organochlorines observed in pollock tissues limited analysis of their composition (Table 2). The only DDT routinely detected was p,p′-DDE and only PCBs 101, 110, 118, 138, and 153 were observed above detection limits more than once in all regions. PCB 101 was the only routinely detected congener found in western Bering Sea pollock, so they were deleted from the compositional analysis. None of the ANCOVAs indicated the presence of an interaction between region and age on the relative concentrations of any of the PCB congeners ($F_{4,55} < 2.01$, $P > 0.105$) or an effect of age ($F_{1,55} < 1.39$, $P > 0.244$). However, there were strong regional effects on the relative concentrations ($F_{4,55} > 3.08$, $P < 0.023$) of PCBs 101, 118, 138, and 153. PCB 110 appeared to be evenly distributed throughout the study area ($F_{4,55} = 0.72$, $P = 0.581$). A consequence of the disparate distribution of PCB congeners among regions (Fig. 7) was that the MANOVA indicated differences in PCB composition among regions (Wilks $\lambda = 0.389$, $P < 0.0005$).

Discussion

Significant differences occurred in the organochlorine content of pollock from different regions, resulting from variation in the availability of PCBs, DDTs, and HCB to regional food webs and not from regional differences in size or age of the fish. Elevated levels of PCBs, DDTs, and HCB were found in the tissues of pollock collected in southeastern Alaska compared to other regions. Further evidence for regional differences in the availability of organochlorines was offered by PCB congener patterns (101, 118, 138, and 153), which all demonstrated that these congeners are acquired at different rates in different regions and further suggest that food webs in different regions have differing PCB compositions. The low levels of organochlorines observed in western Bering Sea samples relative to those from other regions should be viewed with some caution. Fish collected from the western Bering Sea were younger than those in the remaining data set, indicating that most were juveniles. Therefore, less time was available for uptake of organochlorines. In addition, juveniles are likely to be less piscivorous than adults and therefore occupy a lower trophic level.

Our ability to detect organochlorines in each of the regions demonstrates that these compounds are ubiquitously distributed in the food webs of the Bering Sea and Gulf of Alaska. Southeastern and western Alaska are remote locations with exceedingly low population densities and few identifiable PCB sources (Barron et al. 2003). The availability of PCBs, DDTs, and HCB in these food webs is therefore likely determined through deposition from the atmosphere (AMAP 1998). Rain and snow are the most efficient scavengers for removing these compounds from the atmosphere and the relatively high organochlorine concentrations in southeastern Alaska pollock are consistent with the observation that average annual precipitation in that region is in excess of 125 cm per year. In particular, precipitation in Auke Bay, Alaska, a location near the Lynn Canal sites, averages 164 cm per year. In contrast, the precipitation levels at Akutan, located near the Akun Island site, averages 71 cm per year. Precipitation at Attu averages 124 cm per year, while precipitation for St. Paul and St. George islands in the Pribilofs, the region with the relatively low DDT and PCB levels, averages 58 cm per year. Precipitation in British Columbia and southeastern Alaska are the source of the Alaska coastal current, which flows from western North America to the Aleutian Islands. Organochlorines precipitated in southeastern Alaska may therefore ultimately be transported to the Bering Sea, effectively exposing all of the southern coast of Alaska.

Regional differences in the trophic level occupied by pollock may offer an alternative explanation for regional variation in organochlorine content. This could describe the relatively low levels observed among pollock collected at the western Bering Sea stations. However, the elevated levels of PCBs, DDTs, and HCB found in southeastern Alaska pollock are consistent with reports involving other species. Barron et al. (2003) indicated that juvenile Steller sea lions from southeastern Alaska had higher average concentrations of ∑PCBS and ∑DDTs than those from the Bering Sea. Similarly, Vander Pol et al. (2004) found higher levels of PCBs and DDTs in common murre eggs collected from southeastern Alaska compared to those from the Pribilof Islands. Conversely, HCB was higher in Pribilof eggs. It is unlikely that all of these species occupy higher trophic levels in southeastern Alaska than in other parts of their range; consequently trophic variation likely does not account for regional variation.

We report levels on a wet mass basis because organochlorines are consumed by pollock predators in wet tissue. However, expressing organochlorine concentrations on a lipid mass basis provides a method for comparing concentrations among species whose lipid contents vary. On a lipid mass basis, southeastern Alaska pollock averaged 184 ng ∑PCBS per g lipid (i.e., concentration divided by % lipid) and those from the northern Bering Sea, the most northerly collection of adults, averaged 103 ng per g lipid. These values are intermediate to those estimated for fourhorn sculpin and bearded seal near Pt. Barrow, Alaska (Hoekstra et al. 2003). In contrast, the lipid-normalized PCB levels reported here are an order of magnitude lower than those reported for polycheates and sandeels in the Hvaler archipelago near Norway (Ruus et al. 2002).

Discounting differences in analytical approaches, comparing our data to that from previous reports suggests levels of some organochlorines are declining in the Bering Sea pollock. Kawano et al. (1986) reported levels of 15.8 ng per g wet weight for ∑PCBs and 13.5 ng per g wet weight for ∑DDTs in whole pollock collected in 1982 (Fig. 1). The comparability between Kawano (1986) and data presented here is unknown, but we report levels of 2.7 and 1.1 ng per g wet weight for ∑PCBs and ∑DDTs, respectively for fish collected from approximately the same locations and average sizes. Beckmen (2001) reported levels of 9 ng per g wet weight for pollock collected from the Bering Sea between 1998 and 2000. This level is intermediate to those reported by Kawano et al. (1986) and this study and is therefore consistent with a temporal decline. While the analytical approach employed by Beckmen (2001) was identical to that used here, the ages of those fish are unknown.

Steller sea lion risk assessment

The risk of organochlorine exposure imposed by pollock to their predators, such as Steller sea lions, depends on where the foraging takes place, and the size and number of fish consumed. Data presented here indicate that Steller sea lions foraging on pollock in southeastern Alaska are likely to encounter higher organochlorine exposures than sea lions in the western stock. This conclusion assumes that sea lions consume equal masses of equally sized pollock, but estimates for the average size of pollock consumed by the western stock range between 359 and 424 mm (Zeppelin et al. 2004) and 410 and 439 mm for the eastern stock (Tollit et al. 2004). Comparison of the regressions between length and natural log $\sum$PCBS for southeastern Alaska pollock and those from eastern Aleutians, Pribilofs, and western Aleutians combined indicate that the average exposure of sea lions in southeastern Alaska is 4.7 ng $\sum$PCBs per g tissue consumed, while those from the west consume 1.8 ng $\sum$PCBs per g tissue. Winship and Trites (2003) estimated a 20% difference in consumption rate between western and eastern stock sea lions, demonstrating that differences in daily consumption rate are unlikely to compensate for differences in exposure. Consequently, the data presented here indicate that recovery of the western stock is not likely impeded by exposure to organochlorines, because eastern stock animals receive higher exposures and have increasing populations (Sease et al. 2001).

An important limitation to the risk assessment offered here is that variation in organochlorine content among other sea lion prey species has not been described. Western stock sea lions have less diverse diets (Merrick et al. 1997) and the rapidly declining populations in the far west rely heavily on lipid rich species such as Atka mackerel and salmon (Sinclair and Zeppelin 2002). This suggests that lipid intake rates vary among populations and our expectation is that variations in lipid intake will ultimately drive variation in exposure. Consequently, a more detailed analysis of exposure depends on accounting for differences in the rate of lipid ingestion and the lipid burdens in various prey. Such an analysis will ultimately provide the best information on the potential role of contaminants in the failed recovery of western stock sea lions.

The contaminants described here appear to be precipitated from the atmosphere in coastal mountain ranges and entrained in marine food webs where they can be detected even in low lipid species such as walleye pollock. These data indicate significant quantities of organochlorines are precipitated in southeastern Alaska where they can be transported westward in the Alaska coastal current, contaminating food webs along the southern coast of Alaska and eastern Bering Sea. Thus, the same geographic features responsible for the relatively high productivity of the northern Pacific and eastern Bering Sea also effectively pump organochlorines into those same food webs (Sambrotto and Lorenzen 1986). While PCB and DDT concentrations may be declining in the region, the general behavior of these compounds may predict the behavior of other lipophilic compounds whose concentrations are increasing, such as polybrominated diphenyl ethers (PBDEs). In addition to seals and sea lions, the dominant fish species in the northern North Pacific Ocean are important to the diets of humans. Consequently, efforts to maintain the health of this ecosystem need to include the development of models that describe the movement of these compounds from their sources to North Pacific food webs, and periodic monitoring of their levels.

Acknowledgments

We wish to thank those who collected samples for this project, including Jim Murphy and Doyne W. Kessler from the Alaska Fisheries Science Center, and Jennifer Stahl from the University of Alaska Fairbanks. We appreciate the contaminant analyses completed by Daryle Boyd and Karen Tilbury of the Northwest Fisheries Science Center. In addition we wish to thank Erin Flynn and Mandy Johnson for sample preparation. This project was funded under the NOAA Steller Sea Lion Initiative.

References

AMAP. 1998. AMAP Assessment report: Arctic pollution issues. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway. 859 pp.

Anthony, J.A., D.D. Roby, and K.R. Turco. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. J. Exp. Mar. Biol. Ecol. 248:53-78.

Barron, M.G., R. Heintz, and M.M. Krahn. 2003. Contaminant exposure and effects in pinnipeds: Implications for Steller sea lion declines in Alaska. Sci. Total Environ. 311:111-133.

Beckmen, K.B. 2001. Contaminants in free-ranging Steller sea lions: Organochlorines in blood, blubber, feces and prey. Workshop to Assess Contaminant Impacts on Steller Sea lions in Alaska, Anchorage, September 5-6. National Marine Fisheries Service, Auke Bay Laboratory, Juneau.

Calkins, D.G. 1998. Prey of Steller sea lions in the Bering Sea. Biosphere Conserv. 1:33-44.

Christie, W.D. 1989. Gas chromatography and lipids: A practical guide. Oily Press, Ayr, UK. 307 pp.

de Brito, A.P.X., D. Ueno, S. Takahashi, and S. Tanabe. 2002. Contamination by organochlorine compounds in walleye pollock (*Theragra chalcogramma*) from the Bering Sea, Gulf of Alaska, and the Japan Sea. Mar. Pollut. Bull. 44:164-177.

Folch, J., M. Lees, and G.H.S. Stanley. 1957. A simple method for the isolation and purification of total lipids from animal tissues. J. Biol. Chem. 226:497-509.

Hoekstra, P.F., T.M. O'Hara, A.T. Fisk, K. Borga, Kr.R. Solomon, and D.C.G. Muir. 2003. Trophic transfer of persistent organochlorine contaminants (OCs) within an Arctic marine food web from the southern Beaufort-Chukchi seas. Environ. Pollut. 124:509-522.

Kawano, M., S. Matsushita, T. Inoue, H. Tananaka, and R. Tatsukawa. 1986. Biological accumulation of chlordane compounds in marine organisms from the northern North Pacific and Bering Sea. Mar. Pollut. Bull. 17:512-516.

Krahn, M.M., G.M. Ylitalo, J. Buzitis, C.A. Sloan, D.T. Boyd, S. Chan, and U. Varanasi. 1994. Screening for planar chlorobiphenyl congeners in tissues of marine biota by high-performance liquid chromatography with photodiode array detection. Chemosphere 29:117-139.

Merrick, R.L., and D.G. Calkins. 1996. Importance of juvenile walleye pollock, *Theragra chalcogramma*, in the diet of Gulf of Alaska Steller sea lions, *Eumetopias jubatus*. NOAA Tech. Rep. NMFS 126.

Merrick, R.L., M.K. Chumbley, and G.V. Boyd. 1997. Diet diversity of Steller sea lions (*Eumetopia jubatus*) and their population decline in Alaska: A potential relationship. Can. J. Fish. Aquat. Sci. 54:1342-1348.

Ruus, A., K.I. Ugland, and J.U. Skaare. 2000. Influence of trophic position on organochlorine concentrations and compositional patterns in a marine food web. Environ. Toxicol. Chem. 21:2356-2364.

Sambrotto, R.N., and C.J. Lorenzen. 1986. Phytoplankton and primary production. In: D.W. Hood and S.T. Zimmerman (eds.), The Gulf of Alaska physical environment and biological resources. NOAA OCS Study 86-0095, Washington, D.C.

Sease, J.L., W.P. Taylor, T.R. Loughlin, and K.W. Pitcher. 2001. Aerial and land-based surveys of Steller sea lions (*Eumetopias jubatus*) in Alaska, June and July 1999 and 2000. NOAA Tech. Memo. NMFS-AFSC-122. 52 pp.

Sinclair, E.H., and T.K. Zeppelin. 2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). J. Mammal. 83:973-990.

Springer, A.M., J.A. Estes, G.B. vanVleit, T.M. Williams, D.F. Doak, E.M. Danner, K.A. Forney, and B. Pfister. 2003. Sequential megafaunal collapse in the north Pacific Ocean: An ongoing legacy of industrial whaling. Proc. Natl. Acad. Sci. 100:12223-12228.

Tollit, D.J., S.G. Heaslip, and A.W. Trites. 2004. Sizes of walleye pollock (*Theragra chalcogramma*) consumed by the eastern stock of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska from 1994 to 1999. Fish. Bull. U.S. 102:522-532.

Vander Pol, S.S., P.R. Becker, J.R. Kucklick, R.S. Pugh, D.G. Roseneau, and K.S. Simac. 2004. Persistent organic pollutants in Alaskan murre (*Uria* spp.) eggs: Geographical, species and temporal comparisons. Environ. Sci. Technol. 38:1305-1312.

Vollenweider, J.J. 2005. Variability in Steller sea lion prey quality in southeastern Alaska. Master's thesis, University of Alaska Fairbanks. 62 pp.

Winship, A., and A.W. Trites. 2003. Prey consumption of Steller sea lions (*Eumetopias jubatus*) off Alaska: How much prey do they require? Fish. Bull. U.S. 101:147-167.

Wise, S.A., M.M. Schantz, B. J. Koster, R. Demiralp, E.A. Mackey, R.R. Greenbert, M. Burow, P. Ostapczuk, and T.I. Lillestolen. 1993. Development of frozen whale blubber and liver reference materials for the measurement of organic and inorganic contaminants. Fresunius' J. Anal. Chem. 345:270-277.

Womble, J.N., and M.F. Sigler. 2006. Temporal variation in Steller sea lion diet at a seasonal haul-out in Southeast Alaska. In: A.W. Trites, S.K. Atkinson, D.P. DeMaster, L.W. Fritz, T.S. Gelatt, L.D. Rea, and K.M. Wynne (eds.), Sea lions of the world. Alaska Sea Grant College Program, University of Alaska Fairbanks.

Zeppelin, T.K., D.J. Tollit, K.A. Call, T.J. Orchard, and C.J. Gundmundson. 2004. Sizes of walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*) consumed by the western stock of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1998 to 2000. Fish. Bull. U.S. 102:509-521.

Characteristics of Vocalizations in Steller Sea Lions

Tae-Geon Park, Kohji Iida, and Tohru Mukai
Hokkaido University, Graduate School of Fisheries Sciences, Hakodate, Hokkaido, Japan

Abstract

We investigated the acoustics of Steller sea lion (*Eumetopias jubatus*) calls in wild individuals hauled out on shore reefs off the west coast of Hokkaido, northern Japan, and in captive sea lions at an aquarium using video camera observations. Steller sea lion calls were classified as "communication," "threat," "wheedling," and "acknowledge" according to associated behaviors. Classified calls were analyzed by means of sonograms for formant frequency (F_1), sound duration (T), and pitch pattern. All sounds emitted by males were lower in formant frequency than those of females, while sounds made by wild animals were lower than those of captive animals. Sounds by males were also longer in duration than those by females, while those made by wild animals were shorter than those by captive ones. Pitch of "communication" calls was a long flat pattern type, "threat" was a short descending type, and "wheedling" was a short ascending type for wild animals and a short wave-like type for the captives. The characteristics of pitch patterns of wild and captive animals suggest that the calls of Steller sea lions are for communication.

Introduction

Steller sea lions are distributed along the North Pacific coast and into the Okhotsk and Bering seas. Between 300 and 500 Steller sea lions migrate annually from the Kamchatka Peninsula and Kuril Islands to the western coast of Hokkaido in northern Japan from November to April (Davies 1958, Scheffer 1958, Peterson and Bartholomew 1967, Schusterman 1981, King 1983, Loughlin et al. 1984). In the long distance migration from the Okhotsk Sea to Hokkaido, roaring sounds of sea lions may have an important role in navigation and communicating with each other. The damage caused by Steller sea lions to the fishing industry of Hokkaido has resulted in studies of migration and breeding areas. However, a study on vocal communication and the acoustic characteristics of calls has not been previously done.

Materials and methods

Data acquisition

The experiments were carried out with Steller sea lions at the Muroran Municipal Aquarium, and with wild sea lions at a winter haul-out on reefs near Cape Ofuyu along the western coast of Hokkaido, northern Japan.

Three captive Steller sea lions (a 3- and a 23-year-old male, and an 18-year-old female) were recorded day and night with video cameras (TC-D5M, Sony, Japan) set atop a fence surrounding a swimming pool at the aquarium (November 1-30, 2001). The entire pool area was recorded from approximately 20 m, which did not affect the sea lions' behaviors. Roaring sounds were recorded simultaneously using a microphone built into the video camera.

Calls and behaviors of 42-66 wild sea lions that migrated to the haul-out near Cape Ofuyu were recorded for five days (April 12-16, 2003). The video camera and a microphone recorded behaviors and vocalizations of the sea lions from sunrise to sunset.

The calls of captive and wild Steller sea lions were analyzed using an oscilloscope, FFT analyzer, and digital sonograph (Kay model DSP Sona-Graph 5500), and were compared with their behaviors recorded on videotape.

We catalogued 185 calls from three captive sea lions in 2001, and 303 calls from wild sea lions in 2003.

Classification of calls

According to activities observed in captive Steller sea lions, each individual had specific calls that corresponded to specific behaviors. These included "communication" calls emitted to communicate with other sea lions, "threat" calls emitted to fight for or defend territory, "wheedling" calls emitted during socialization or when eating prey, and "acknowledge" calls emitted in response to other sea lions (Fig. 1). These specific calls were also used to distinguish vocalizations of wild sea lions. Unfortunately, it was difficult to accurately classify the activities of wild individuals due to various environmental factors. In particular, the large numbers of sea lions at the haul-out made it almost impossible to identify individuals, as was done for captive sea lions. The characteristics of calls were classified based on the above four call types related to behaviors of captive sea lions. Three types of calls were classified (communication, threat, and wheedling) and examined in relation to the behaviors of the wild sea lions.

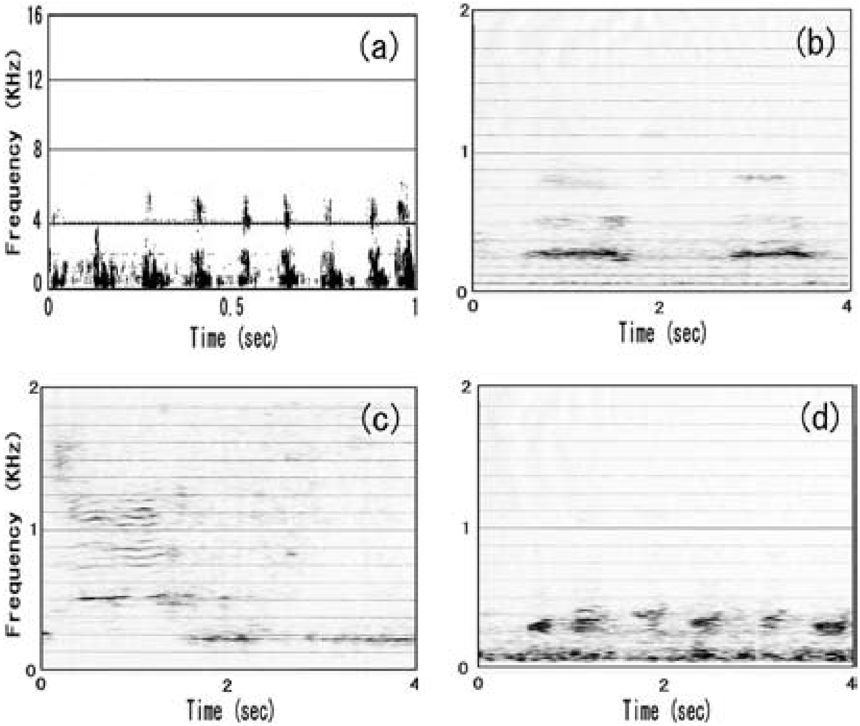


Figure 1. Vocalization classification by Steller sea lion behaviors: (a) "wheedling" sound in captive male, (b) "communication" sound in wild male, (c) "acknowledge" sound in captive female, and (d) "threat" sound in wild male.

We analyzed and classified the acoustical characteristics for wild (three types) and captive sea lions (four types) according to formant frequency (F_1), sound duration (T), and pitch pattern of the vocalizations.

Results

Formant frequency (F_1)

The F_1 of "communication," "wheedling," and "threat" calls for females was generally higher than those for males (Fig. 2). The F_1 of the "communication" sound of females was higher than that of males for both wild and captive sea lions. The F_1 of "wheedling" and "threat" sounds of wild females were higher than those of wild males. The F_1 of wild sea lions was lower than that of captive ones. The F_1s of the "threat" sound for males and females were similar.

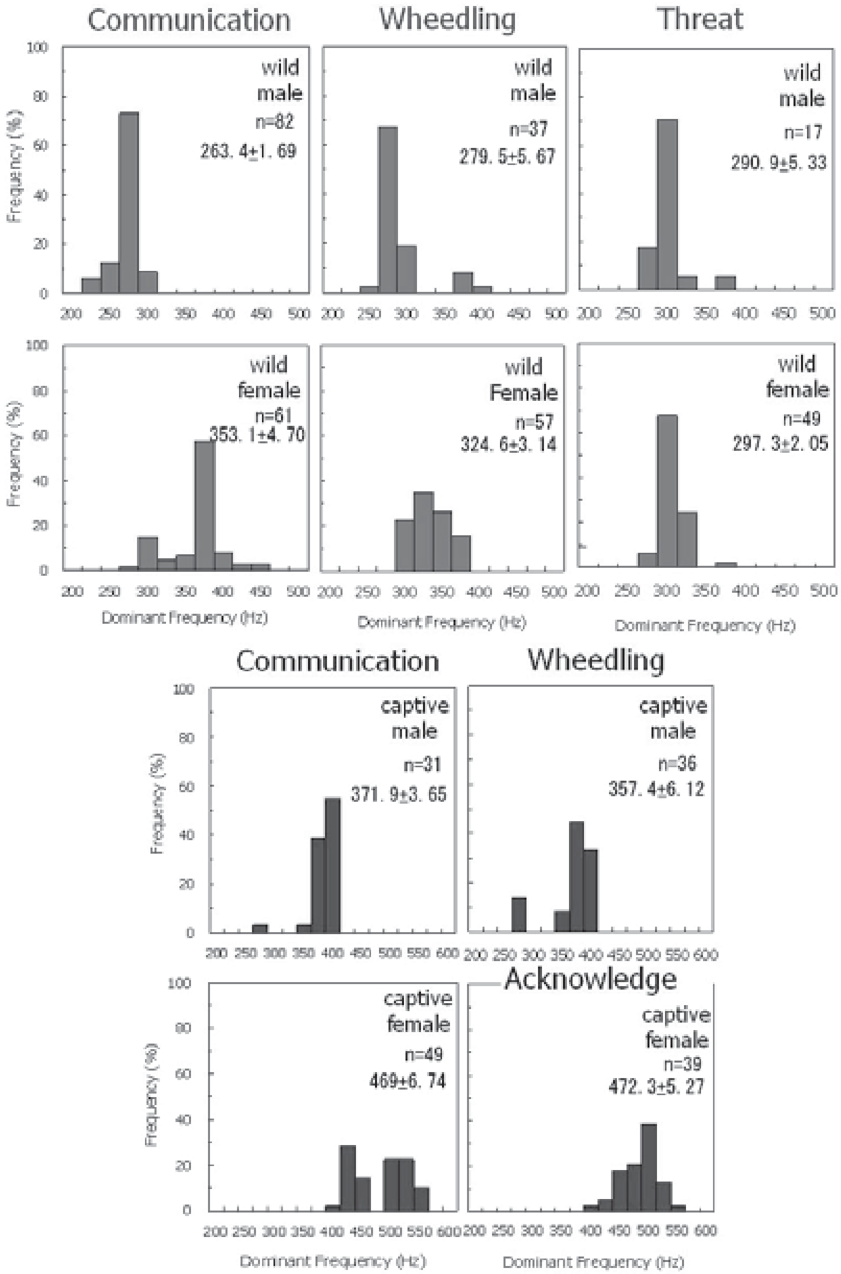


Figure 2. Comparison of formant frequency between males and females for wild and captive Steller sea lions.

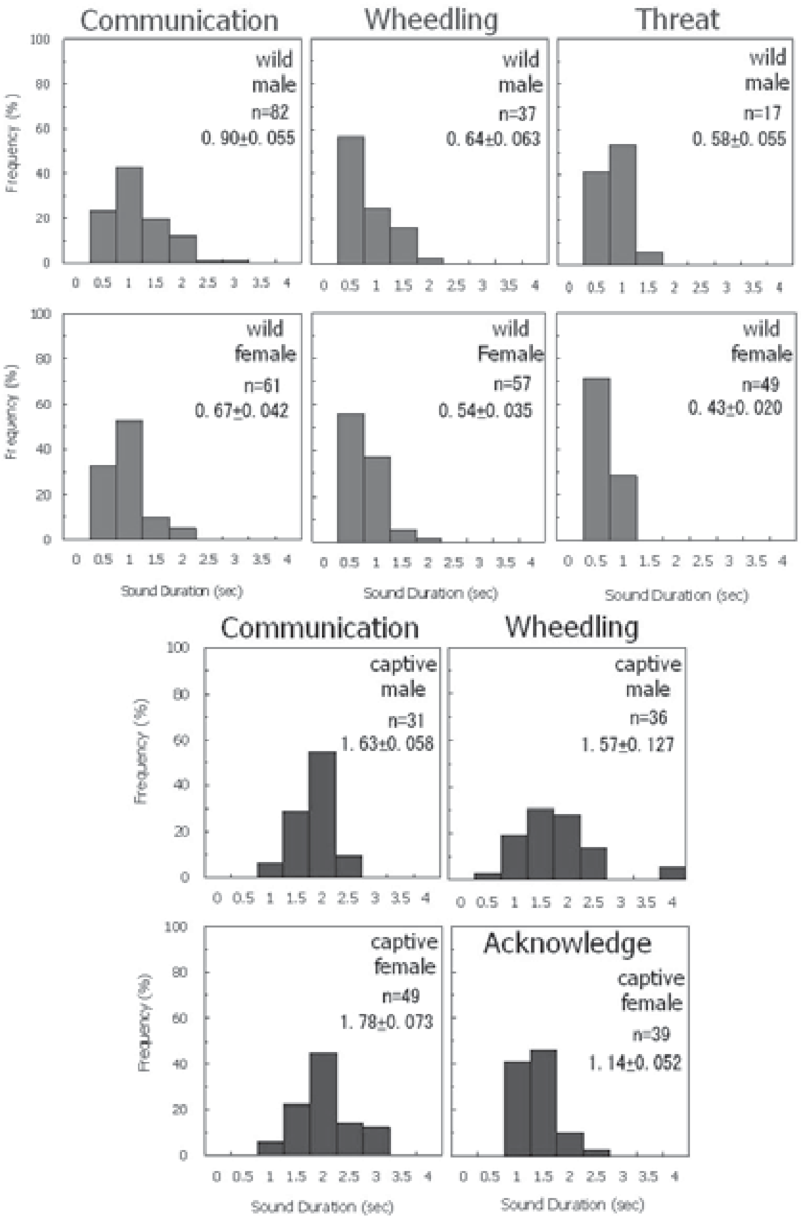


Figure 3. **Comparison of sound duration between males and females for wild and captive Steller sea lions.**

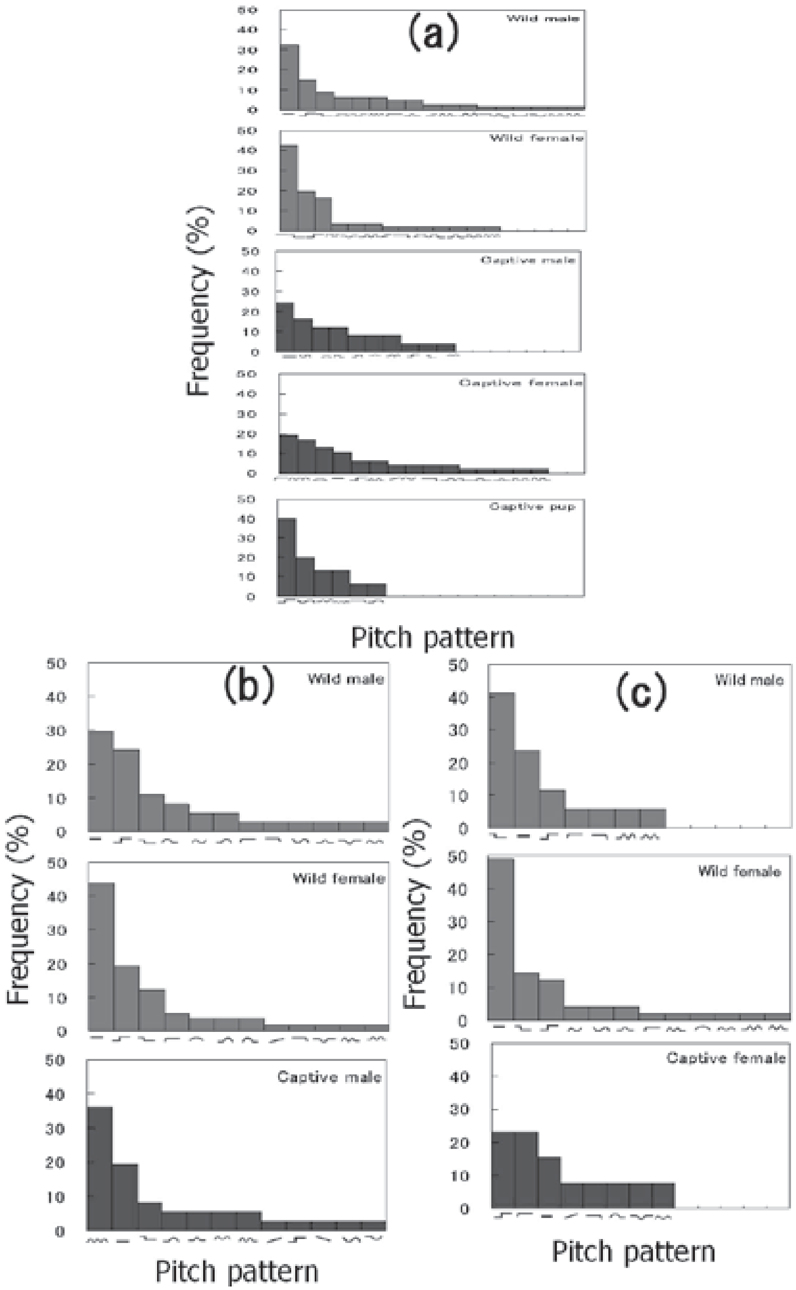


Figure 4. Pitch pattern distributions of (a) "communication" sound, (b) "wheedling" sound, and (c) "threat" sound, for Steller sea lions.

Table 1. Pitch pattern distributions of "communication" sound for Steller sea lions. The number is a frequency that the Steller sea lions used.

Gradation of utilization	Wild				Captive					
	male		female		male		female		pup	
1		4		4		4		2		5
2		5		4		2		4		2
3		4		5		4		4		3
4		4		2		4		4		4
5		2		2		3		5		4
6		4		3		4		3		3
7		2		3		3		3		
8		4		4		5		2		
9		3		4		4		4		
10		1		4		3		3		
11		3		4				4		
12		4		3				4		
13		4		4				4		
14		1						3		
15		1						3		
16		3								
17		3								

Sound duration (T)

Figure 3 shows the sound durations of classified call types of wild and captive Steller sea lions. The histograms for the wild individuals show sound durations of both males and females were shorter for threat sounds than for wheedling sounds, which were shorter in turn than communication sounds. Additionally, sound duration of the calls of captive lions was longer than those of the wild ones.

Common feature of pitch patterns

Figure 4a shows pitch pattern of "communication" for captive sea lions and wild ones. The frequency distribution of pitch patterns of "wheedling" and "threat" sounds for captive sea lions and wild ones were similar (Figs. 4b and 4c).

Table 1 shows the common features of pitch patterns in the order of frequency of "communication" sound for both wild and captive sea lions based on Fig. 4a (Dreher 1961). The numbers of pitch pattern types used in the "communication" calls were 17 for wild males, 13 for the wild females, 10 for a captive male, 15 for a captive female, and 6 for the captive juvenile.

The main pitch pattern of "communication" was the "long flat" type. The number 5 means it was a more common feature of pitch patterns,

Table 2. Pitch pattern distributions of "wheedling" sound for Steller sea lions. The number is a frequency that the Steller sea lions used.

Gradation of utilization	Wild				Captive	
	male		female		male	
1		3		3		1
2		3		3		3
3		3		3		3
4		2		2		3
5		1		1		2
6		3		3		2
7		2		2		2
8		2		2		2
9		2		2		3
10		2		2		1
11		2		2		2
12		2		1		1

and the number 1 means it was a less common feature. Common features are indicative of animals that share the same environment; few common features of males and females implies they use different environments.

In the common feature of pitch pattern for the captive juvenile, 3 out of 6 types showed features in common. It can be considered as the result of learning "communication" sound from their parents in the same group. The reason that there were only a few pitch patterns was likely because juveniles are in the middle of learning.

Table 2 shows 12 pitch patterns of "wheedling" for captive male Steller sea lions and wild male and female sea lions. The primary pattern of "wheedling" was short and ascending for the wild sea lions and a short waveform for the captive male. The captive male and wild Steller sea lions had a relatively high degree of common features for "wheedling."

For pitch patterns used in the "threat" sound of Steller sea lions, the wild males showed 7 types, the wild females 12 types, and captive female 8 types (Table 3). The main pattern was short and descending for the wild animals. The common characteristic was low for "threat" and high for "wheedling."

Discussion

The English language has 26 letters of which some are repeatedly used more than other letters (Shannon 1948, Witten 1990). Information coding can be studied by analyzing the frequency of use of letters (Shannon

Table 3. Pitch pattern distributions of "threat" sound for Steller sea lions. The number is a frequency that the Steller sea lions used.

Gradation of utilization	Wild				Captive	
	male		female		female	
1		2		3		3
2		3		2		3
3		3		3		3
4		3		1		1
5		2		1		2
6		2		1		1
7		1		3		1
8				1		2
9				1		
10				2		
11				2		
12				1		

1948, Cherry 1978). Plotting the frequency of occurrence on a log-probability plot is one means of uncovering the relationship between information theory and language (Dreher and Evans 1964). Therefore, the calls of sea lions could be inferred to hold valuable information if the occurrence frequency of call types falls on the line in a log probability plot (Fig. 5).

Pitch pattern arrangement graphs of the three call types were used to confirm whether the calls that were classified by their activities had meanings of information exchange with each other. The graphs plotted pitch pattern frequency against the logarithm of probability (where the number of their calls was converted to 1,000). They showed that the pitch patterns used by each Steller sea lion fell on a straight line for "communication," which suggests that "communication" has a meaning of information interchange among individuals. "Wheedling" and "threat" sounds also have a meaning of information interchange (Fig. 6).

It can be concluded that calls can be identified between males, females, and juveniles based on the characteristics of calls. The results showed sea lions may have the ability to find their offspring using vocalizations, as northern fur seals do (Takemura et al. 1983, Riedman 1990, Insley 1992). Moreover, the calls of sea lions appear to be used to exchange information, as echolocation does for whales (Watkins and Schevill 1977). Thus it can be concluded that the calls of sea lions are important to maintain their groups, and may even play a role in facilitating sea lion navigation.

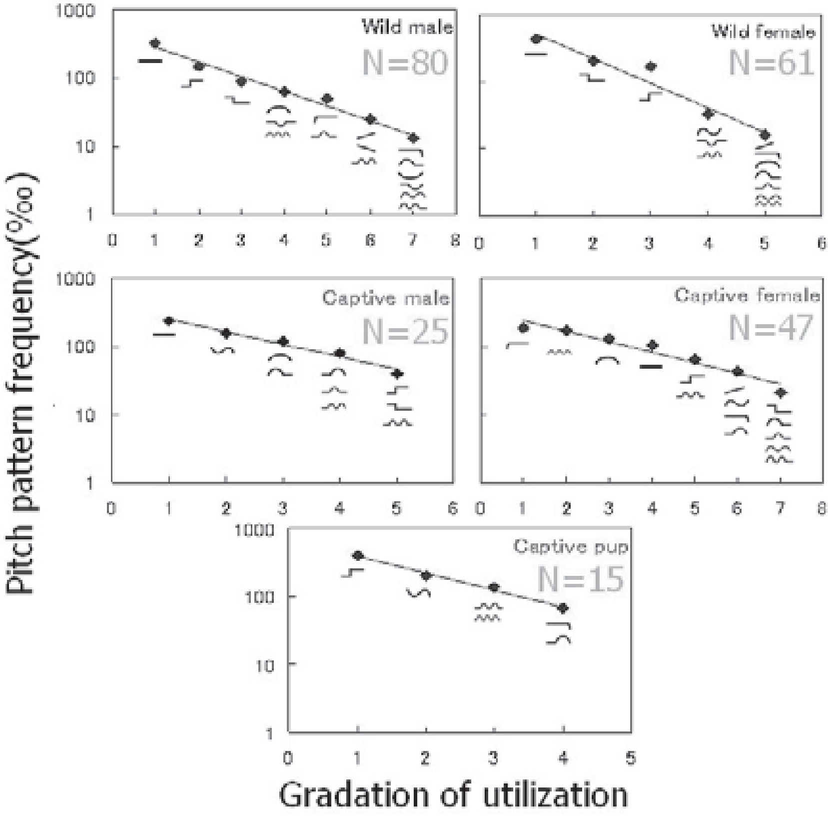


Figure 5. Pitch pattern frequency relative to pattern types of "communication" sound for Steller sea lions.

Acknowledgments

The authors thank Emeritus Professor Haruo Ogi of Hokkaido University, who motivated us to begin this research. We also thank Dr. Donhyug Kang, Dr. Myounghee Kang, Dr. Kyounghoon Lee, Mr. Takuma Takayama, and Mr. Shoji Kotani for their assistance with the experiments and in collecting material. We wish to thank the Muroran Municipal Aquarium for providing captive Steller sea lions.

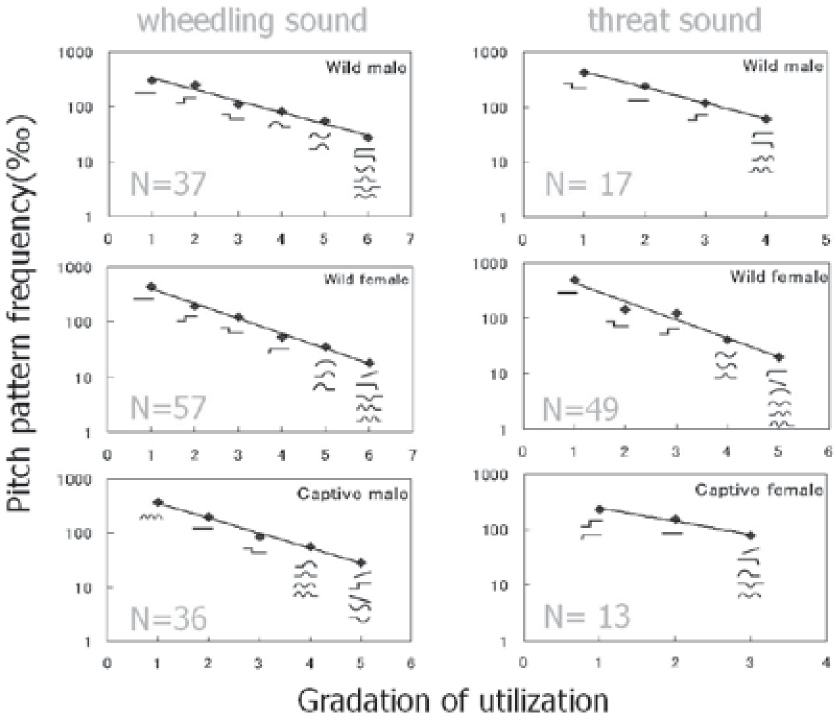


Figure 6. Pitch pattern frequency relative to pattern types of "wheedling" sound and "threat" sound for Steller sea lions.

References

Cherry, C. 1978. On human communication. 3rd edn. MIT Press.

Davies, J.L. 1958. The Pinnipedia: An essay in zoogeography. Geogr. Rev. 48:1817-1832.

Dreher, J.J. 1961. Linguistic considerations of porpoise sounds. J. Acoust. Soc. Amer. 33:1799-1800.

Dreher, J.J., and W.E. Evans 1964. Cetacean communication. Marine Bio Acoustics, Academic Press, pp. 373-393.

Insley, S.J. 1992. Mother-offspring separation and acoustic stereotypy: A comparison of call morphology in two species of pinnipeds. Behaviour 120:103-121.

King, J.E. 1983. Seals of the world. Oxford University Press, Oxford. 240 pp.

Loughlin, T.R., D.J. Rugh, and C.H. Fiscus. 1984. Northern sea lion distribution and abundance: 1956-80. J. Wildl. Manag. 48:719-740.

Peterson, R.S., and G.A. Bartholomew 1967. The natural history and behavior of the California sea lion. Amer. Soc. Mamm. Special Publ. No. 1.

Riedman, M. 1990. The pinnipeds: Seals and sea lions. University of California, Berkeley.

Scheffer, V.B. 1958. Seals, sea lions, and walruses: A review of the Pinnipedia. Stanford University Press, Palo Alto, California. 179 pp.

Schusterman, R.J. 1981. Steller sea lion, *Eumetopias jubatus* (Schreber 1776). In: S.H. Ridgway and R.J. Harrison (eds.), Handbook of marine mammals. Vol. 1. Walrus, sea lions, fur seals and sea otters. Academic Press, New York, pp. 119-141.

Shannon, C.E. 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27:379-423, 623-656.

Takemura, A., K. Yoshida, and N. Baba. 1983. Distinction of individual northern fur seal pups, *Callorhinus ursinus*, through their call. Bull. Fac. Fish. Nagasaki Univ. 54:29-34.

Watkins, W.A., and W.E. Schevill. 1977. Sperm whale codas. J. Acoust. Soc. Amer. 62(6):1485-1490.

Witten, H. 1990. Source models for natural language text. Int. J. Man-Machine Studies 32:545-579.

Organochlorines in Walleye Pollock from the Bering Sea and Southeastern Alaska

Ron Heintz
NOAA Fisheries, Alaska Fisheries Science Center, Auke Bay Laboratory, Juneau, Alaska

Margaret M. Krahn and G.M. Ylitalo
NOAA Fisheries, Northwest Fisheries Science Center, Environmental Conservation Division, Seattle, Washington

Frank Morado
NOAA Fisheries, Alaska Fisheries Science Center, Resource Assessment and Conservation Engineering Division, Seattle, Washington

Abstract

The ubiquitous distribution and toxicity of organochlorines in high latitude food webs has been suggested as one factor in preventing the recovery of the western Steller sea lion stock. However, there are few data describing the bio-availability of these contaminants in the sub-arctic Bering Sea and Gulf of Alaska. We measured concentrations of dioxin-like and other selected polychlorinated biphenyls (PCBs), DDTs, and hexachlorobenzene (HCB) in a prey species of Steller sea lions (walleye pollock) that is distributed throughout the range of these marine mammals, to test the hypothesis that contaminant loads in western stock food webs would be higher than those of the eastern stock. More than 110 fish were collected from six regions: western Bering Sea, western Aleutians, eastern Aleutians, Pribilof Islands, northern Bering Sea, and southeastern Alaska. Organochlorine levels were found to correlate with fish age and size ($r^2 > 0.390$), but were uncorrelated with lipid content. Pollock from southeastern Alaska were significantly more contaminated than Bering Sea pollock ($P < 0.01$) with length-corrected concentrations of 5.00 ng per g wet weight, 4.93 ng per g, and 1.15 ng per g for total PCBs ($\sum$PCBs), total DDTs ($\sum$DDTs), and HCB, respectively. Aerial transport and precipitation likely account for the relatively high levels of contamination in southeastern Alaska. Eastern stock sea lion populations have been increasing while apparently consuming prey with higher organochlorine loads. Consequently, presence of organochlorines in high latitude food webs does not appear to be a major factor inhibiting the recovery of the western sea lion stock.

Introduction

The toxic effects of organochlorines have been proposed as one of the causes for the decline of the western stock of Steller sea lions and its failure to recover. Steller sea lions populations from Cape Yakutaga westward through the Aleutian Islands (Western stock) have been declining rapidly since the 1980s. In contrast, Steller sea lion populations in British Columbia and southeastern Alaska have been slowly increasing during the same period. Included among the organochlorines are the polychlorinated biphenyls (PCBs), hexachlorobenzene (HCB), and many pesticides including the dichlorodiphenytrichloroethanes (DDTs). The high volatility of these compounds allows them to be carried into the upper atmosphere at low latitudes and transported to colder northern latitudes where they condense and precipitate back to the earth's surface (AMAP 1998). Organochlorines are lipophilic and are therefore readily entrained in food webs, where they can be concentrated in the lipid-rich tissues of apex predators such as Steller sea lions. Although there are programs in place for monitoring organochlorine levels and trends in Arctic regions, much less effort has been directed at the subarctic Bering Sea and northern Gulf of Alaska, an area where populations of Steller sea lions and other apex predators have been declining over the last 20 years (Springer et al. 2003). Few Steller sea lion samples are available for contaminant analysis, because of the logistical difficulty associated with the capture and biopsy of individuals in this extremely remote region. In addition, captive animals are few which precludes controlled exposure studies.

Steller sea lions primarily acquire organochlorines through ingestion, so one way to understand the risk imparted by organochlorines to Steller sea lions is to evaluate their potential exposure by examining their prey in different parts of the sea lion range. Such an analysis depends on sampling a prey item that is ubiquitously distributed throughout the sea lion range; thus the confounding effects of trophic level, ecology, and lipid content can be minimized. Fortunately, walleye pollock (*Theragra chalcogramma*) are a frequently encountered prey item (Merrick and Calkins 1996, Calkins 1998, Womble and Sigler 2006). Estimates of the frequency of pollock in juvenile Steller sea lion scats range from 75% in the western Aleutians to 85% in southeastern Alaska.

Previous reports have measured organochlorines in walleye pollock, but these data shed little light on the relationship of organochlorine ex-

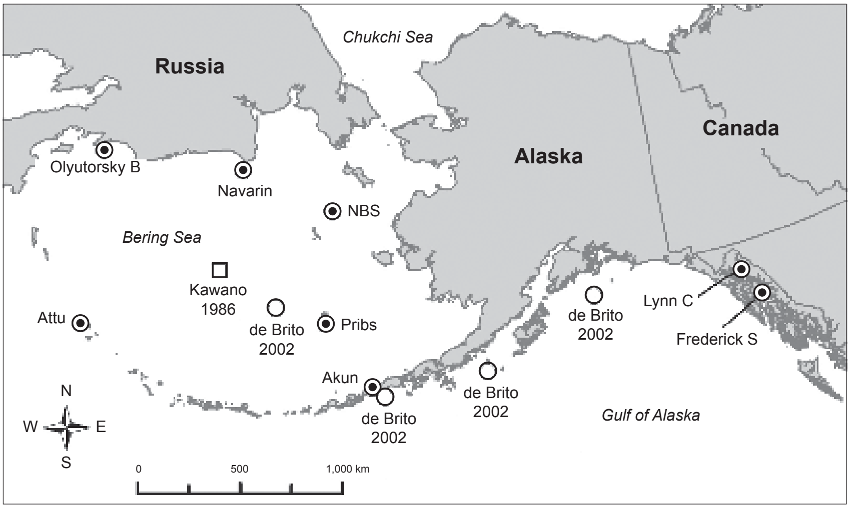


Figure 1. Sampling locations for pollock used in this study and those sampled by Kawano et al. (1986) and de Brito et al. (2002).

posure to declining populations of pollock predators, such as Steller sea lions. The first observation (Kawano et al. 1986) measured DDT, PCB, HCB, and chlordane levels in the whole bodies of three pollock collected from the mid-shelf of the Bering sea in 1982 (Fig. 1). In 1992, de Brito et al. (1992) estimated concentrations of these same compounds in the livers of 29 pollock collected from three locations in the Bering Sea and three in the Gulf of Alaska (Fig. 1). All of these samples were collected from the region in which apex predator populations are declining, but there are no comparable data from areas where predator populations are stable. Furthermore, time trends in organochlorine levels cannot be determined from these limited data sets because different tissues were used. Beckmen (2001) describes a third set of pollock analyzed for these compounds, but the specific sampling locations are not described.

The objective of this report is to understand spatial variation of organochlorines in a prey species of Steller sea lions. We present data describing the concentrations of 15 PCB congeners, five DDTs, and HCB in the tissues of walleye pollock collected from the Bering sea and southeastern Alaska, collected opportunistically in 2002 and 2003. In particular, we tested the hypothesis that the availability of organochlorines to apex predators from the Bering Sea is the same as that in southeastern Alaska by using the levels of these organochlorines in pollock as an index to their availability in local food webs. In addition we examine the relative concentrations of individual PCB congeners in pollock samples to determine if the PCB composition in the food webs varies among different geographic regions.

Methods

Sample collection and preparation

Walleye pollock samples were collected in the Bering Sea and southeastern Alaska in 2002 and 2003. In some cases, samples from locations relatively near each other were pooled to make collections representative of a region. Locations sampled during the summer and fall of 2002 included Frederick Sound in southeastern Alaska, Attu Island in the western Aleutian Islands, and Akun Island in the eastern Aleutians, a series of points along a transect between St. Lawrence and St. Matthew islands in the northern Bering Sea, Cape Navarin, and Olyutorsky Bay on the western shore of the Bering Sea. In February 2003 pollock were collected during the commercial fishery near the Priblilof Islands. Additional samples were collected from Lynn Canal in southeastern Alaska during April 2003 and added to the Frederick Sound samples to represent southeastern Alaska. Each of these sites is located on Fig. 1. Sampling dates, specific locations, and fish sizes are listed in Table 1. Samples chosen for processing were representative of the size range available at those sites during collection, with the exception of the Russian sites where size of the fish was limited by the logistics of transport back to the United States.

After collection, samples were immediately frozen and shipped as soon as possible to the NOAA Auke Bay Laboratory for preparation. Otoliths were removed and whole fish were cut in small pieces and homogenized in a commercial meat grinder. The resulting paste was spread over a 25 by 45 cm cutting board and two 5 gram samples were composited from randomly selected aliquots. One of the samples was kept for lipid extraction and the other was shipped frozen to the NOAA Montlake Laboratory in Seattle for organochlorine analysis. Samples for organochlorine analysis were stored in certified jars with Teflon lined lids. All homogenized samples were topped with nitrogen and stored at –80ºC prior to analysis. Temperature of the homogenates never exceeded 0ºC during processing. All grinding and sampling equipment was washed with hot soapy water between samples and rinsed with hexane between sets of samples from different locations. Ages of fish were determined from the otoliths at NOAA's ageing laboratory in Seattle, Washington, by two independent readers. Their age estimates agreed 90% of the time.

Organochlorine analysis by HPLC/PDA

Whole body homogenate samples of pollock were analyzed for selected organochlorines, including dioxin-like polychlorinated biphenyls (PCBs)

Table 1. Location names and sample information for walleye pollock collected for organochlorine analysis.

Region	Location	Latitude	Longitude	Collection date	Sample size	Average length (mm)	Average weight (g)	Average age (years)
SEAK	Lynn Canal	58°30'N	134°48'W	08-Apr-03	10	306.0 (73.4)	300.0 (323.4)	3.2 (1.8)
SEAK	Frederick Sound	58°21'N	134°08'W	03-Apr-02	10	489.0 (92.7)	1159.2 (744.1)	7.5 (1.0)
WAI	Attu Is.	52°48'N	172°24'E	21-Jun-02	12	456.7 (28.8)	627.1 (185.2)	4.6 (1.5)
EAI	Akun Is.	54°24'N	165°30'W	19-May-02	15	475.3 (28.8)	752.6 (132.6)	6.4 (1.1)
PRIBS	Pribilof Is.	56°44'N	170°21'W	26-Feb-03	15	443.3 (47.6)	583.3 (162.3)	6.1 (1.2)
NBS	Northern Bering Sea	60°57'N	171°31'W	28-Sep-02	27	353. (154.9)	537.2 (448.1)	5.1 (4.0)
WBS	Cape Navarin	61°35'N	178°36'E	1-Oct-02	15	124.8 (79.5)	37.6 (61.7)	0.6 (1.1)
WBS	Olyutorsky Bay	59°30'N	167°03'E	22-Sep-02	7	227.6 (20.4)	122.4 (29.5)	1.8 (0.4)

EAI = eastern Aleutian Islands, NBS = northern Bering Sea, PRIBS = Pribilof Islands, SEAK = southeastern Alaska, WAI = western Aleutian Islands, WBS = western Bering Sea. Numbers in parentheses represent 1 standard deviation.

and DDTs, by a high-performance liquid chromatography photodiode array (HPLC/PDA) method (Krahn et al. 1994). Briefly, whole fish homogenate (1.7-3.0 g), hexane/pentane (1:1 v/v), sodium sulfate (5 g), and a surrogate standard were homogenized and separated from interfering compounds (e.g., lipids, aromatic compounds) on a gravity flow cleanup column that contained neutral, basic, and acidic silica gels eluted with hexane/methylene chloride (1:1 v/v). Eight dioxin-like congeners (PCBs 77, 105, 118, 126, 156, 157, 169, 189) were resolved from other selected PCBs (PCBs 99/101/149, 110, 128, 138, 153, 170/194, and 180) and six additional organochlorines [*o,p′*-DDD, *p,p′*-DDD, *p,p′*-DDE, *o,p′*-DDT, *p,p′*-DDT, hexachlorobenzene (HCB)] by HPLC on two Cosmosil PYE analytical columns, connected in series and cooled to 16°C. The congeners were measured by an ultraviolet (UV) photodiode array detector and were identified by comparing their UV spectra (200-310 nm) and retention times to those of reference standards in a library. The analyte purity was confirmed by comparing spectra within a peak to the apex spectrum.

Summed PCB (∑PCB) concentrations were calculated using the following formula: ∑PCBs = ∑concentrations of 15 PCBs listed above (based on individual response factor) + ∑concentrations of other PCB congeners (calculated by summing areas of peaks identified as PCBs and using an average PCB response factor). Summed DDT (∑DDTs) concentrations were calculated by summing the concentrations of five DDTs (*o,p′*-DDD, *p,p′*-DDD, *p,p′*-DDE, *o,p′*-DDT, *p,p′*-DDT).

Lipid extraction

Lipid was extracted using a modification of Folch's method (1957) outlined by Christie (1989) using a Dionex Accelerated Solvent Extractor (ASE) 200. Approximately 1 g of wet homogenate was mixed with a drying agent (Hydromatrix) and masticating agent (sand) and loaded into ASE cells. Samples were extracted using a 2:1 (v:v) chloroform:methanol solvent at 1,200 psi and 120°C. Following extraction, the filtrate was washed to remove the coextractables with a 0.88% KCl solution followed by a solution of 1:1 (v:v) methanol:deionized water, both in a volume equal to 25% of the extract volume. Excess solvent was evaporated to reduce the sample volume to 1 ml. Percent lipid was calculated gravimetrically.

Quality assurance

During lipid extraction, quality assurance samples were extracted with each batch of 17 samples and these included (1) a blank, (2) a replicate sample consisting of a second aliquot of homogenate of one of the samples in the batch, and (3) a reference sample of herring homogenate, which had been previously characterized for lipid content. Accuracy of the estimate for the reference sample, repeatability, and method cleanliness were required to meet laboratory criteria or the batch was re-extracted.

To monitor the accuracy of our HPLC/PDA method, a National Institute of Standards and Technology (NIST) Standard Reference Material (blue mussel SRM1974b or fish homogenate SRM1946) was analyzed with each sample set and results met laboratory criteria (Wise et al. 1993). Approximately 10% of fish homogenate samples were analyzed in duplicate to measure precision of the method, and the laboratory quality assurance criteria were met for all analytes detected in these samples. Method blanks also met laboratory criteria.

Statistical analysis

Sample collections varied in average fish size and age (Table 1), suggesting the presence of important covariates with location in the analysis of the sample collections. Consequently, statistical analysis began by understanding how age, size, and lipid content related to the observed organochlorine concentrations. The observed concentrations of ∑PCBs, ∑DDTs, and HCB were plotted against length, age, and lipid content (percent wet weight) for the entire data set and the resulting relationship evaluated by linear regression. Observations below detection limit were set to zero. In addition, the relationships between the covariates were also examined by linear regression.

Spatial variation in organochlorine content was examined by ordinal logistic regression with region as a factor and age as a covariate. Logistic regression was used because organochlorine concentrations in different regions were not normally distributed and had heterogeneous variances. Ordinal logistic regression requires categorical response variables, so the organochlorine contents of all specimens were sorted and assigned to deciles. Consequently, the regression examined the frequency distribution of deciles within each region, while accounting for differences in age. When assigning deciles to observations of ∑DDTs, 32 of the 111 samples were found to have undetectable DDT levels; these were removed from the analysis. Finally, ANCOVA was used to calculate least square mean organochlorine contents for fish from each region using age as a covariate. These values were not tested, but are used here to report representative age-normalized values for contaminant load in different regions. In the event that an interaction between age and region was found to influence organochlorine levels, the slopes of the age and organochlorine relationships between regions were compared using Student's *t* test.

Compositional differences in the organochlorines found in fish from different geographical regions were examined by a combination of ANCOVA and multivariate analysis of covariance (MANCOVA). The observed concentrations of PCB congeners found to be above the detection limit in at least two fish from each region were examined individually by ANCOVA with region as the main factor and age as the covariate. Prior to analysis, the concentrations were transformed by dividing each congener's concentration by the observed ∑PCBs to generate relative con-

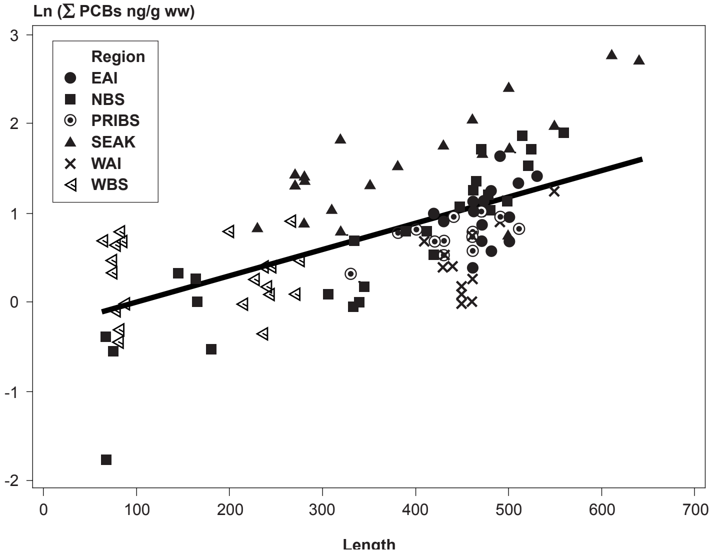


Figure 2. Relationship between natural log of ∑PCBs (ng per g wet weight) and length (mm) for pollock in the Bering Sea and southeastern Alaska. The line depicts the regressed fit for all samples. Abbreviations: EAI = eastern Aleutian Islands, NBS = northern Bering Sea, PRIBS = Pribilof Islands, SEAK = southeastern Alaska, WAI = western Aleutian Islands, WBS = western Bering Sea.

centrations. In addition, the entire group of congeners was subsequently examined together by MANCOVA to test the hypothesis that the relative concentrations of the congeners varied among regions.

Results

Relationships between covariates and organochlorine concentrations

There were strong relationships between the organochlorine content of pollock and their lengths. Average values (±1 s.d.) for ∑PCBs ranged from 1.40±0.55 to 5.79±4.00 ng per g wet weight in samples from western Bering Sea and southeastern Alaska, respectively (Table 2). Coincidently, these two collections represent those with the smallest and largest pollock, respectively (Table 1). The linear regression between the ∑PCBs and length for all of the fish sampled was significant ($P < 0.0005$, $r^2 = 0.252$). However, a scatter plot of the relationship indicated an exponential curve was better at describing this relationship (Fig. 2). This was confirmed by

Table 2. Observed average lipid content and organochlorine concentrations in walleye pollock from different locations. Only those congeners are shown for which concentrations were above detection limits.

Region	Location	% Lipid	PCB congener ng per g					ΣPCB ng per g	ΣDDT ng/g	HCB ng/g
			101	110	118	138	153			
SEAK	Lynn Canal	2.18 (0.68)	1.78 (0.77)	0.05 (0.11)	0.382 (0.34)	0.24 (0.33)	0.82 (0.64)	4.28 (2.65)	3.80 (3.34)	0.89 (0.28)
SEAK	Frederick Sound	4.02 (1.71)	1.53 (0.91)	0.24 (0.18)	0.80 (0.51)	0.44 (0.62)	1.54 (0.84)	7.30 (4.61)	8.36 (6.81)	1.62 (0.54)
WAI	Attu Is.	2.48 (1.33)	0.65 (0.28)	0.03 (0.09)	0.05 (0.12)	0.37 (0.16)	0.82 (0.27)	1.70 (0.74)	1.33 (0.63)	0.30 (0.41)
EAI	Akun Is.	3.55 (1.03)	1.17 (0.40)	0.07 (0.19)	0.35 (0.38)	0.31 (0.19)	0.90 (0.26)	2.88 (0.98)	1.65 (0.58)	1.37 (0.40)
PRIBS	Pribilof Is.	3.72 (1.65)	1.18 (0.28)	0.06 (0.11)	0.10 (0.11)	0.08 (0.11)	0.61 (0.11)	2.17 (0.38)	0.89 (0.22)	1.47 (0.41)
NBS	Northern Bering Sea	4.16 (2.29)	1.18 (1.30)	0.12 (0.15)	0.11 (0.15)	0.13 (0.22)	0.38 (0.35)	2.54 (1.85)	0.81 (0.98)	1.09 (0.46)
WBS	Cape Navarin	5.56 (1.34)	1.12 (0.56)	0.06 (0.11)	nd	nd	0.07 (0.15)	1.35 (0.53)	nd	0.92 (0.18)
WBS	Olyutorsky Bay	5.25 (1.68)	1.26 (0.76)	n.d	nd	nd	0.15 (0.16)	1.50 (0.63)	nd	0.76 (0.21)

EAI = eastern Aleutian Islands, NBS = northern Bering Sea, PRIBS = Pribilof Islands, SEAK = southeastern Alaska, WAI = western Aleutian Islands, WBS = western Bering Sea.
All concentrations are expressed as ng compound per g wet weight. Numbers in parentheses represent 1 standard deviation.
nd = analytes were not detected.

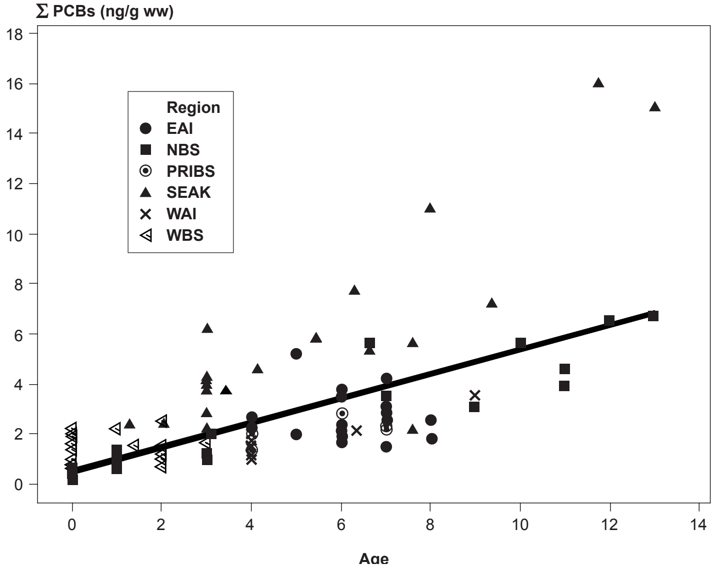


Figure 3. Relationship between ∑PCBs (ng per g wet weight) and age of walleye pollock collected from the Bering Sea and southeastern Alaska. Line depicts regression fit for all samples. Abbreviations are the same as those in Fig. 2.

regressing the natural logarithm of ∑PCBs against length ($P < 0.005$, $r^2 = 0.398$). Similarly, the concentrations of ∑DDTs varied with fish size, ranging from non-detectable to 6.08±5.72 ng per g wet weight for fish from the western Bering Sea and southeastern Alaska, respectively. While the regressed relationships between fish length and the natural logarithms of ∑DDTs and HCB were also significant ($P < 0.0005$), they were weakly correlated ($r^2 < 0.140$).

Age was directly related to contaminant load (Fig. 3). There was a linear relationship between age and ∑PCBs ($P < 0.0005$, $r^2 = 0.392$). Similarly, the relationships between age and ∑DDTs and HCB did not require transformation to natural logarithms ($P < 0.0005$, $0.140 < r^2 < 0.250$). This was consistent with the observed relationships between contaminant loads and size; as fish age they grow. The difference in the shapes of the relationships between age and length with organochlorine levels resulted from the asymptotic relationship between age and length in the pollock (Fig. 4). As pollock age, their contaminant levels apparently increase, but their growth rates level off resulting in a nonlinear relationship between size and contaminant level.

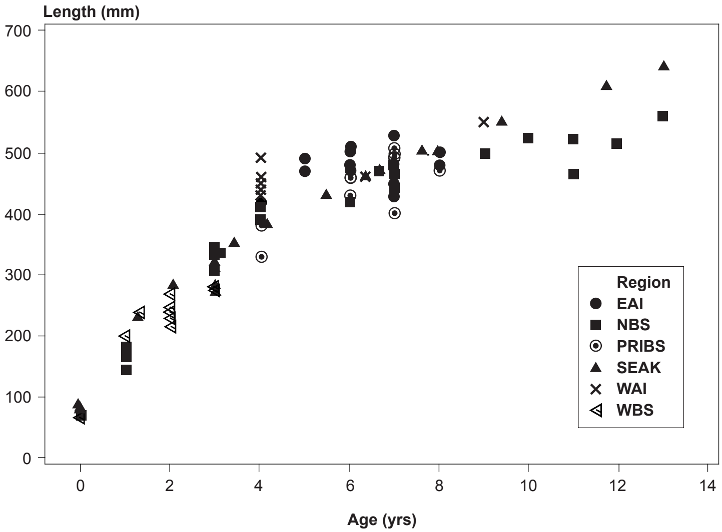


Figure 4. Relationship between age and length for walleye pollock collected from the Bering Sea and southeastern Alaska.

The lipid content, expressed as a percentage of wet mass, was unrelated to organochlorine level in pollock. Linear regression between ∑PCBs and the percent lipid content was not significant ($P = 0.854$, $r^2 = 0.0$). Inspection of a scatter plot revealed little indication of any relationship between lipid content and ∑PCBs (Fig. 5). Similarly, there was no relationship between lipid content and ∑DDTs ($P = 0.724$, $r^2 = 0.0$). However, there was a weakly correlated relationship between lipid and HCB ($P < 0.0005$, $r^2= 0.189$). The general lack of relationship between percentage lipid and organochlorine content was consistent with a lack of relationship between lipid content and size of the pollock ($P = 0.071$, $r^2 = 0.021$), which has been previously described (Anthony et al. 2000, Vollenweider 2005).

Spatial variation in organochlorine concentrations

Ordinal logistic regression of the ∑PCBs levels in pollock from different regions indicated a significant elevation in the availability of ∑PCBs to pollock in southeastern Alaska. There was a significant interaction between age and region on ∑PCB level ($\chi^2 = 14.8$, $P = 0.011$) indicating that pollock in different regions acquire ∑PCBs at different rates with respect to time. Removing the northern Bering Sea collection from the regression resulted in no interaction ($\chi^2 = 7.81$, $P = 0.099$) and a significant difference among regions ($\chi^2 = 14.00$, $P = 0.007$). Age-corrected estimates of

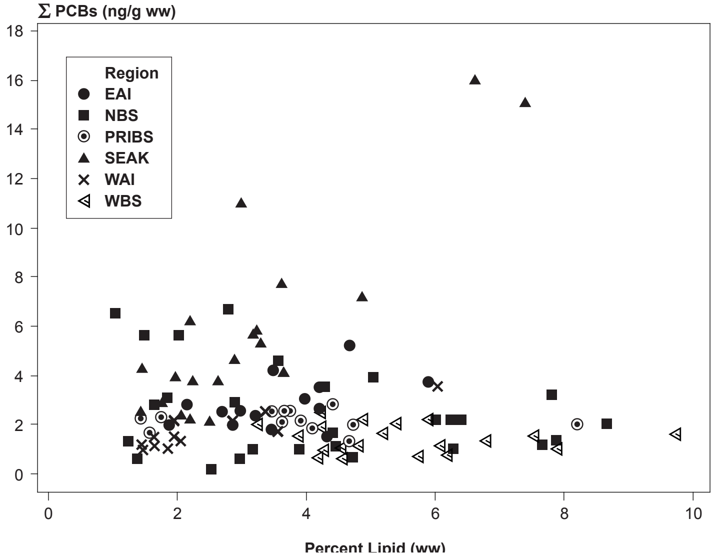


Figure 5. Relationship between ∑PCBs (ng per g wet weight) and lipid content (% wet weight) of pollock collected from the Bering Sea and southeastern Alaska. No relationship was detected by regression. Abbreviations are the same as those in Fig. 2.

the mean ∑PCBs, derived by ANCOVA (Fig. 6) indicated pollock from southeastern Alaska had greater ∑PCBs than those from the western Aleutians and western Bering Sea. Pollock, aged 4.6 years, averaged 5.0 ng ∑PCBs per g wet weight while those from the western Aleutian Islands and western Bering Sea averaged less than 1.7 ng ∑PCBs per g wet weight (Table 2). Pollock from the eastern Aleutians and Pribilofs averaged 3.3 and 2.0 ng per g, respectively. Heterogeneous variances and interactions prevent direct comparison of these means, but comparison of the slopes relating age and ∑PCBs for pollock from southeastern Alaska and northern Bering Sea indicated that pollock from southeastern Alaska acquire PCBs at nearly two and one-half times the rate of those in the northern Bering Sea and western Aleutians ($t > 14.0$, $P < 0.0005$). However, there was no difference in the slopes relating age and ∑PCBs for pollock from the northern Bering Sea and western Aleutians ($t = 1.71$, $P = 0.115$) (Fig. 3). Other comparisons of slopes were not made due to the narrowness of the age ranges in collections from the remaining regions (Table 1).

DDT content of pollock depended on the region in which fish were collected ($\chi^2 = 28.83$, $P < 0.0005$). There was no interaction between region and age on DDT content ($\chi^2 = 3.76$, $P = 0.440$). Pollock from southeastern

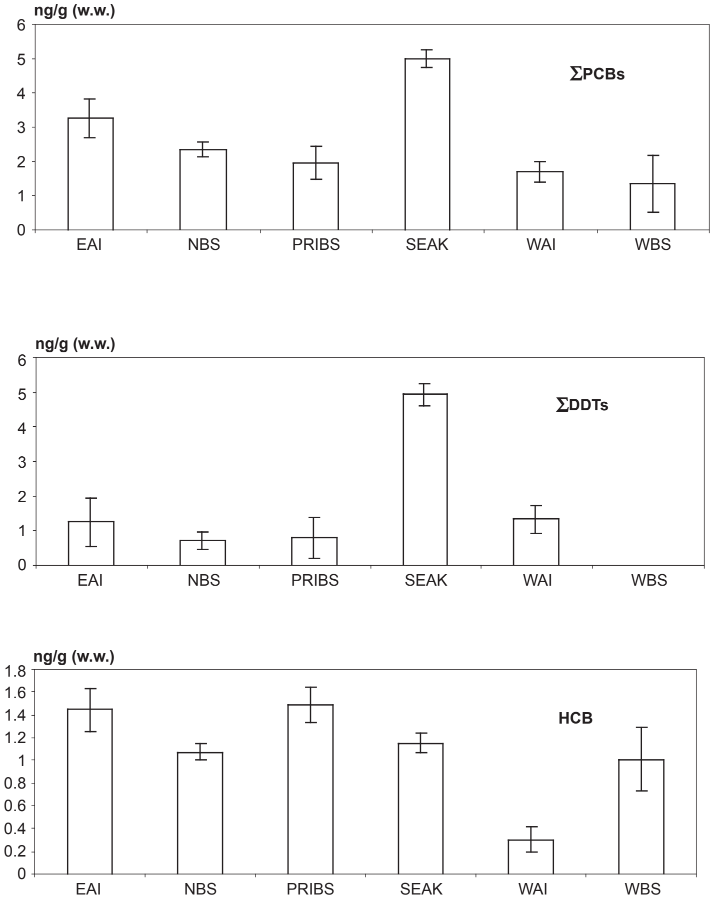


Figure 6. Age adjusted organochlorine (OC) concentrations (ng OC per g wet weight) (± 1 s.e.) in pollock collected from different locations in the Bering Sea and southeastern Alaska. Top panel: ∑PCBs, middle: ∑DDTs, and lower: HCB. Abbreviations are the same as those in Fig. 2.

Alaska had the greatest DDT concentrations with age 4.6 pollock averaging 4.9 ng ∑DDTs per g wet weight in contrast to those from the western Aleutians, eastern Aleutians, Pribilofs, and northern Bering Sea, which averaged less than 1.33 ng ∑DDTs per g wet. No DDTs were detected in tissues of fish from the western Bering Sea (Table 2) (Fig. 6).

HCB content also varied regionally ($\chi^2 = 14.30$, $P = 0.014$). No interaction between age and region was observed for HCB content ($\chi^2 = 8.06$,

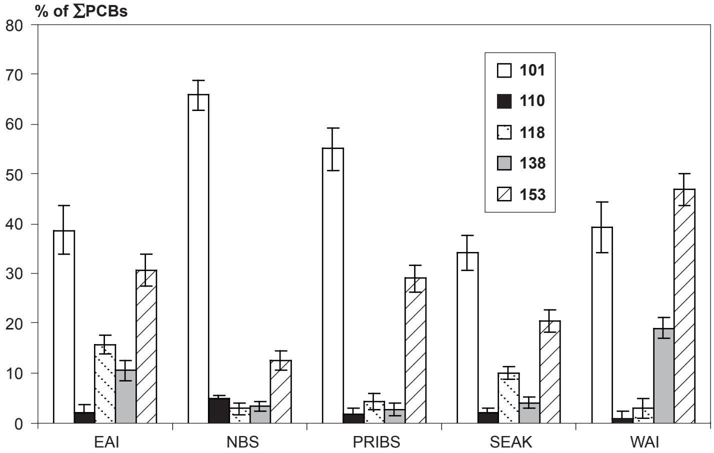


Figure 7. **Relative concentrations of selected PCB congeners (age adjusted by ANCOVA) in tissues of pollock from different regions in the Bering Sea and southeastern Alaska.**

$P = 0.153$). The regional differences arose from the relatively low levels of HCB observed among pollock from the western Aleutians (Table 2) (Fig. 6). Age 4.6 pollock from the western Aleutians averaged 0.30 ng HCB per g wet weight, in contrast to those from the other regions, whose HCB levels exceeded 1.01 ng HCB per g wet weight.

Spatial variation in composition

The generally low levels of organochlorines observed in pollock tissues limited analysis of their composition (Table 2). The only DDT routinely detected was p,p′-DDE and only PCBs 101, 110, 118, 138, and 153 were observed above detection limits more than once in all regions. PCB 101 was the only routinely detected congener found in western Bering Sea pollock, so they were deleted from the compositional analysis. None of the ANCOVAs indicated the presence of an interaction between region and age on the relative concentrations of any of the PCB congeners ($F_{4,55} < 2.01$, $P > 0.105$) or an effect of age ($F_{1,55} < 1.39$, $P > 0.244$). However, there were strong regional effects on the relative concentrations ($F_{4,55} > 3.08$, $P < 0.023$) of PCBs 101, 118, 138, and 153. PCB 110 appeared to be evenly distributed throughout the study area ($F_{4,55} = 0.72$, $P = 0.581$). A consequence of the disparate distribution of PCB congeners among regions (Fig. 7) was that the MANOVA indicated differences in PCB composition among regions (Wilks $\lambda = 0.389$, $P < 0.0005$).

Discussion

Significant differences occurred in the organochlorine content of pollock from different regions, resulting from variation in the availability of PCBs, DDTs, and HCB to regional food webs and not from regional differences in size or age of the fish. Elevated levels of PCBs, DDTs, and HCB were found in the tissues of pollock collected in southeastern Alaska compared to other regions. Further evidence for regional differences in the availability of organochlorines was offered by PCB congener patterns (101, 118, 138, and 153), which all demonstrated that these congeners are acquired at different rates in different regions and further suggest that food webs in different regions have differing PCB compositions. The low levels of organochlorines observed in western Bering Sea samples relative to those from other regions should be viewed with some caution. Fish collected from the western Bering Sea were younger than those in the remaining data set, indicating that most were juveniles. Therefore, less time was available for uptake of organochlorines. In addition, juveniles are likely to be less piscivorous than adults and therefore occupy a lower trophic level.

Our ability to detect organochlorines in each of the regions demonstrates that these compounds are ubiquitously distributed in the food webs of the Bering Sea and Gulf of Alaska. Southeastern and western Alaska are remote locations with exceedingly low population densities and few identifiable PCB sources (Barron et al. 2003). The availability of PCBs, DDTs, and HCB in these food webs is therefore likely determined through deposition from the atmosphere (AMAP 1998). Rain and snow are the most efficient scavengers for removing these compounds from the atmosphere and the relatively high organochlorine concentrations in southeastern Alaska pollock are consistent with the observation that average annual precipitation in that region is in excess of 125 cm per year. In particular, precipitation in Auke Bay, Alaska, a location near the Lynn Canal sites, averages 164 cm per year. In contrast, the precipitation levels at Akutan, located near the Akun Island site, averages 71 cm per year. Precipitation at Attu averages 124 cm per year, while precipitation for St. Paul and St. George islands in the Pribilofs, the region with the relatively low DDT and PCB levels, averages 58 cm per year. Precipitation in British Columbia and southeastern Alaska are the source of the Alaska coastal current, which flows from western North America to the Aleutian Islands. Organochlorines precipitated in southeastern Alaska may therefore ultimately be transported to the Bering Sea, effectively exposing all of the southern coast of Alaska.

Regional differences in the trophic level occupied by pollock may offer an alternative explanation for regional variation in organochlorine content. This could describe the relatively low levels observed among pollock collected at the western Bering Sea stations. However, the elevated levels of PCBs, DDTs, and HCB found in southeastern Alaska pollock are consistent with reports involving other species. Barron et al. (2003) indicated that juvenile Steller sea lions from southeastern Alaska had higher average concentrations of $\sum$PCBS and $\sum$DDTs than those from the Bering Sea. Similarly, Vander Pol et al. (2004) found higher levels of PCBs and DDTs in common murre eggs collected from southeastern Alaska compared to those from the Pribilof Islands. Conversely, HCB was higher in Pribilof eggs. It is unlikely that all of these species occupy higher trophic levels in southeastern Alaska than in other parts of their range; consequently trophic variation likely does not account for regional variation.

We report levels on a wet mass basis because organochlorines are consumed by pollock predators in wet tissue. However, expressing organochlorine concentrations on a lipid mass basis provides a method for comparing concentrations among species whose lipid contents vary. On a lipid mass basis, southeastern Alaska pollock averaged 184 ng $\sum$PCBS per g lipid (i.e., concentration divided by % lipid) and those from the northern Bering Sea, the most northerly collection of adults, averaged 103 ng per g lipid. These values are intermediate to those estimated for fourhorn sculpin and bearded seal near Pt. Barrow, Alaska (Hoekstra et al. 2003). In contrast, the lipid-normalized PCB levels reported here are an order of magnitude lower than those reported for polycheates and sandeels in the Hvaler archipelago near Norway (Ruus et al. 2002).

Discounting differences in analytical approaches, comparing our data to that from previous reports suggests levels of some organochlorines are declining in the Bering Sea pollock. Kawano et al. (1986) reported levels of 15.8 ng per g wet weight for $\sum$PCBs and 13.5 ng per g wet weight for $\sum$DDTs in whole pollock collected in 1982 (Fig. 1). The comparability between Kawano (1986) and data presented here is unknown, but we report levels of 2.7 and 1.1 ng per g wet weight for $\sum$PCBs and $\sum$DDTs, respectively for fish collected from approximately the same locations and average sizes. Beckmen (2001) reported levels of 9 ng per g wet weight for pollock collected from the Bering Sea between 1998 and 2000. This level is intermediate to those reported by Kawano et al. (1986) and this study and is therefore consistent with a temporal decline. While the analytical approach employed by Beckmen (2001) was identical to that used here, the ages of those fish are unknown.

Steller sea lion risk assessment

The risk of organochlorine exposure imposed by pollock to their predators, such as Steller sea lions, depends on where the foraging takes place, and the size and number of fish consumed. Data presented here indicate that Steller sea lions foraging on pollock in southeastern Alaska are likely to encounter higher organochlorine exposures than sea lions in the western stock. This conclusion assumes that sea lions consume equal masses of equally sized pollock, but estimates for the average size of pollock consumed by the western stock range between 359 and 424 mm (Zeppelin et al. 2004) and 410 and 439 mm for the eastern stock (Tollit et al. 2004). Comparison of the regressions between length and natural log ∑PCBS for southeastern Alaska pollock and those from eastern Aleutians, Pribilofs, and western Aleutians combined indicate that the average exposure of sea lions in southeastern Alaska is 4.7 ng ∑PCBs per g tissue consumed, while those from the west consume 1.8 ng ∑PCBs per g tissue. Winship and Trites (2003) estimated a 20% difference in consumption rate between western and eastern stock sea lions, demonstrating that differences in daily consumption rate are unlikely to compensate for differences in exposure. Consequently, the data presented here indicate that recovery of the western stock is not likely impeded by exposure to organochlorines, because eastern stock animals receive higher exposures and have increasing populations (Sease et al. 2001).

An important limitation to the risk assessment offered here is that variation in organochlorine content among other sea lion prey species has not been described. Western stock sea lions have less diverse diets (Merrick et al. 1997) and the rapidly declining populations in the far west rely heavily on lipid rich species such as Atka mackerel and salmon (Sinclair and Zeppelin 2002). This suggests that lipid intake rates vary among populations and our expectation is that variations in lipid intake will ultimately drive variation in exposure. Consequently, a more detailed analysis of exposure depends on accounting for differences in the rate of lipid ingestion and the lipid burdens in various prey. Such an analysis will ultimately provide the best information on the potential role of contaminants in the failed recovery of western stock sea lions.

The contaminants described here appear to be precipitated from the atmosphere in coastal mountain ranges and entrained in marine food webs where they can be detected even in low lipid species such as walleye pollock. These data indicate significant quantities of organochlorines are precipitated in southeastern Alaska where they can be transported westward in the Alaska coastal current, contaminating food webs along the southern coast of Alaska and eastern Bering Sea. Thus, the same geographic features responsible for the relatively high productivity of the northern Pacific and eastern Bering Sea also effectively pump organochlorines into those same food webs (Sambrotto and Lorenzen 1986). While PCB and DDT concentrations may be declining in the region, the general behavior of these compounds may predict the behavior of other lipophilic compounds whose concentrations are increasing, such as polybrominated diphenyl ethers (PBDEs). In addition to seals and sea lions, the dominant fish species in the northern North Pacific Ocean are important to the diets of humans. Consequently, efforts to maintain the health of this ecosystem need to include the development of models that describe the movement of these compounds from their sources to North Pacific food webs, and periodic monitoring of their levels.

Acknowledgments

We wish to thank those who collected samples for this project, including Jim Murphy and Doyne W. Kessler from the Alaska Fisheries Science Center, and Jennifer Stahl from the University of Alaska Fairbanks. We appreciate the contaminant analyses completed by Daryle Boyd and Karen Tilbury of the Northwest Fisheries Science Center. In addition we wish to thank Erin Flynn and Mandy Johnson for sample preparation. This project was funded under the NOAA Steller Sea Lion Initiative.

References

AMAP. 1998. AMAP Assessment report: Arctic pollution issues. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway. 859 pp.

Anthony, J.A., D.D. Roby, and K.R. Turco. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. J. Exp. Mar. Biol. Ecol. 248:53-78.

Barron, M.G., R. Heintz, and M.M. Krahn. 2003. Contaminant exposure and effects in pinnipeds: Implications for Steller sea lion declines in Alaska. Sci. Total Environ. 311:111-133.

Beckmen, K.B. 2001. Contaminants in free-ranging Steller sea lions: Organochlorines in blood, blubber, feces and prey. Workshop to Assess Contaminant Impacts on Steller Sea lions in Alaska, Anchorage, September 5-6. National Marine Fisheries Service, Auke Bay Laboratory, Juneau.

Calkins, D.G. 1998. Prey of Steller sea lions in the Bering Sea. Biosphere Conserv. 1:33-44.

Christie, W.D. 1989. Gas chromatography and lipids: A practical guide. Oily Press, Ayr, UK. 307 pp.

de Brito, A.P.X., D. Ueno, S. Takahashi, and S. Tanabe. 2002. Contamination by organochlorine compounds in walleye pollock (*Theragra chalcogramma*) from the Bering Sea, Gulf of Alaska, and the Japan Sea. Mar. Pollut. Bull. 44:164-177.

Folch, J., M. Lees, and G.H.S. Stanley. 1957. A simple method for the isolation and purification of total lipids from animal tissues. J. Biol. Chem. 226:497-509.

Hoekstra, P.F., T.M. O'Hara, A.T. Fisk, K. Borga, Kr.R. Solomon, and D.C.G. Muir. 2003. Trophic transfer of persistent organochlorine contaminants (OCs) within an Arctic marine food web from the southern Beaufort-Chukchi seas. Environ. Pollut. 124:509-522.

Kawano, M., S. Matsushita, T. Inoue, H. Tananaka, and R. Tatsukawa. 1986. Biological accumulation of chlordane compounds in marine organisms from the northern North Pacific and Bering Sea. Mar. Pollut. Bull. 17:512-516.

Krahn, M.M., G.M. Ylitalo, J. Buzitis, C.A. Sloan, D.T. Boyd, S. Chan, and U. Varanasi. 1994. Screening for planar chlorobiphenyl congeners in tissues of marine biota by high-performance liquid chromatography with photodiode array detection. Chemosphere 29:117-139.

Merrick, R.L., and D.G. Calkins. 1996. Importance of juvenile walleye pollock, *Theragra chalcogramma*, in the diet of Gulf of Alaska Steller sea lions, *Eumetopias jubatus*. NOAA Tech. Rep. NMFS 126.

Merrick, R.L., M.K. Chumbley, and G.V. Boyd. 1997. Diet diversity of Steller sea lions (*Eumetopia jubatus*) and their population decline in Alaska: A potential relationship. Can. J. Fish. Aquat. Sci. 54:1342-1348.

Ruus, A., K.I. Ugland, and J.U. Skaare. 2000. Influence of trophic position on organochlorine concentrations and compositional patterns in a marine food web. Environ. Toxicol. Chem. 21:2356-2364.

Sambrotto, R.N., and C.J. Lorenzen. 1986. Phytoplankton and primary production. In: D.W. Hood and S.T. Zimmerman (eds.), The Gulf of Alaska physical environment and biological resources. NOAA OCS Study 86-0095, Washington, D.C.

Sease, J.L., W.P. Taylor, T.R. Loughlin, and K.W. Pitcher. 2001. Aerial and land-based surveys of Steller sea lions (*Eumetopias jubatus*) in Alaska, June and July 1999 and 2000. NOAA Tech. Memo. NMFS-AFSC-122. 52 pp.

Sinclair, E.H., and T.K. Zeppelin. 2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). J. Mammal. 83:973-990.

Springer, A.M., J.A. Estes, G.B. vanVleit, T.M. Williams, D.F. Doak, E.M. Danner, K.A. Forney, and B. Pfister. 2003. Sequential megafaunal collapse in the north Pacific Ocean: An ongoing legacy of industrial whaling. Proc. Natl. Acad. Sci. 100:12223-12228.

Tollit, D.J., S.G. Heaslip, and A.W. Trites. 2004. Sizes of walleye pollock (*Theragra chalcogramma*) consumed by the eastern stock of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska from 1994 to 1999. Fish. Bull. U.S. 102:522-532.

Vander Pol, S.S., P.R. Becker, J.R. Kucklick, R.S. Pugh, D.G. Roseneau, and K.S. Simac. 2004. Persistent organic pollutants in Alaskan murre (*Uria* spp.) eggs: Geographical, species and temporal comparisons. Environ. Sci. Technol. 38:1305-1312.

Vollenweider, J.J. 2005. Variability in Steller sea lion prey quality in southeastern Alaska. Master's thesis, University of Alaska Fairbanks. 62 pp.

Winship, A., and A.W. Trites. 2003. Prey consumption of Steller sea lions (*Eumetopias jubatus*) off Alaska: How much prey do they require? Fish. Bull. U.S. 101:147-167.

Wise, S.A., M.M. Schantz, B. J. Koster, R. Demiralp, E.A. Mackey, R.R. Greenbert, M. Burow, P. Ostapczuk, and T.I. Lillestolen. 1993. Development of frozen whale blubber and liver reference materials for the measurement of organic and inorganic contaminants. Fresunius' J. Anal. Chem. 345:270-277.

Womble, J.N., and M.F. Sigler. 2006. Temporal variation in Steller sea lion diet at a seasonal haul-out in Southeast Alaska. In: A.W. Trites, S.K. Atkinson, D.P. DeMaster, L.W. Fritz, T.S. Gelatt, L.D. Rea, and K.M. Wynne (eds.), Sea lions of the world. Alaska Sea Grant College Program, University of Alaska Fairbanks.

Zeppelin, T.K., D.J. Tollit, K.A. Call, T.J. Orchard, and C.J. Gundmundson. 2004. Sizes of walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*) consumed by the western stock of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1998 to 2000. Fish. Bull. U.S. 102:509-521.

A Review of the Potential Effects of Disturbance on Sea Lions: Assessing Response and Recovery

Laura Kucey and Andrew W. Trites
University of British Columbia, Marine Mammal Research Unit, Fisheries Centre, Vancouver, British Columbia, Canada

Abstract

Human intrusion within areas of sea lion habitat is increasing worldwide, leading to concerns about disruption of distribution and daily activities of sea lions. Sea lion responses to disturbance can be quantified by recording changes in behavioral patterns, documenting numbers of animals on shore before, during, and after the disturbance, or by measuring physiological stress of individual animals. However, assessing recovery is not so straightforward, as highlighted by an example from a study of the short-term effects of disturbance on Steller sea lions. Recovery is generally recognized as a return to an original state or normal condition, but is often operationally defined as a percent-return to pre-disturbance numbers or behaviors. Simple interpretation of disturbance effects can be easily confounded by concurrent natural seasonal changes in behaviors or haul-out patterns, or by daily variability in numbers of animals present that can be attributed to weather, tidal cycle stage, and other factors. Overall, a range of recovery criteria needs to be simultaneously applied when assessing the effects of human disturbance on sea lion populations. Insights gained from research on the effects of disturbance on Steller sea lions may help guide the development of studies undertaken on other species of sea lions.

Introduction

Human intrusion within sea lion habitat has increased worldwide as development, resource exploitation, tourism, and research activities have expanded. Incursions may cause sea lions to deviate from their normal or reference behavioral state. They may also disrupt sea lion daily activities and cause them to move to new areas or redistribute themselves on their existing haul-outs. Severe disturbances may even interrupt community interactions or ecosystem functioning (Forbes et al. 2001).

Knowing how populations and individuals respond to disruptions to daily activities is necessary for assessing viability of populations faced with human pressures (Andersen et al. 1996). However, field experiments on a wide range of species have yielded conflicting conclusions about the effects of human disturbance on wild populations (e.g., Andersen 1996, Engelhard 2002, Kerley 2002). This inconsistency of results suggests that studies need to be species-specific.

Recent pinniped studies have focused on two types of disturbance: anthropogenic (Salter 1979, Lewis 1987, Suryan and Harvey 1999, Engelhard et al. 2001, Boren et al. 2002, Born et al. 2002, Blackwell et al. 2004, Cassini et al. 2004) and non-anthropogenic (Ono et al. 1987, Grellier et al. 1996, Porter 1997, Deecke et al. 2002). Human forms of potential sea lion disturbance include noise, vessel and aircraft traffic, human approach (both scientific and recreational), industrial activities, and development. Non-human disturbances can involve environmental changes, storms, birds, other sea lions, other species, predators, and landslides.

The following provides an overview of some of the scientific considerations that need to be addressed when evaluating the effects of disturbance on sea lions. Our insights stem from a detailed study of human disturbance on Steller sea lions (*Eumetopias jubatus*) (Kucey 2005) and have general applicability to pinnipeds. We examine how sea lions might respond to disturbances in time and space, and how their response can be measured. We also consider what is meant by recovery from a disturbance, and how it might be assessed. Finally, we provide an example from our study of Steller sea lions that highlights some of the difficulties in assessing recovery.

Response

Response of animals to disturbance may vary both temporally and spatially among groups within an area, and may result in greater avoidance or tolerance of certain areas depending on the source of the disturbance (Suryan and Harvey 1999, Gill et al. 2001a). Elements that might affect how animals respond to disturbance events can include the quality of the occupied site, the distance, availability, and quality of other sites, the risk of predation, density of competitors, or the investment that an individual or group has made in a site (Gill et al. 2001a). Responses may also be specific to an individual, or may occur at a group or population level. In general, behaviors of individual sea lions tend to be narrower and more specific than those of the population. However, preferences and response of individuals shape group behavior and can determine how the group will collectively act during any event or population change (Gentry 1998).

Animals may also have physiological responses to disturbance. One of the most promising means of assessing this is by measuring the concentration of stress hormones released by animals into their bloodstream, or passed through urine and feces (Whitten et al. 1998, Wingfield 2003). Research on a wide range of terrestrial birds and mammals suggests that differences in stress hormone concentrations pre- and post-disturbance are valid measures of response to disturbance (e.g., Wasser et al. 1997, Foley et al. 2001, Millspaugh et al. 2001).

In the short-term, the source of disturbance and whether it causes temporary displacements can usually be determined. However, knowing whether the disturbance impacts the population is another matter. Activities with no immediate, short-term effects may have the potential to cause cumulative effects that do not become apparent until the disturbance has continued for some time. Conversely, disturbances that cause immediate effects may not necessarily generate cumulative effects over time (Riffell et al. 1996). Disturbance thresholds and habituation are difficult to measure in wild populations and may affect response and recovery time. From a population viewpoint, species with high fitness costs and few habitat choices are the ones most likely to be adversely affected by disturbance. Displacement may reduce reproductive success for rare or declining species as well as reduce parental care and prey intake rates. It may also increase levels of vigilance and stress responses (Andersen et al. 1996, Riffell et al. 1996, Gill et al. 2001b, Engelhard et al. 2002).

Recovery

Determining what is meant by recovery is essential for assessing whether there is an effect of disturbance on sea lion haul-out behavior. This is critical for the design of experiments, and ultimately affects the methodologies that will be employed, as well as the length of time that observations need to be conducted.

In the strictest sense, recovery can be defined as a return to an original state or normal condition. However, operational definitions of recovery tend to be less rigorous. Some studies have considered recovery to be attained when 50% of the animals present at the time of flushing return to shore (Allen et al. 1984, Henry and Hammill 2001). Other criteria that might be employed include setting higher percent-return-targets (e.g., 75%, 90%, or 100%), or applying statistical approaches that consider average densities and daily variation in numbers on shore. For example, the grand mean number of animals on shore before a disturbance could be used as the benchmark for comparison with numbers of animals that return to the haul-out. Such a measure would likely be a more accurate means of assessing recovery due to the large daily variation in number of sea lions that tend to haul out each day.

Describing the average state of a group of sea lions before a disturbance is challenging given the wide daily variability in numbers and behaviors that can be attributed to weather, tidal cycle stage, and other factors. Similarly, identifying the period over which the average state is to be described is an equally important consideration, as is controlling for natural seasonal changes in behaviors or haul-out patterns that could confound the simple interpretation of disturbance effects. In the case of Steller sea lions, documenting average conditions for 1 to 2 weeks prior to disturbance resulted in seven of ten sites reaching recovery in the following week to 50-75% of the pre-disturbance levels (Kucey 2005). Whether this applies to other species of sea lions remains to be tested.

Overall, it is appropriate to use a range of recovery criteria rather than locking into any single measure of recovery. Knowledge of how various measures of recovery are attained provides a method for assessing the rate of return to a pre-disturbance state. As such, point counts, daily means, and grand mean post-disturbance counts are all valid measures of recovery.

Experimentally assessing disturbance: A Steller example

Steller sea lions tend to avoid people, and generally appear to be skittish while on shore. Disruptions often affect entire haul-outs and rookeries (Lewis 1987, Loughlin 2002). Sea lions that are approached directly (as with scat collection) tend to become agitated, and increase the frequency and level of their vocalizations and head movements. Animals that are startled may stampede into the water, or may gradually enter the water if the disturbance (or disturbance stimulus) is moderate and prolonged. Those that enter the water may leave the area, while some may remain in the vicinity and vocalize toward the haul-out from the water. Some animals may also swim in front of the haul-out in small groups with their heads oriented toward the researchers, occasionally vocalizing. Sudden movements by researchers may cause individual animals to dive under water, possibly initiating a group response.

The apparent susceptibility of Steller sea lions to disturbance raises behavioral and physiological concerns for populations that experience high levels of intrusion. Only one study to date has addressed the effects of research disturbance on Steller sea lions. It consisted of observations that documented sea lions responding to biologists walking through a rookery, and led to recommendations to improve census counts and reduce disturbance to pups (Lewis 1987).

We conducted a study of short-term effects of disturbance of Steller sea lions at haul-outs and rookeries in British Columbia and Southeast

Alaska (Kucey 2005). Our approach was to observe haul-out patterns at six sites between May and August of 2003, and to repeat our observations between February and April in 2004. Counts were performed at 20-minute intervals, 12 hours a day during the summer season, and during daylight hours in the winter and spring months. Observations were performed from a fixed location blind with the aid of binoculars and spotting scopes to avoid detection by the sea lions. At each site, the study occurred from 1-2 weeks before, to 1-2 weeks after a predetermined research disturbance to collect fecal samples (scats) for dietary analysis. Researchers approached the haul-outs and guided the sea lions into the water using slow arm movements. They were typically on shore for less than 2 hours.

Counts documenting the number of animals hauled out before, during, and after a directed research disturbance are shown in Fig. 1 and illustrate the large daily variation in number of animals hauled out. The data are from one of the 12 sets of observations, and are representative of the other sites studied. The particular site shown in Fig. 1 was a year-round Steller sea lion haul-out located in Southeast Alaska (SW Brothers Island) that was composed of mixed age and sex classes, and was greatly influenced by tidal fluctuations. Plotting the grand mean numbers of animals present pre- and post-disturbance shows that mean numbers were lower at this site following the disturbance (Fig. 1a). However, one of the 20-minute counts made on the day following the disturbance equaled the mean number of sea lions counted during all 8 days preceding the disturbance (Fig. 1b). Similarly, recovery could also have been deemed to have occurred quickly based on mean daily counts that reached 50% of the pre-disturbance mean less than 6 hours after the disturbance (Fig. 1c). Using more conservative recovery criteria, these data suggest that recovery occurred between 1 and 6 days later when the mean daily counts were respectively 75% or 100% of the pre-disturbance mean (Fig. 1c). Thus the assessment of recovery very much depends on the criteria used.

Conservation

The example from Steller sea lions highlights how difficult it is to assess the effects of disturbance as well as determine when recovery has occurred. Experiments such as ours are useful for assessing short-term effects of disturbance, but cannot evaluate potential long-term consequences, thus indicating the need for additional methodologies for long-term studies. Intuitively, preventing human disturbance of land-based sea lion activities such as breeding, nursing, resting, and maintenance of a cohesive social structure should enhance reproductive success and species perpetuation (Kruse et al. 2001). However, disturbing non-reproducing individuals at haul-outs may not have immediate life history consequences. Measuring the physiological stress of individual animals

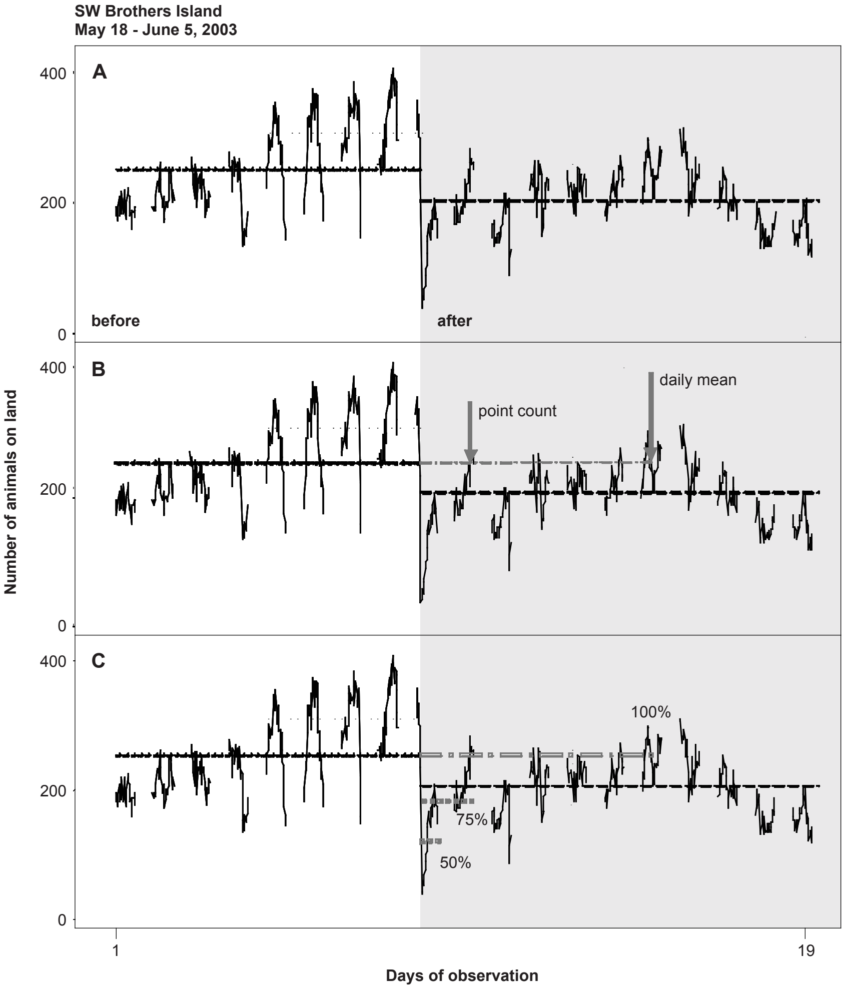


Figure 1. Counts made before and after scat collection at SW Brothers Island from May 19 to June 5, 2003. Total number of Steller sea lions on land were recorded every 20 minutes from 0800 to 2000. Gaps in counts reflect night-time when no observations were made. Shaded area represents counts made after scat collection. Dashed lines indicate the grand mean number of animals on land before and after the experimental disturbance (A, B, and C). Point count and daily mean recovery of the number of sea lions hauled out to the pre-disturbance grand mean (B). Daily mean recovery levels to 50, 75, and 100% of the pre-disturbance grand mean (C).

can be used as an alternative method for determining biological ramifications of disturbance (Andersen et al. 1996). Addressing changes in stress levels with hormone analysis, either through blood or scat analysis, can indicate changes in glucocorticoid levels (Andersen et al. 1996, Creel et al. 2002, Hunt et al. 2004). However, in wild populations, it is extremely difficult to obtain baseline physiological measurements without the confounding effects of research handling. Therefore, documenting changes in behavior and numbers is an alternative and accessible method to monitor the effects of disturbance on individual populations.

Understanding the effects of human disturbance on endangered wildlife populations is critical to conservation efforts (Kerley et al. 2002). Only by knowing whether animals are physiologically affected or significantly modify their behaviors in response to disturbance can effective protection measures be applied. The insights that can be gained by assessing the effects of disturbance on sea lions may help to guide research activities, air and boat operations, and human approaches within areas of sea lion habitat. Similarly, the lessons gained by thinking critically about what a disturbance response is and how recovery should be evaluated may also help to guide the development of other studies of disturbance that might be undertaken on other species of sea lions.

Acknowledgments

Funding was provided by NOAA to the North Pacific Universities Marine Mammal Research Consortium through the North Pacific Marine Science Foundation. Field research was performed under Federal Marine Mammal permits: 358-1564 and 715-1457 and University of British Columbia Animal Care certificate: Category B, Protocol Number A02-0190.

References

Allen, S.G., D.G. Ainley, G.W Page, and C.A. Ribic. 1984. The effect of disturbance on harbor seal haul out patterns at Bolinas Lagoon, California. Fish. Bull. U.S. 82:493-500.

Andersen, R., J.D.C. Linnell, and R. Langvatn. 1996. Short term behavioural and physiological response of moose *Alces alces* to military disturbance in Norway. Biol. Conserv. 77:169-176.

Blackwell, S.B., J.W. Lawson, and M.T. Williams. 2004. Tolerance by ringed seals (*Phoca hispida*) to impact pipe-driving and construction sounds at an oil production island. J. Acoust. Soc. Amer. 115:2346-2357.

Boren, L.J., N.J. Gemmell, and K.J. Barton. 2002. Tourist disturbance on New Zealand fur seals *Arctocephalus forsteri.* Austral. Mammal. 24:85-95.

Born, E.W., J. Teilmann, and F.F. Riget. 2002. Haul-out activity of ringed seals (*Phoca hispida*) determined from satellite telemetry. Mar. Mamm. Sci. 18:167-181.

Cassini, M.H., D. Szteren, and E. Fernández-Juricic. 2004. Fence effects on the behavioural responses of South American fur seals to tourist approaches. J. Ethol. 22:127-133.

Creel, S., J.E. Fox, A. Hardy, J. Sands, B. Garrott, and R.O. Peterson. 2002. Snowmobile activity and glucocorticoid stress responses in wolves and elk. Conserv. Biol. 16:809-814.

Deecke, V.B., P.J.B. Slater, and J.K.B. Ford. 2002. Selective habituation shapes acoustic predator recognition in harbour seals. Nature 420:171-173.

Engelhard, G.H., A.N.J. Baarspul, M. Broekman, J.C.S. Creuwels, and P.J.H. Reijnders. 2002. Human disturbance, nursing behaviour, and lactational pup growth in a declining southern elephant seal (*Mirounga leonina*) population. Can. J. Zool. 80:1876-1886.

Engelhard, G.H., J. van den Hoff, M. Broekman, A.N.J. Baarspul, I. Field, H.R. Burton, and P.J.H. Reijnders. 2001. Mass of weaned elephant seal pups in areas of low and high human presence. Polar Biol. 24:244-251.

Foley, C.A.H., S. Papageorge, and S.K. Wasser. 2001. Noninvasive stress and reproductive measures of social and ecological pressures in free-ranging African elephants. Conserv. Biol. 15:1134-1142.

Forbes, B.C., J.J. Ebersole, and B. Strandberg. 2001. Anthropogenic disturbance and patch dynamics in circumpolar arctic ecosystems. Conserv. Biol. 15:954-969.

Gentry, R.L. 1998. Behavior and ecology of the northern fur seal. Princeton University Press, Princeton.

Gill, J.A., K. Norris, and W.J. Sutherland. 2001a. Why behavioural responses may not reflect the population consequences of human disturbance. Biol. Conserv. 97:265-268.

Gill, J.A., K. Norris, and W.J. Sutherland. 2001b. The effects of disturbance on habitat use by black-tailed godwits *Limosa limosa*. J. Appl. Ecol. 38:846-856.

Grellier, K., P.M. Thompson, and H.M. Corpe. 1996. The effect of weather conditions on harbour seal (*Phoca vitulina*) haulout behaviour in the Moray Firth, northeast Scotland. Can. J. Zool. 74:1806-1811.

Henry, E., and M.O. Hammill. 2001. Impact of small boats on the haulout activity of harbour seals (*Phoca vitulina*) in Métis Bay, Saint Lawrence Estuary, Québec, Canada. Aquat. Mamm. 27:140-148.

Hunt, K.E., A.W. Trites, and S.K. Wasser. 2004. Validation of a fecal glucocorticoid assay for Steller sea lions (*Eumetopias jubatus*). Physiol. Behav. 80:595-601.

Kerley, L.L., J.M. Goodrich, D.G. Miquelle, E.N. Smirnov, H.B. Quigley, and M.G. Hornocker. 2002. Effects of roads and human disturbance on Amur tigers. Conserv. Biol. 16:97-108.

Kruse, G.H., M. Crow, E.E. Krygier, D.S. Lloyd, K.W. Pitcher, L.D. Rea, M. Ridgway, R.J. Small, J. Stinson, and K.M. Wynne. 2001. A review of proposed fishery management actions and the decline of Steller sea lions *Eumetopias jubatus* in Alaska: A report by the Alaska Steller sea lion restoration team. Alaska Department of Fish and Game, Regional Information Report, 5J01-04.

Kucey, L. 2005. Human disturbance and the hauling out behaviour of Steller sea lions (*Eumetopias jubatus*). M.S. thesis, University of British Columbia, Vancouver. 75 pp.

Lewis, J.P. 1987. An evaluation of a census-related disturbance of Steller sea lions. M.S. thesis, University of Alaska Fairbanks. 93 pp.

Loughlin, T.R. 2002. Steller sea lion. In: W.F. Perrin, B. Wursig, and J.G.M. Thewissen (eds.), Encyclopedia of marine mammals. Academic Press, San Diego, p. 1414.

Millspaugh, J.J., R.J. Woods, K.E. Hunt, K.J. Raedeke, G.C. Brundige, B.E. Washburn, and S.K. Wasser. 2001. Fecal glucocorticoid assays and the physiological stress response in elk. Wildl. Soc. Bull. 29:899-907.

Ono, K.A., D.J. Boness, and O.T. Oftedal. 1987. The effect of a natural environmental disturbance on maternal investment and pup behavior in the California sea lion. Behavior. Ecol. Sociobiol. 21:109-118.

Porter, B. 1997. Winter ecology of Steller sea lions (*Eumetopias jubatus*) in Alaska. M.S. thesis, University of British Columbia, Vancouver. 84 pp.

Riffell, S.K., K.J. Gutzwiller, and S.H. Anderson. 1996. Does repeated human intrusion cause cumulative declines in avian richness and abundance? Ecol. Appl. 6:492-505.

Salter, R.E. 1979. Site utilization, activity budgets, and disturbance responses of Atlantic walruses during terrestrial haul-out. Can. J. Zool. 57:1169-1180.

Suryan, R.M., and J.T. Harvey. 1999. Variability in reactions of Pacific Harbor seals, *Phoca vitulina richardsi*, to disturbance. Fish. Bull. U.S. 97:332-339.

Wasser, S.K., K. Bevis, G. King, and E. Hanson. 1997. Noninvasive physiological measures of disturbance in the northern spotted owl. Conserv. Biol. 11:1019-1022.

Whitten, P.L., D.K. Brockman, and R.C. Stavisky. 1998. Recent advances in noninvasive techniques to monitor hormone-behavior interactions. Yearb. Phys. Anthropol. 41:1-23.

Wingfield, J.C. 2003. Control of behavioural strategies for capricious environments. Anim. Behav. 66:807-815.

Southern Sea Lions and Artisanal Fisheries in Piriápolis, Uruguay: Interactions in 1997, 2001, and 2002

Diana Szteren
Universidad de la República, Facultad de Ciencias, Montevideo, Uruguay; and CICIMAR-IPN, Laboratorio de Mamíferos Marinos, La Paz, B.C.S, México

Cecilia Lezama
Universidad de la República, Facultad de Ciencias, Montevideo, Uruguay

Abstract

Interactions between marine mammals and fisheries are a worldwide problem that occur whenever fishing activities coincide spatially with marine mammals feeding grounds. In Uruguay this topic was first studied in 1997, and continued in 2001 and 2002. Here we compare the interactions over 3 years at Piriápolis fishing port. Onboard observations during fishing operations were done between July and January, totaling 16 samplings in 1997, 15 in 2001, and 9 in 2002.

The frequency of sea lion sightings decreased over time (56.3%, 46.7%, and 22.2%), as did the mean number of sea lions (1.13, 0.80, 0.44), but not significantly. Sea lion interactions also decreased with time from 75% in 1997 to 33.3% in 2002. CPUEs with longlines diminished with time, but with gillnets were higher in 2001. The frequency of interactions diminished with time (from 75% to 33%), but this was not clearly reflected in an increase of CPUE, because in most cases they were not significantly related to the presence of interactions. Since interactions or the record of predation during fishing operations were not reflected in lower CPUE, we conclude that sea lions were not the only cause of the low and variable catches.

Introduction

Interactions between marine mammals and fisheries are a worldwide problem, which occur whenever fishing activities coincide spatially with marine mammals feeding grounds. This is because many marine mammal species are distributed and feed in coastal areas. Conflicts in a higher or lesser extent may affect the conservation of the marine mammal or the fishing activity. Two kinds of interactions have been defined: operational and biological. Operational interactions take place during fishing activities where marine mammals interact with fishing gear, causing damage to the gear or to the catch. Interactions depend on the fishing gear, the ecology, the behavior of the marine mammal, and the target fish species. In biological interactions marine mammals and fisheries conflict for trophic resources, resulting in a competition whenever those resources are limiting (Northridge 1985, Wickens 1995).

Many pinniped species have developed the capacity of recognizing fishing boats, as their engines act as a “calling bell” (Bonner 1982). In this way they would obtain their food easily, instead of investing more energy in locating it on their own. This strategy would represent a lower energetic cost in searching and capturing their prey. In recent years the global increase of coastal fisheries and the greater use of passive gear (static fishing gear) have caused an increase in conflicts with marine mammals (Harwood 1987).

Artisanal fisheries in Uruguay

In Uruguay, artisanal fisheries use simple fishing gear and rely basically on manual labor (Crossa et al. 1991). Landings and effort vary widely because this activity is highly dependent on climate and resource availability (Altez et al. 1988). There is an alternation between periods of heavy activity and others with very scarce activity of fishing fleets.

In coastal areas the fishing gear generally used are gillnets and longlines. Both are usually set in the bottom, and are passive. Gillnets are between 50 and 100 m long and between 2 and 4 m high. The mesh size most frequently used is from 10 to 12 cm for the main target species (weakfish *Cynoscion guatucupa*, croaker *Micropogonias furnieri,* and narrownose smoothhound *Mustelus schmitti*). Gear is set at dawn or morning and retrieved 2-5 hours later. Longlines are usually 100 m long with 100 secondary lines that have a baited hook at the end. The main target species at Piriápolis port are *Urophycis brasiliensis* (Brazilian codling), and *C. guatucupa* and *M. schmitti* to a lesser extent. Gear is usually set at night and retrieved at dawn.

Artisanal fishermen frequently complain about sea lion predation, claiming that they are responsible for their low catches. In some ports on the Atlantic coast, sea lions are considered as a serious problem in fishers’ activity and are a restriction to the fishing activity (Crossa et al. 1991).

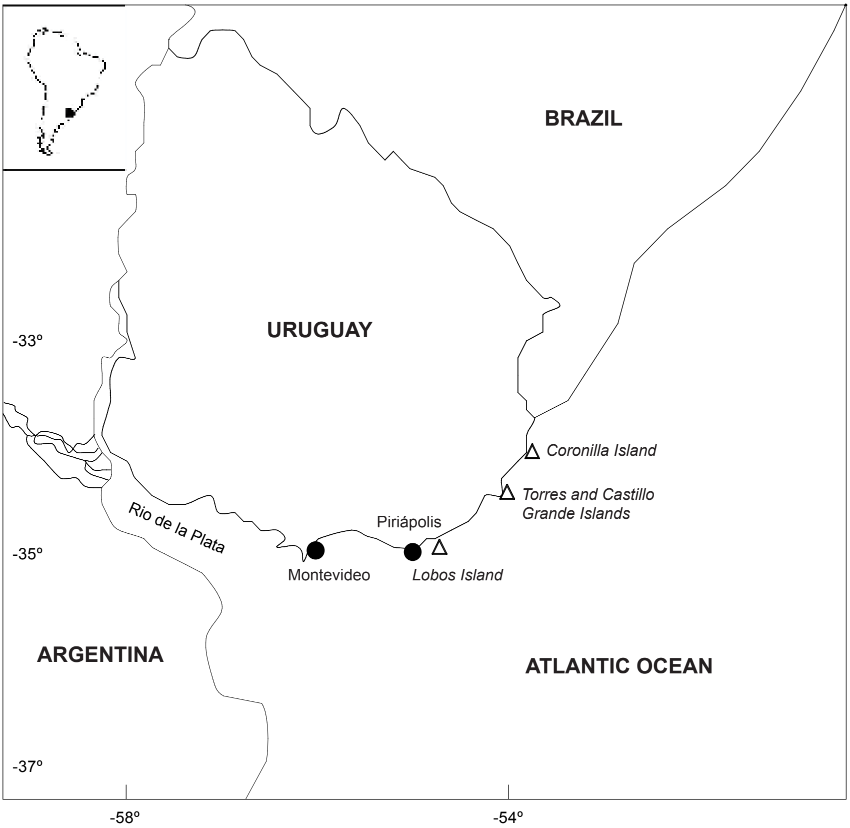


Figure 1. Location of Piriápolis (circle) (the sampled fishing port) and sea lion rookeries (triangle) on the Uruguayan coast.

Conflicts with Otaria flavescens

Southern sea lions (*Otaria flavescens*) prey mainly on fish, but they can also feed on crustaceans and mollusks. They forage in coastal areas less than 5 miles from the coast (Vaz-Ferreira 1976). According to some authors (George-Nascimento et al. 1985, Koen Alonso et al. 2000, Naya et al. 2000) they are broad-spectrum and opportunistic feeders, and they are able to exploit a wide range of trophic resources. In Uruguay, the southern sea lion might be the main factor responsible of damage to fishing gear and losses to catches (Vaz-Ferreira 1976).

Southern sea lion distribution extends from Rio de Janeiro (Brazil) south to Tierra del Fuego (Argentina) in the Atlantic Ocean and on the coast of Chile and Perú in the Pacific. The population in Uruguay is located in three areas: Isla de Lobos (35º01′S-54º53′W) where roughly half of the population lives; Torres islands (Rasa, Encantada, and Marco islands) (34º24′S-53º46′W); and La Coronilla islands (33º56′S-58º29′W) (Vaz Ferreira 1976) (Fig. 1). By 1995-1996 there were about 12,000 individuals, and the population was declining between 5% and 7% yearly (Páez 1996). The causes of this decline are unknown.

Studies focusing the interactions between *Otaria flavescens* and fisheries in South America include all the countries where this species is distributed (Perú, Chile, Argentina, Uruguay, and Brazil). In Argentina, Fazio et al. (2000) found attacks by sea lions to coastal gillnets in Cabo San Antonio (Pcia. de Buenos Aires). On the Patagonian coast (Argentina) the southern sea lion diet overlaps industrial fisheries of the area, mainly for hake (*Merluccius hubbsi*) (Crespo et al. 1997). In Brazil, the most intense interactions occurred when gillnets were used in coastal areas, near sea lions rookeries (Carvalho et al. 1996). In Rio Grande do Sul, Ott et al. (1996) reported interactions with fishing operations, including entanglement in fishing gear and damage to catches.

In Uruguay this topic was first studied in 1997-1998; before that, no quantitative or qualitative evaluation of damage existed (Szteren 1999). In that research, four fishing localities were studied, and Piriápolis was the place where the highest levels of interactions were found. In this study, we summarize those results together with new data collected in 2001 and 2002 in the same locality. Our main objective was to compare the three sampling years, in order to know if the interactions are increasing, and also to analyze if they are related to fishers' lower catches. The importance of analyzing these conflicts is crucial to understand and evaluate the problem. This study is a useful tool in making management decisions directed to the conservation of southern sea lions and the optimization of artisanal fisheries.

Methods

This research involved three different sampling periods, all of them in Piriápolis. This location has important artisanal fishing activity, with around 25 boats year-round. It is located about 42 km from the Isla de Lobos rookery (Fig. 1).

Data collection

Observations were done onboard fishing boats during routine fishing journeys. The first sampling period was July to December 1997 (Szteren 1999) where 12 fishing trips were observed totaling 16 fishing events. We considered a "fishing event" as the catch during a fishing journey with a certain gear. It includes a variable number of gillnets or longlines set together in groups of three to five (Szteren 1999). From August to December 2001 10 trips were done, recording 15 fishing events (Lezama

2002); and from October 2002 to January 2003, in 7 trips 9 fishing events were observed.

At each fishing event we counted the number of sea lions near the boat during fishing activities, and recorded sea lion presence, predation, and damages to fish or gear. We calculated the frequency of sea lion sightings as the number of fishing events in which sea lions were sighted or predation recorded in relation to the total fishing events. We then analyzed if the number of sea lions had significantly changed in time.

Fishing catches

We calculated the CPUE (catch per unit of effort) for each fishing event, as the catch divided by the number of gillnets or longlines used (net surface or number of hooks), and the time in hours that the gear was set in the water. We express it as kg per h per 1,000 m^2 or hooks. We transformed CPUEs to logarithms in order to meet normality assumptions. This variable was compared through our sampling years using one-way analysis of variance, and assessed if it was related with the number of sea lions using regression.

Damage

We considered three types of sea lion–related damage to the fishery: (1) fish consumption stolen from the fishing gear (predation), (2) bitten fish (fish caught with wounds), and (3) damage to fishing gear (considered only when sea lions were observed). Indirect clues of sea lion predation were also considered as presence of interactions whenever sea lions were seen eating in the vicinity. These were pullings from the set gear (gillnets or longlines) and opened hooks of longlines. These two elements indicated that a sea lion was stealing caught fish (Szteren 1999). We calculated the frequency of predation as the number of fishing events in which sea lions consumed fish and/or bit fish, in relation with the total number of fishing events.

Interactions

We considered presence of interaction whenever sea lions were observed, or predation or gear damage was recorded; and absence when nothing related to sea lions was detected. The frequency of interactions is a gross indicator of sea lion activity near the fishing gear. We then analyzed if CPUE varied in the presence or absence of interactions, using *t*-tests of variance of log-transformed CPUE.

Table 1. Mean number of sea lion and frequency of sightings for each year and fishing gear. Frequency of predation and interactions for each fishing gear, in relation to the total number of fishing trips each year at Piriápolis, Uruguay.

	Gear	1997	2001	2002
Number of sea lions	G	0.60 ± 0.89	1.14 ± 0.89	1.0 ± 1.73
	L	1.36 ± 1.57	0.50 ± 1.07	0.17 ± 0.41
Frequency of sightings	G	40.0% (5)	71.4% (7)	33.3% (3)
	L	63.6% (11)	25% (8)	16.7% (6)
Frequency of predation	G	40% (5)	71.4% (7)	66.7% (3)
	L	72.7% (11)	62.5% (8)	0% (6)
Frequency of interactions	G	80% (5)	71.4% (7)	66.7% (3)
	L	72.7% (11)	62.5% (8)	16.7% (6)

In parentheses is the number of fishing events recorded.
Fishing gear: G = gillnets; L = longlines.

Results

Sea lion presence

In 1997-1998, 1-4 sea lions were observed in 56.3% of the sampled fishing events. In 2001 and 2002 a maximum of 3 individuals were observed in 46.7% and 22.2% of the recorded fishing events (Lezama and Szteren 2003). The mean number of sea lions tended to decrease in time, but not significantly ($F = 0.964$, d.f. = 2, $P = 0.391$). In these three years interacting animals were always adult females and/or subadult males (not distinguishable).

Neither the mean number of sea lions nor the frequency of sightings varied with fishing gear, although the trend was to decrease with time in the case of longlines, and were highest in 2001 and minimum in 1997 with gillnets (Table 1). Furthermore, CPUEs were not significantly different in the presence or absence of sea lions, except in 2001 where CPUEs with longlines were higher in absence of sea lions (Table 2).

Catches

The greatest CPUEs with gillnets were recorded in 2001 (averaging 85.89 kg per h per 1,000 m^2 ± 112.75), in 2002 decreased to 8.59 kg per h per 1,000 m^2 in average (± 8.79 kg per h per 1,000 m^2), and in 1997-1998 they were 11.15 ± 23.71 kg per h per 1,000 m^2. There were no significant differences between the three years ($F = 3.28$, d.f. = 2, $P = 0.073$).

With longlines CPUEs differed in time, increasing in each successive sampling period ($F = 9.69$, d.f. = 2, $P = 0.001$). In 1997-1998 they averaged

Table 2. Results of the *t*-test comparing CPUE in the presence or absence of sea lion sightings (P/A sea lions) and interactions (P/A interaction), with each fishing gear and year of study.

Fishing gear	Year	N	Log CPUE vs. P/A sea lions	Log CPUE vs. P/A interaction
Gillnets	1997	5	$T = 0.76$, d.f. = 3, $P = 0.50$	$T = -9.72$, d.f. = 3, $P = 0.002$[a]
	2001	7	$T = -2.34$, d.f. = 5, $P = 0.07$	$T = 2.34$, d.f. = 5, $P = 0.07$
	2002	3	$T = -0.12$, d.f. = 1, $P = 0.925$	$T = -1.34$, d.f. = 1, $P = 0.41$
Longlines	1997	11	$T = -0.42$, d.f. = 9, $P = 0.68$	$T = -0.19$, d.f. = 9, $P = 0.85$
	2001	8	$T = 3.55$, d.f. = 6, $P = 0.012$[a]	$T = -0.50$, d.f. = 6, $P = 0.64$
	2002	6	$T = -1.49$, d.f. = 4, $P = 0.21$	$T = -1.49$, d.f. = 4, $P = 0.21$

[a] Significant at $P < 0.05$.

3.25 ± 2.75 kg per h per 1,000 hooks, in 2001 they were 9.68 ± 6.22 kg per h per 1,000 hooks, and in 2002 they increased to 24.80 ± 18.44 kg per h per 1,000 hooks.

In 1997-1998 there was no relationship between CPUE and the number of sea lions with any fishing gear (Szteren 1999, Szteren and Páez 2002). However, in 2001 CPUEs with longlines decreased with the number of sea lions ($r_s = -0.71$, $P = 0.05$), while with gillnets no significant relationship was found. In 2002 CPUEs with longlines increased with the number of sea lions ($r_s = 0.84$, $P = 0.04$).

Damages

The frequency of fishing trips with predation was maximum in 2001 and minimum in 1997 (Table 1). Damage to gillnets was recorded in one fishing event in a single gillnet in 2002 and was minimum in relation with the overall number of gillnets set in all fishing events. However, it should be mentioned that set nets already had old holes, making it very difficult to determine which were new holes or if some holes had been enlarged.

The frequency of predation in longline fishing events also decreased in time, from 72.7% to 0% (Table 1). Damage to the gear was recorded only in two fishing events in 2001.

Frequency of interactions

The frequency of interactions decreased from 1997 to 2002 with both fishing gears (Table 1). Overall, sea lions caused interactions in 75% of the sampled fishing events in 1997, 66.7% in 2001, and 33.3% in 2002. It is interesting to note that, in general, CPUEs did not show significant differences with or without interactions. Only in 1997 were CPUEs significantly higher in absence of interactions with gillnets (Table 2). In Fig. 2 we show

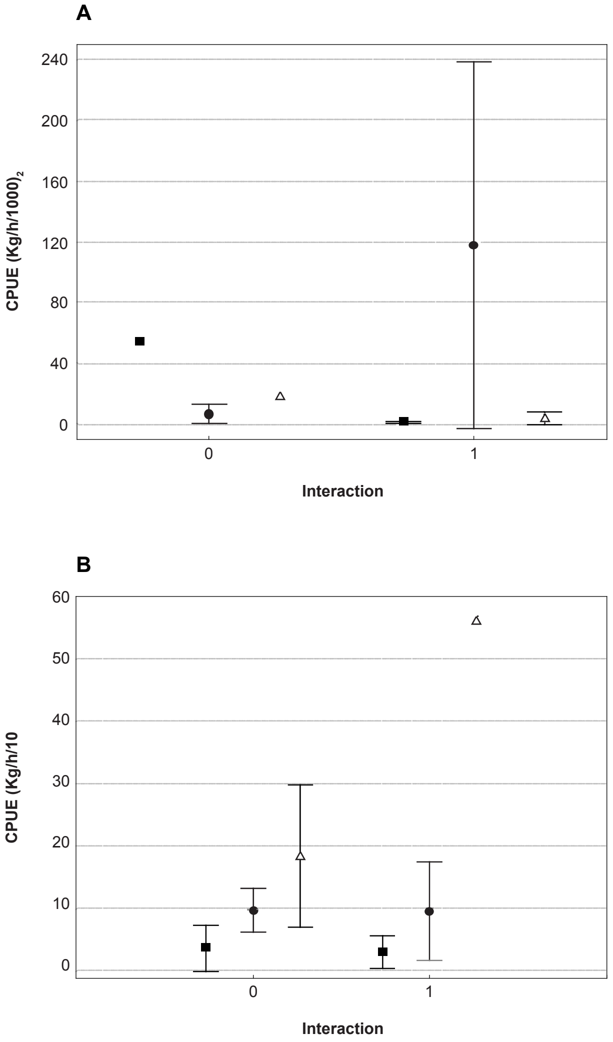


Figure 2. CPUE with (1) and without (0) interactions with both fishing gears each year at Piriápolis, Uruguay. A = with gillnets; B = with longlines. ■ = CPUE1997, ● = CPUE2001, △ = CPUE2002.

CPUEs in the presence and absence of interactions for both fishing gears and for each year. It is noticeable that broad variability had an important role in statistical results, as well as the small sample sizes.

Discussion

Our results over three sampling periods are not conclusive to indicate a significant change in interactions between southern sea lions and artisanal fisheries in time, or an important influence of sea lion predation on lower CPUEs. Furthermore, different trends were found according to the fishing gear. When the fishery used longlines, the mean number of sea lions, the frequency of sightings, and the frequency of damages and interactions decreased in the three successive years. However, CPUEs did not increase with a low number of sea lions and were similar with and without interactions. When gillnets were used, the mean number of sea lions, the frequency of sightings, and the frequency of predation was maximum in 2001. This may imply that in 2001 the impact of sea lion interactions would be the greatest. However, this coincided with an increase in CPUE. Moreover, there was no relationship between the presence or absence of interactions and lower CPUEs.

Despite the fact that sea lions were less common over time, the frequency of damage did not decrease significantly, possibly because the number of interactions was not associated with lower CPUE, except in 1997 with gillnets. In that case, interactions were apparently reflected in lower CPUE, but the number or frequency of sea lions was not related to interactions.

Possibly, a small number of rogue animals has specialized in eating caught fish, and use this feeding strategy. Concordantly, in many cases it has been demonstrated that most damage was caused by a small number of pinnipeds; e.g., in Scotland (Harwood and Greenwood 1985), on Australia (Pemberton and Shaughnessy 1993), and in South Africa (Wickens 1995). In Australia, David and Wickens (2003) reported that the number of seals was not related to the intensity of the problem, because in general they were small groups habituated to this easy way of obtaining food. In some cases the presence of a vessel seemed to attract sea lions; e.g., the number of sea lions in central Chile was not different in successful or unsuccessful sets (Hückstädt and Antezana 2003).

In this sense, sea lion sightings were frequent throughout our samplings but the number of sea lions was small (1 to 4). These figures are similar to those found in similar studies with the same species and types of fishery; e.g., 2-4 sea lions in Rio Grande do Sul (Brazil) (Soto et al. 2000), and an average of 1.6 (Arias-Schreiber 1996) and 1.8-6 in Perú (Arias and Garayar 1991). Nevertheless, they are smaller than those reported in Chile (groups of 3-6 animals per gillnet) (Oporto et al. 1991). The frequencies of sea lion sightings at Piriápolis are in the range found by Rodríguez and

Stotz (2002) in IV Region, Chile, who reported 59% of fishing journeys with sea lion sightings (67% with gillnets and 42% with longlines).

Our range of occurrence of interactions with gillnets (66% to 80%) tended to be higher than other studies with *Otaria flavescens*: 32% of gillnets in Cabo San Antonio (Argentina) (Fazio et al. 2000), 25% at Rio Grande do Sul (Brasil) (Ott et al. 1996), and 46% in Puerto de Huacho (Perú) (Arias-Schreiber 1996). However, in Pto. San Juan de Marcona (Perú) the presence of damage was similar (71%, Arias-Schreiber 1993).

Evidence in Uruguay is still not conclusive to indicate that sea lions are related to lower catches. Only in 2001 did CPUEs with longlines decrease with the mean number of sea lions, and the following year, 2002, they increased with the number of sea lions. Trends were not constant in time nor were they consistent within a fishing gear. This is probably related to the wide variation in CPUE. Moreover, if predation values were high, we should have found differences between fishing journeys with and without interactions. Rodríguez and Stotz (2002) in Chile came to the same conclusion, but in Cabo San Antonio (Argentina), CPUEs with gillnets showed small variations and were significantly different with and without interactions (Fazio et al. 2000).

In our case, as we found no solid proof to claim that the presence of sea lions or the damage they cause are related with lower catches, we conclude that sea lions would not be the only responsible factor in the wide variability in catches.

Management of the problem

When analyzing the interactions between sea lions and fisheries in Uruguay, two areas of conflict are apparent: (1) purely biological aspects related to the population of southern sea lions, fish prey populations, target fish populations, and fishermen as predators; and (2) socioeconomic features affecting artisanal fisheries as a commercial activity.

Biological aspects

While pinnipeds represent just one component of the multispecies system that involves fisheries, they very conspicuous, and the most often encountered by fishermen (David and Wickens 2003). It is extremely difficult to demonstrate competition and to determine to which extent both groups are competing for the same species. In many cases fish taken by sea lions would not be available for the fisheries or would be discarded (FAO 1978, Northridge 1985).

Long-term benefits of a population reduction will depend on density-dependent processes controlling the abundance of fish populations, predator dynamics, trophic relationships, and prey use and availability (Harwood and Greenwood 1985, Wynne 1990). For a basic level of decision, it would be appropriate to establish if sea lion predation is really affecting fishery catches. We should also have a confident estimation that the fishery will increase after the reduction of a sea lion population, and that this increase could be effectively used by the commercial fishery (DeMaster and Sisson 1992).

More basic information related to sea lion feeding is necessary, including daily consumption by the population, diet composition (prey species and sizes) and their temporal and spatial variations, foraging areas, prey energetic content, and feeding strategies. With the scarce knowledge of the interactions between fish, pinnipeds, and humans, it is very difficult to assess the effects of each group on the rest, let alone to justify a pinniped reduction to protect fishing activities (FAO 1978). Recently, there is a debate in which some authors have pointed out that cullings of top predators have not resulted in increased fishing yields. This is because of the complexity of marine ecosystems, characterized by many species that must be considered (Yodzis 2001).

Socioeconomic aspects

It seems obvious that possible solutions should not involve culling, but rather should imply changes in the fishery, directed to increase catches and incomes. In Uruguay the artisanal fishery is a highly unstable activity, with difficult and irregular working conditions because of its high dependence on climate and resource variability (Szteren 1999). Regarding their economy, fishers greatly depend on intermediate buyers (Astori and Buxedas 1986). This results in low incomes, and a difficulty to be independent or to gather in cooperative initiatives. Furthermore, substantial catches by industrial fisheries keep fish prices low in the market. In this way, artisanal fisheries in Uruguay suffer because industrial large-scale fisheries dominate in the domestic market and exportations (Bertola et al. 1996). Solutions to alleviate these problems will need to be focused in particular areas, gear, and times when fishing is taking place (David and Wickens 2003).

Acknowledgments

Authors are very grateful to the artisanal fishery community of Piriápolis; special thanks to Alfredo Hargain, Luis, and Camarón who allowed us to board their boats. Diana Perez and Mariana Rios helped in 2002 field season. Programa de Maestría en Manejo de Vida Silvestre, Universidad Nacional de Córdoba (Argentina) financed the 1997-1998 study, and the KARUMBE Project financed in 2002. We also acknowledge the two referees for their valuable suggestions.

References

Altez, M.C., S. Campos, M. Crossa, C. de la Fuente, L. Guirin, W. Magallanes, A. Martinote, and E. Salgueiro. 1988. Encuesta Nacional de Pescadores Artesanales Uruguay. Ministerio de Trabajo y Seguridad Social, Dirección Nacional de Fomento Cooperativo (1). 43 pp. (In Spanish.)

Arias-Schreiber, M. 1993. Interacciones entre lobos marinos *Otaria byronia* y la pesquería artesanal en el puerto San Juan de Marcona, Perú. Graduate thesis, Univ. Nacional Agraria La Molina, Lima, Perú. 29 pp. (In Spanish.)

Arias-Schreiber, M. 1996. Interacciones entre lobos marinos *Otaria byronia* y la pesca con redes de cortina en el Puerto de Huacho, Perú. Abstract 7a. Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur, Viña del Mar, Chile. Addendum. (In Spanish.)

Arias, M., and L. Garayar. 1991. Efecto de la presencia de lobos marinos (fam. Otaridae) en la pesquería artesanal de Puerto San Juan de Marcona, Perú. Abstract. Pesca artesanal. Fuente de alimentación y trabajo. III Seminario Latinoamericano de pesca artesanal y III Reunión Regional desarrollo costero integrado, Lima, Perú. p. 94-95

Astori, D., and M. Buxedas. 1986. La pesca en el Uruguay: Balance y perspectivas. CIEDUR. Ediciones de la Banda Oriental, Montevideo. 208 pp. (In Spanish.)

Bertola, L., L. Bermúdez, and M. Camou. 1996. Pesca, sinsabores y esperanzas. Síntesis de las acciones del CCU en el área de la pesca artesanal en los últimos 25 años. Ediciones del Centro Cooperativista Uruguayo, Montevideo. 142 pp. (In Spanish.)

Bonner, N. 1982. Seals and man: A study of interactions. Washington Sea Grant and University of Washington Press, Seattle. 170 pp.

Carvalho, R.V., KG. Silva, and L.T. Messias. 1996. Os pinnipedes e a pesca artesanal no litoral do Rio Grande do Sul, Brasil. Abstract 7a. Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur, Viña del Mar, Chile. Addendum. (In Portuguese.)

Crespo, E.A., S.N. Pedraza, S.L. Dans, M. Koen Alonso, L.M. Reyes, N. García, and M. Coscarella. 1997. Direct and indirect effects of the high seas fisheries on the marine mammal populations in the northern and central Patagonian coast. J. Northw. Fish. Sci. 22:189-207.

Crossa, M., R. Pereiro, J. Pinieiro, G. Sorachu, F. Mateo, and D. Trujillo. 1991. Análisis de las pesquerías artesanales del Uruguay. I. Documento de Trabajo al Foro. Centro Cooperativista Uruguayo. Sistema de Programas de Pesca Artesanal, Montevideo, Uruguay. 236 pp. (In Spanish.)

David, J., and P. Wickens 2003. Management of cape fur seals and fisheries in South Africa. In: N. Gales, M. Hindell, and R. Kirkwood (eds.), Marine mammals: Fisheries, tourism and management issues. CSIRO Publishing, Australia, pp.116-135

DeMaster, D.P., and J.E. Sisson. 1992. Pros and cons of pinniped management along the North American coast to abet fish stocks. In: D.R. McCullough and R.H. Barrett (eds.), Wildlife 2001: Populations. Elsevier Applied Science, London, pp.321-329.

FAO. 1978. Mammals in the seas. Report of the FAO Advisory Committee on Marine Resources Research. Working Party on Marine Mammals. FAO Fish. Ser. 1(5). 264 pp.

Fazio, A., A. Palmerio, M. Mendez, S. Botta, and P. Bordino. 2000. Interacción entre lobos marinos de un pelo *Otaria flavescens* y la pesquería artesanal del Cabo San Antonio, Buenos Aires, Argentina. Abstract 9a. Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur, Buenos Aires, p. 44. (In Spanish.)

George-Nascimento, M., R. Bustamante, and C. Oyarzun. 1985. Feeding ecology of the South American sea lion *Otaria flavescens*: Food contents and food electivity. Mar. Ecol. Prog. Ser. 21:135-143.

Harwood, J. 1987. Competition between seals and fisheries. Sci. Prog., Oxf. 71:429-437.

Harwood, J., and J.J.D. Greenwood. 1985. Competition between British grey seals and fisheries. In: J.R. Beddington, R.J.H. Beverton, and D.M. Lavigne (eds.), Marine mammals and fisheries. George Allen & Unwin, London, pp. 153-169.

Hückstädt, L.A., and T. Antezana. 2003. Behaviour of the southern sea lion (*Otaria flavescens*) and consumption of the catch during purse-seining for jack mackerel (*Trachurus symmetricus*) off central Chile. ICES J. Mar. Sci. 60:1003-1011.

Koen Alonso, M., E.A. Crespo, S.N. Pedraza, N.A. Garcia, and M.A. Coscarella. 2000. Food habits of the South American sea lion, *Otaria flavescens*, off Patagonia, Argentina. Fish. Bull. U.S. 98:250-263.

Lezama, C. 2002. Daños ocasionados por el león marino sudamericano (*Otaria flavescens*) a la pesca artesanal en el puerto de Piriápolis. Informe de Pasantía. Opción Zoología de Vertebrados, Facultad de Ciencias, Universidad de la República, Montevideo. 24 pp. (In Spanish.)

Lezama, C., and D. Szteren. 2003. Interacción entre el león marino sudamericano (*Otaria flavescens*) y la flota pesquera artesanal de Piriápolis, Uruguay. Abstract from 2º Jornadas de Conservación y Uso Sustentable de la Fauna Marina, Montevideo, Uruguay, p. 48. (In Spanish.)

Naya, D.E., R. Vargas, and M. Arim. 2000. Análisis Preliminar de la dieta del león marino del sur (*Otaria flavescens*) en Isla de Lobos, Uruguay. Bol. Soc. Zool. Uruguay 12:14-21. (In Spanish.)

Northridge, S.P. 1985. Estudio mundial de las interacciones entre los mamíferos marinos y la pesca. FAO Inf. Pesca 251. 234 pp. (In Spanish.)

Oporto, J., C. Mercado, and L. Brieva. 1991. Conflicting interactions between coastal fisheries in southern Chile. Report on the Benguela Ecology Programme workshop on seal-fishery biological interactions, University of Cape Town. Working Paper BEP/SW91/R8. 21 pp.

Ott, P.H., I. Moreno, D. Danilevicz, and L.R. Olivera. 1996. Leones marinhos (*Otaria flavescens*) e a pesca costeira no sul do Brasil: Uma analise preliminar das competicoes e conflictos. Abstract 7a. Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur, Viña del Mar, Chile, p. 62. (In Portuguese.)

Páez, E. 1996. Simulaciones estocásticas en la población de *Otaria flavescens* en Uruguay. Abstract 7. Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur, Viña del Mar, Chile, p. 116. (In Spanish.)

Pemberton, D., and P.D. Shaughnessy. 1993. Interaction between seals and marine fish-farms in Tasmania, and management of the problem. Aquat. Conserv. Mar. Freshw. Ecosys. 3:149-158.

Rodríguez, L., and W. Stotz. 2002. Descripción de la interacción del lobo marino común *Otaria flavescens* (Shaw, 1800) en la actividad de los pescadores artesanales de las Caletas de Coquimbo y Peñuelas, IV Región, Chile. Abstract 10a. Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur, Valdivia, Chile, p. 46. (In Spanish.)

Soto, J.M., M.B. Souza-Filho, and M.M. Mincarone. 2000. Interaçao do leão-marinho, *Otaria flavescens* (Shaw, 1800), com a pesca de emalhe na costa do Rio Grande do Sul, Brasil. Anais da XIII Semana Nacional de Oceanografia, Itajaí-SC, Brasil, pp. 733-735. (In Portuguese.)

Szteren, D. 1999. Impacto económico del león marino sudamericano (*Otaria flavescens*) en la pesca artesanal en Uruguay. M.Sc. thesis, Centro de Zoología Aplicada, Universidad Nacional de Córdoba, Argentina. 59 pp. (In Spanish.)

Szteren, D., and E. Páez. 2002. Predation by southern sea lions (*Otaria flavescens*) on artisanal fishing catches in Uruguay. Mar. Freshw. Res. 53:1161-1167.

Vaz-Ferreira, R. 1976. *Otaria flavescens* (Shaw) southern sea lion. Advisory Committee on Marine Resources Research, Scientific Consultation on Marine Mammals, Bergen, Norway. 20 pp.

Wickens, P.A. 1995. A review of operational interactions between pinnipeds and fisheries. FAO Fish. Tech. Pap. 346. 86 pp.

Wynne, K. 1990. Marine mammal interactions with the salmon drift gillnet fishery on the Copper River Delta, Alaska 1988-1989. Alaska Sea Grant College Program. University of Alaska Fairbanks. 36 pp.

Yodzis, P. 2001. Must top predators be culled for the sake of fisheries? Trends Ecol. Evol. 16(2):78-84.

Telemetry Instruments and Analysis

Summary of a workshop held at the Sea Lions of the World Symposium
Anchorage, Alaska
October 3, 2004

Participants in the telemetry roundtable discussed some common issues encountered when using behavior-recording technology to answer questions about sea lion ecology.

Behavior recording and relay technologies

The choice between archival dive- and location-recording technologies, such as time-depth recorders (TDRs), dead-reckoning systems, and associated loggers of physiology and other information, and satellite-relay technologies, such as satellite data recorders (SDRs) and satellite relay data loggers (SRDLs), largely depends on recoverability of instruments from the study animal. Archival tags provide greater quantity and resolution of dive information, but must be retrieved; satellite-relay tags do not require recovery, but provide dive data in a less-frequent, more generalized form. Frequently, TDRs are combined with location-only Argos PTTs (platform terminal transmitters) to provide both dive and position fixes, because—notes Peter Olesiuk—the light-based geolocation systems carried by TDRs can be less accurate than Argos location estimation. NOAA National Marine Mammal Lab and Alaska SeaLife Center are testing new Advanced Telemetry Systems, Inc. remote-release devices that have not yet been successful in the field. Peter Olesiuk has great success retrieving floating TDRs that molt off harbor seals; however, these seals are confined to fjords and range over only tens of kilometers. Mary-Anne Lea and Ben Wilson (University of British Columbia) have recovered only 1 of 10 floating TDRs deployed on farther-ranging Steller sea lions. Gabrielle Müller has good success recovering tags using a release mechanism triggered by an airgun pellet fired from within 10 meters.

Newer archival technologies in use for sea lions include dead-reckoning systems, which provide finer-scale position and animal orientation information. Location accuracy is subject to drift; correction of this drift at each known haul-out location is not as accurate as ongoing correction that might be made using new GPS tags. Dead-reckoning systems in use include the Driesen and Kern system (www.driesen-kern.de/englischeseiten/products/biologgere) used by Nikolai Liebsch and Gabrielle Müller, the Little Leonardo system (polaris.isc.nipr.ac.jp/~penguin/oogataHP/procabst/leo.html) described by Russ Andrews, and the DTAG (dtag.whoi.edu) manufactured in-house (not commercially available) at the Woods Hole Oceanographic Institution. Russ Andrews further discussed acoustic pingers as a way to identify sea lion location while using multiband sonar to track foraging within fish schools in real-time.

Satellite-relay systems in use among sea lions include dive- and location- or location-only tags manufactured by Wildlife Computers (www.wildlifecomputers.com), Sirtrack (www.sirtrack.com) and Sea Mammal Research Unit (www.smru.st-and.ac.uk). With Steller sea lions, only 13% of radio signals made by the tags reach the satellite. Also there is a problem with antenna breakage, partly mitigated by use of thicker antennae. SDRs provide more generalized but more complete data; SRDLs provide greater dive detail but data are less complete. For both systems, programming decisions can optimize data collection to best suit study design and subject species. Roger Hill says that a GPS system under development should be able to provide higher-accuracy locations at greater frequency, relayed via Argos, than currently available with the Argos location estimation system; GPS power consumption may be an issue. Cell phone relay devices were mentioned as a possibility in areas with cell coverage; satellite phone–based systems would require a great deal of power.

Movement analysis technique

A problem with data analysis was cited: there are no standards for the editing/processing of data, and many groups have taken independent approaches to location processing. It would be useful to share information on the techniques used by different labs. One concern was that most current techniques for filtering and analyzing movement data were developed using animals that move relatively long distances during long trips-to-sea. However, some sea lions make very short trips-to-sea, during which few Argos locations are collected, which complicates filtering and analysis using these methods. New, model-based approaches to analysis of Argos location data may provide a better alternative, and are getting started among sea lion researchers. The work of Gina Himes Boor at Montana State University and Mark Hindell of the Antarctic Wildlife Research Unit (University of Tasmania) were cited.

Recommended analysis software

Seaturtle.org: Michael Coyne provides a variety of Argos location filters and mapping tools.

eMAMVIS: The Sea Mammal Research Unit (University of St Andrews, Fife, Scotland) is developing a public SRDL data visualization package, www.smru.st-and.ac.uk.

Australian Antarctic Division: This group is currently preparing software to visualize dive data along PTT location tracks.

The R Project for Statistical Computing: This general statistical analysis software has numerous add-on packages including spatial analysis, using the S language, similar to the commercial S-Plus system, www.r-project.org.

GMT (Generic Mapping Tools): This freely available GIS software appears to be a favorite of oceanographers, gmt.soest.hawaii.edu.

Researchers who know of, or are developing analysis software, are asked to please spread the word.

Capture technique

Capture of specific individuals or age classes is necessary for longitudinal studies of physiology, and also for behavior study if using archival instruments. Simon Goldsworthy explained a method to “dip” for sea lions using a box-shaped net suspended below a trawler-processor between tows while far offshore (60 km).

Future communication

Contact information and a summary of interests were circulated among all participants via email to facilitate further communication on these topics.

Session chairs

Session chairs for the Telemetry and Instrument Attachment roundtable discussion were Michael Rehberg (Alaska Department of Fish and Game, Anchorage) and Mary-Anne Lea (University of British Columbia, B.C., Canada).

Telemetry and Instrument Attachment roundtable participants.

Name	Affiliation	Study animals	Technologies	Comments
Russel Andrews	University of Alaska Fairbanks and Alaska SeaLife Center, USA		TDR, Stomach temperature, Jaw opening, Heart rate, respiration, body temperature and other physiological parameters, Flipper stroking, 3-D orientation, Swim speed, PTT, GPS, Video	
Carrie Beck	Alaska Department of Fish and Game, USA	Steller sea lion, Grey seal	TDR, SDR, PTT	
Holly Briggs	Texas A&M University, USA	Steller sea lion	SDR T-16, SPOT-2	Looking at general dive patterns, locations and habitat of Steller sea lions in Prince William Sound. Just looking to glean more information about satellite telemetry.
Tony Fischbach	USGS Alaska Science Center, Biological Science Office, USA	Pacific walrus	PTT with saltwater switch and haul-out timeline, remotely attached	
Pat Gearin	National Marine Mammal Laboratory, USA			
Tom Gelatt	National Marine Mammal Laboratory, USA			

Telemetry and Instrument Attachment roundtable participants (continued.)

Name	Affiliation	Study animals	Technologies	Comments
Simon Goldsworthy	South Australian Research and Development Institute and Aquatic Sciences Centre	Australian fur seal, New Zealand fur seal, Antarctic fur seal, Sub-Antarctic fur seal, Australian sea lion	TDRs, PTTs, VHF, Head-mounted digital camera	Need for spatial analysis free-ware, standardized approaches to filtering data and estimating time in area, distribution of foraging effort data etc.
Kaoru Hattori	Hokkaido National Fisheries Research Institute, Japan	Steller sea lion, Sea otter		
Roger Hill	Wildlife Computers, Inc.	n/a		Manufacturer of tags for all species.
Gina Himes Boor	Montana State University, USA	Steller sea lion		Stochastic spatial modeling using satellite telemetry data.
Kohji Iida	Hokkaido University, Japan	Steller sea lion	Acoustics, Vocalization, Auditory activity, Behavior	How do acoustics contribute to Steller sea lion behaviors?
Lisa Laceby	Lotek Wireless, Inc.	n/a	GPS, Argos, VHF, Acoustic, Archival	
Michelle Lander	National Marine Mammal Laboratory and University of Washington, USA	Steller sea lion	SRDL, SDR	

Telemetry and Instrument Attachment roundtable participants (continued.)

Name	Affiliation	Study animals	Technologies	Comments
Mary-Anne Lea	Marine Mammal Research Unit, University of British Columbia, Vancouver, B.C., Canada	S. elephant seal, Antarctic fur seal, Steller sea lion	TDR-Mk 3, 5, 6, 7, 9; heart rate and stomach temperature; PTT: SMRU SRDL, Sirtrack KiwiSat; VHF; Head-mounted digital camera; Acoustic tag (VEMCO)	
Nikolai Liebsch	IFM-GEOMAR, Kiel, Germany	Harbor seal, Weddell seal	Dead-reckoners for 3-D movement, Jaw sensors to record feeding events, Release mechanisms (timed “popup” and remote), Analysis software	
Rob Mattlin	Ministry of Fisheries, Wellington, New Zealand			
Lori Mazzuca	National Marine Mammal Laboratory and Alaska SeaLife Center, USA	Killer whale/cetacean and predation studies		
Sharon Melin	National Marine Mammal Laboratory, USA	California sea lion, Northern fur seal	SDR, TDR, Sirtrack KiwiSat PTT, VHF	
Gabriele Müller	IFM-GEOMAR, Germany	South American sea lion	Dead reckoners (12-channel), Satellite tags, Non-electronic release mechanism	To determine locations at-sea, movements and diving.

Telemetry and Instrument Attachment roundtable participants (continued.)

Name	Affiliation	Study animals	Technologies	Comments
Sarah E. Norberg	Alaska SeaLife Center, USA	3 captive Steller sea lions, juveniles and wild rehabilitated seals	Head-mounted digital camera, Acceleration data loggers, VHF and SPOT/PTT tags, ATS remote release	
Padraic O'Flaherty	Lotek Wireless, Inc.	n/a	GPS, Argos, VHF, Acoustic, Archival	
Peter Olesiuk	Department of Fisheries and Oceans, Canada	Harbor seal, Steller sea lion, California sea lion	TDR, Stomach temperature transmitter, VHF, Argos PTT, Sonic telemetry	
Kathryn Ono	University of New England, Department of Biological Sciences, USA	Harbor seal, Steller sea lion, California sea lion	SDR T16, SPLASH	Meeting was very informative for me (just starting out in this technology) to hear all these ideas from experts in the field.
Tony Orr	National Marine Mammal Laboratory and University of Washington, USA	California sea lion	Satellite tags: PTT; Archival tags: TDR	
Federico Riet Sapriza	Massey University, New Zealand			
Karin Soto	Marine Mammal Research Unit, University of British Columbia, Vancouver, B.C., Canada			

Telemetry and Instrument Attachment roundtable participants (continued.)

Name	Affiliation	Study animals	Technologies	Comments
Kim Raum-Suryan	Alaska Department of Fish and Game, USA	Steller sea lion	SDR, PTT, Radio transmitters	Would be nice to have a listserv for sea lion researchers so we could all keep in touch and share ideas.
Michael Rehberg	Alaska Department of Fish and Game and University of Alaska Anchorage, USA	Steller sea lion, Harbor seal	SRDL, SDR, SPOT	Understanding behavior at haul-out, bout and trip scales.
Diego Rodríguez	Mar del Plata University, Argentina	Southern sea lion	SPOT, SDRs, Short-term marks	
Jeremy Sterling	National Marine Mammal Laboratory, USA	Northern fur seal, Steller sea lion, Antarctic fur seal	SDR; SPLASH; TDR-Mk 5, 7, 9; Sirtrack KiwiSat 101 PTT	

Telemetry Attachment Techniques

Summary of a workshop held at the Sea Lions of the World Symposium Anchorage, Alaska October 3, 2004

Telemetry devices are deployed on otariids and phocids in a variety of ways, some of which are species specific. The successes and failures of these different techniques are not usually discussed in the literature. The Sea Lions of the World Symposium presented a rare opportunity for telemetry specialists and pinniped researchers to discuss the pros and cons of many techniques. The following summary details some the techniques used across sea lion species and their rates of success.

General recommendations

- Apply epoxies as thinly as possible to avoid excess heat generation and possible burning (more difficult with sea lions than fur seals).
- Reduce the size of neoprene or mesh footprints. They may not be necessary at all depending on the length of deployment.
- "Male" Velcro may be used as a substrate for coating with epoxy under devices.
- Apply epoxies and/or cements to the surface of the fur. It is not necessary to work deep into the fur. Applying to the surface reduces likelihood of burning. S. Goldsworthy recommends using tongue depressors to temporarily hold tag off skin while epoxy sets.
- Consider using small areas of epoxy rather than coating a large surface area (N. Liebsch and S. Goldsworthy). This promotes better flexibility and water circulation.
- If using an epoxy try to reduce sharp edges in order to reduce rubbing under fur. Apply thinly—less is best!

- Conduct your own tests in the lab with various brands of adhesives and substrates. R. Andrews has a paper on this coming out in the future.
- All methods have their pros and cons, and some techniques may suit some species and deployment lengths better than others. There is no hard and fast rule. Contact people on the list if you need any advice.
- A group order could be coordinated to purchase quantities of adhesives too large for an individual project.

Adhesives and epoxies

Quick setting adhesives

5-minute epoxy + mesh (e.g., Devcon)

Pros:	Fast setting, comes in pre-mixed syringes or self-mix bottles.
Cons:	Can reach up to 80°C. There is a risk of burning the animal, and skin necrosis, if it is applied too thickly. Not made to withstand UV and saltwater. It may become brittle and flaky when applied thinly.
Application:	Apply in very fine layers.
Duration:	Five-minute epoxy has lasted 8-9 month deployments on Californian sea lions (S. Melin) and to 8 months on spotted seal in Russia. P. Olesiuk has used 5-minute with success on harbor seals by storing epoxy in the cooler, which slows the setting time and reduces the amount of heat it generates.

10-minute epoxy (e.g., Devcon and Vantico)

Pros:	More flexible than 5 minute, less heat, comes in pre-mixed syringes.
Cons:	Slower than 5 minute (actually 15-20 minutes), may need to keep warm if in very cold conditions (e.g., Bering Sea, Antarctic).
Application:	Pre-mixing in plastic cups before application reduces mess.
Duration:	Alaska Department of Fish and Game results from 2002 deployment on juvenile Steller sea lions—most 6-9 months. University of British Columbia results on 2003 deployment on juvenile Steller sea lions—many deployments lasted 9-10 months (rubbing detected in some cases).

SARDI used 10-minute epoxy on Antarctic, New Zealand, and Australian fur seals (S. Goldsworthy).

15-minute 2-part epoxy (e.g., System Three)

Pros: Works very well, mixes perfectly every time.
Cons: Need sufficient time for epoxy to set.
Duration: For information on successful 3-month deployments, contact R. Andrews. See www.systemthree.com/p_t_88.asp.

Non-toxic Vetbond or 500280 (WPI)

Marbled murrelet biologists who used to use Bird Grip (see below, a flexible quick-setting adhesive) now use Vetbond.

Pros: Nontoxic and quick-setting (similar to superglue).
Cons: It needs some testing. It is probably only good for short deployments, e.g., deploying a small TDR for 1-2 foraging trips (could be great for fur seals).
Not cheap. Vetbond US$21 for a 3 ml package (need only a very small amount). 500280 US$44 for a 2 ml package.
Contact: WPI Telephone 1 (941) 371-1003. www.wpiinc.com/WPI_Web/Lab/Application_Curing.html. Shipping costs may be waived for group or large orders.

Slow-setting adhesives

Neoprene and neoprene cement (R. Andrews and H. Briggs)

Neoprene attachment technique may also work well with small amounts of epoxy.

Pros: When dry it is a very flexible and reliable adhesive.
Cons: A slow technique used for animals under sedation (~45 minutes).
Neoprene contains toluene (toxic). It may result in temporary skin irritation.
Application: Need to apply in layers. Small footprint of neoprene suggested if necessary at all (Rob Mattlin).
Duration: 3 months average duration and up to 6 months.
Neoprene supplier: Canal Rubber, USA
Duration: No difference in longevity with epoxy-mesh and neoprene cement techniques (over 2-6 month deployments).

Previously available adhesives

- Evercoat Tenset is no longer available.
- Bird grip (Eclectic Industries, Titan, Oregon) is very strong, viscous (easier application), flexible, and fast setting. (The Titan corporation was contacted; it is definitely not possible to obtain this product.)

Remote release devices

Advanced Telemetry Systems release mechanism

Contacts: T. Gelatt or J. Sterling, R. Andrews, S. Melin or P. Olesiuk regarding success.

Comments: This design is still under development. Currently the release trigger mechanism is large to carry around and is easier to use with two people. The maximum detection range is 0.2-1.6 km. Contact ATS for further details.

Venus camera release mechanism

Contacts: Wild Insight Ltd, UK (www.wildinsight.com.uk), B. Wilson, and M-A Lea, regarding use on juvenile Steller sea lions.

Disc-triggered release mechanism

Contacts: G. Müller for details regarding use on male southern sea lions (5/5 success rate).

Comments: 4-5 m range, 2.5 cm disc, need to be a good shot and have the right angle!

Russ Andrews custom-made release

Used with 50% success rate (7/15)

Floating tags (alternative to release mechanisms)

Tags are potted in syntactic foam and have been used with good success.

Pros: Enables the use of archival tags on species that are difficult to recapture.

Cons: Makes tags larger in an era when miniaturization is preferable.
Searching effort required once tags have molted off the sea lion.

Contacts: Harbor seals, P. Olesiuk and J. Womble.
Juvenile Steller sea lions, M-A Lea and B. Wilson.

Session chairs

Session chairs were Mary-Anne Lea (University of British Columbia, Vancouver, Canada) and Michael Rehberg (Alaska Department of Fish and Game, Anchorage). Rapporteur was Diana Szteren (CICIMAR, La Paz, Mexico).

Telemetry Attachment Techniques workshop participants.

Name	Affiliation	City	State/ Province	Country
Russ Andrews	Alaska SeaLife Center	Seward	AK	USA
Carrie Beck	Alaska Department of Fish and Game	Anchorage	AK	USA
Melinda Braun	Wildlife Computers	Redmond	WA	USA
Holly Briggs	Texas A&M University	Galveston	TX	USA
Vladimir Burkanov	National Marine Mammal Lab	Seattle	WA	USA
Tony Fishbach	U.S. Geological Survey	Anchorage	AK	USA
Tom Gelatt	National Marine Mammal Lab	Seattle	WA	USA
Simon Goldsworthy	South Australian Research and Development Inst. (SARDI)	Adelaide	SA	Australia
Roger Hill	Wildlife Computers	Redmond	WA	USA
Gina Himes Boor	Montana State University	Bozeman	MT	USA
Kohji Iida	Hokkaido University	Hakodate		Japan
Mary-Anne Lea	Marine Mammal Research Unit, University of British Columbia	Vancouver	BC	Canada
Nikolai Liebsch	IFM-Geomar	Kiel		Germany
Evgeniy Mamaev	Vyatka State Agricultural Academy	Kirov		Russia
Sharon Melin	National Marine Mammal Lab	Seattle	WA	USA
Gabriele Müller	IFM-Geomar	Kiel		Germany
Sarah E. Norberg	Alaska SeaLife Center	Seward	AK	USA
Padraic O'Flaherty	Lotek Wireless Inc.	St. Johns	NL	Canada

Telemetry Attachment Techniques workshop participants (continued.)

Name	Affiliation	City	State/ Province	Country
Peter Olesiuk	Department of Fisheries and Oceans	Nanaimo	BC	Canada
Kathryn Ono	University of New England	Biddeford	ME	USA
Tony Orr	National Marine Mammal Lab	Seattle	WA	USA
Kim Raum-Suryan	Alaska Department of Fish and Game	Anchorage	AK	USA
Mike Rehberg	Alaska Department of Fish and Game	Anchorage	AK	USA
Diego Rodríguez	Mar del Plata University	Mar del Plata		Argentina
Karim H. Soto	Marine Mammal Research Unit, University of British Columbia	Vancouver	BC	Canada
Jeremy Sterling	National Marine Mammal Lab	Seattle	WA	USA
Jamie Womble	National Marine Mammal Service	Auke Bay	AK	USA
Kate Wynne	University of Alaska Fairbanks	Kodiak	AK	USA
Carlos Francisco Yaipen-Llanos	ORCCAMM	Lima		Peru

References

Andrews, R. 1998. Remotely releasable instruments for monitoring the foraging behavior of pinnipeds. MEPS 175:289-294.

Baranov, E.A. 1996. A device for data retrieval and recapture of diving animals in open water. Mar. Mamm. Sci. 12:465-468.

Ellis, G.M., and A.W. Trites. 1992. The RAM-packs came back: A method for attaching and recovering pinniped data recorders. Aquat. Mamm. 18:61-64.

Hammill, M.O., V. Lesage, G. Lobb, and P. Carter. 1999. A remote release mechanism to recover time-depth recorders from marine mammals. Mar. Mamm. Sci. 15:584-588.

Mellor, D.J., N.J. Beausoleil, and K.J. Stafford. 2004. Marking amphibians, reptiles and marine mammals: Animal welfare, practicalities and public perceptions in New Zealand. Department of Conservation Science Publishing, Wellington, New Zealand. 55 pp. science.publications@doc.govt.nz.

Quantifying Predation on Sea Lions: Identifying Key Parameters and Data Needs

Summary of a workshop held at the Sea Lions of the World Symposium
Anchorage, Alaska
October 3, 2004

Predation events on sea lions can be dramatic, yet in many cases the roles of natural predators in the dynamics of sea lion populations are poorly understood. Predator-prey and ecosystem models quantify the ecological interactions between sea lions and their predators, but often suffer from a lack of information regarding key parameters. The following summarizes a workshop held at the Sea Lions of the World conference, which brought together researchers in an effort to outline the key data necessary to quantify the impacts of predators on sea lion populations and to discuss methods of obtaining and interpreting these data.

To quantify predation on sea lion populations it is necessary to know (1) the abundance of their predators, (2) the predators' rates of food intake, (3) the proportion of the predators' diets composed of sea lions, and (4) the component of the sea lion population that is vulnerable to predation. The workshop discussion primarily focused on methods for determining the second and third items.

The first method for determining the diet and rate of prey intake by predators of sea lions is direct observation. Killer whales are known predators of at least three sea lion species (Jefferson et al. 1991), and direct observation has been employed with some success in the quantification of their predation on sea lions and other marine mammals (e.g., Hoelzel 1991, Baird and Dill 1995). Focal groups of whales are followed for extended periods of time and the rates of observed attacks and kills on sea lions (and other prey) are determined. The remains of prey are sometimes collected after an observed predation event to identify the species. Observation is often limited to daytime. The technique is potentially biased toward larger prey that take more time and effort to kill. Underwater predation events on smaller prey may go unnoticed. Also, noise from an observation vessel may impair whales' abilities to acoustically locate prey, which could bias observations of predation events.

When continuous observation of predators or direct observation of predation events are not feasible, the simple presence of predators in the vicinity of sea lions has been used as an index of predation rate. For example, in Australia great white sharks have been tagged with VHF transmitters (Bruce et al. 2005). Receiving stations are located near sea lion foraging and breeding areas and monitor the presence of sharks in these areas. Video cameras have been used to observe the presence of killer whales in the vicinity of Steller sea lion haul-outs. Satellite tags are another option for monitoring predator movements, and have the advantage of covering a wide area without the need for active tracking or numerous receiving stations/cameras. The development of a satellite tag for killer whales is currently under way. A limitation of simply tracking predator movements is that it is not possible to measure the actual predation rate.

Acoustic monitoring has the potential to quantify both the presence and predation rates of killer whales. Deecke et al. (2005) have observed that the vocalization rates of mammal-eating killer whales consistently increase after a kill. Thus, killer whale vocalizations could potentially be used to calculate predation rates. Deecke is currently ground-truthing the use of stationary hydrophones for passive acoustic monitoring of killer whale predation events in Southeast Alaska. Acoustic monitoring has the advantage that predation events underwater can be recognized. However, it may be difficult to determine the type of prey taken unless vocalizations vary with the species of prey. Whether or not vocalization types or rates vary with prey species is currently unknown. A method that has been used to assess the species of prey taken by predators of sea lions is stomach content analysis. Stomach contents of sharks are often obtained through the capture of live animals while data on the contents of killer whale stomachs come mainly from stranded animals. The stomach of one killer whale stranded in Alaska contained 14 flipper tags from Steller sea lions, highlighting the potential importance of killer whale predation on this sea lion species (Heise et al. 2003).

Sleeper shark stomachs have also been examined in Alaska, but so far there is not much evidence of predation on sea lions. In Australia great white sharks are a protected species, so there are few carcasses to examine stomach contents. Predation of Australian sea lions has been documented in bronze whaler sharks, *Carcharhinus brachyurus*, south of Kangaroo Island (R. McIntosh unpubl. data). While stomach contents reveal the species of prey taken, quantification of the diet from stomach contents is complicated by feeding frequency, rate of digestion and the retention of prey parts in the stomach. Captive feeding experiments could be used to examine these biases, but are unlikely to occur with large predators of marine mammals.

A second method that has been used to assess the diet composition of predators of sea lions is fatty acid analysis. Fatty acid analysis has been done with killer whales and the technique can currently distinguish between broad classes of prey (e.g., fish, pinnipeds, large whales). Blubber samples for fatty acid analysis are obtained by biopsying wild whales using a dart gun (Barrett-Lennard et al. 1996). The innermost blubber layer has been found to be more active than the outer blubber layer in cetaceans (Koopman et al. 1996) and thus it may be the most relevant with respect to predicting diet. However, it is currently difficult to obtain blubber cores that are long enough to reach the inner layer. In general, there is uncertainty regarding potential differences in fatty acid signatures at different blubber depths and locations on the body. Captive feeding experiments could potentially reduce these biases. Analysis of the mechanics of feeding can potentially be used to assess the prey that predators are capable of consuming.

A study is currently under way to examine the mechanics of killer whale feeding. Presumably the ability of a whale to get a purchase on the body or appendage of a marine mammal prey is reflected in the success of an attack, and thus the predator's overall diet, according to optimal foraging theory. Rates of predation on sea lions can also be estimated by studying sea lions themselves. Scarring has been used to assess predation on Australian sea lions by sharks (P. Shaughnessy unpubl. data). Scars from killer whale bites are sometimes observed on other cetaceans (Shelden et al. 2003), but are not commonly observed on sea lions, possibly because attacks are more often fatal. M. Horning is currently developing a mortality tag that can be implanted in the body cavity of a sea lion. When a tagged sea lion is killed and/or consumed by a predator the tag would transmit a message via satellite that the sea lion was dead.

Data on the diet and prey intake of sea lion predators, obtained using the above methods, are critical to models that explore the impact of predation on individuals and populations of sea lions. These models can be static or dynamic, individual-based or population-level, and have a high spatial/temporal resolution or a decadal, ecosystem-wide scope. Each model incorporates predation in a different way. For example, an individual-based model being developed by C. Alvarez considers the risk of predation (or probability of encountering a predator) experienced by a foraging sea lion in different areas and at different depths on a fine time scale. Regardless of the specific modeling approach, it is important to have quantitative estimates of the number of predators and the number of sea lions consumed by those predators.

The methods discussed in this workshop all show promise for improving estimates of predation, but no single technique can currently provide accurate, unbiased, quantitative estimates of the impact of predators on sea lion populations. The role of predation in sea lion ecology and evolution is often not well understood. In Australia, sea lions and fur seals are sympatric and yet have different foraging strategies, behaviors, and life histories. It is not understood why the Australian sea lion has such a unique life history. It could be related to many things such as environmental parameters or foraging ecology, but the role of predation in this relationship has not been examined at this stage. In Alaska, the Steller sea lion has experienced a drastic decline in numbers. It seems unlikely that killer whale predation was the sole cause of that decline, but it may have been an important contributing factor, particularly its interaction with other factors (e.g., nutrition, disease). Further research quantifying predation on the sea lions of the world will help us better understand their ecology and evolution.

Workshop attendees

Juan Jose Alava
Carlos Alvarez
Russ Andrews
John Bengtson
Paul Breen
Aurelie Castinel
Andrea Coombs
Douglas DeMaster
Gavin Fay
Sylvie Guénette
Caroline Jezierski
Jennifer Katalinich
Lori Mazzuca
Rebecca McIntosh
Bob Small
Ward Testa
Brad Warren
Arliss Winship
Nicholas Wolf

References

Baird, R.W., and L.M. Dill. 1995. Occurrence and behaviour of transient killer whales: Seasonal and pod-specific variability, foraging behaviour, and prey handling. Can. J. Zool. 73:1300-1311.

Barrett-Lennard, L.G., T.G. Smith, and G.M. Ellis. 1996. A cetacean biopsy system using lightweight pneumatic darts, and its effect on the behavior of killer whales. Mar. Mamm. Sci. 12:14-27.

Bruce, B.D., J.D. Stevens, and R.W. Bradford. 2005. Site fidelity, residence times and home range patterns of white sharks around pinniped colonies. Final Report to the Australian Government Department of the Environment and Heritage, CSIRO Marine and Atmospheric Research, Hobart. 41 pp.

Deecke, V.B., P.J.B. Slater, and J.K.B. Ford. 2005. The vocal behaviour of mammal-eating killer whales: Communicating with costly calls. Anim. Behav. 69:395-405.

Heise, K., L.G. Barrett-Lennard, E. Saulitis, C. Matkin, and D. Bain. 2003. Examining evidence for killer whale predation on Steller sea lions in British Columbia and Alaska. Aquat. Mamm. 29:325-334.

Hoelzel, A.R. 1991. Killer whale predation on marine mammals at Punta Norte, Argentina: Food sharing, provisioning and foraging strategy. Behav. Ecol. Sociobiol. 29:197-204.

Jefferson, T.A., P.J. Stacey, and R.W. Baird. 1991. A review of killer whale interactions with other marine mammals: Predation to co-existence. Mamm. Rev. 21:151-180.

Koopman, H.N., S.J. Iverson, and D.E. Gaskin. 1996. Stratification and age-related differences in blubber fatty acids of male harbor porpoise (*Phocoena phocoena*). J. Comp. Physiol. B 165:628-639.

Shelden, K.E.W., D.J. Rugh, B.A. Mahoney, and M.E. Dalheim. 2003. Killer whale predation on belugas in Cook Inlet, Alaska: Implications for a depleted population. Mar. Mamm. Sci. 19:529-544.

Assessing the Diets of Sea Lions: Current Techniques and Future Challenges

Summary of a workshop held at the Sea Lions of the World Symposium Anchorage, Alaska October 3, 2004

Roundtable participants reviewed the techniques used to determine what sea lions eat, with a view to understanding the problems posed by the different species. They also discussed a range of methods to estimate numbers and biomass of prey consumed, and looked to the challenges that lie ahead.

Current techniques by species

California sea lions

Extensive numbers of scats have been collected in California, Washington, and British Columbia. Most of the California sea lion diet work in British Columbia has focused on winter diets. Prior to 1980, diet studies relied on identifying only otoliths, which failed to account for species such as dogfish and sharks. However, all hard parts have been used since the 1990s, and stomachs have been collected in the past in Washington to compare with scat analysis. Visual observations have also been used to identify large prey brought to the surface by California sea lions.

Steller sea lions

Diets were determined from stomach contents until the 1990s when scat analysis became the preferred technique. However, Japan relies on stomachs from shot Steller sea lions (mostly males). Thousands of scats have been collected since 1990 throughout most of the North Pacific, and species of fish have been identified using the all structure technique. Interest in assessing diets from fatty acids has developed since 1998, and recent work with captive animals has investigated the use of DNA to identify prey species. Stable isotope analysis is also being explored to identify the timing of weaning.

South American sea lions

Diets differ significantly between the Atlantic and Pacific Ocean populations. There are also significant latitudinal differences. Generally, diets of South American sea lions have been identified from the otoliths and beaks recovered from stomachs. Otoliths tend to be destroyed in scats because they are fragile and easily crushed by gastroliths. This has been noted on the Falkland Islands. Timing of weaning has been studied by measuring mercury concentrations in muscle. Mercury is a good tracer of diet history (varying between <1 ppm and 15 ppm in a month) and can indicate increasing consumption of fish. Different tracers for detecting squid have not been tested yet. Researchers tend to rely on otoliths rather than the all structure technique because otoliths are easy to recover and identify with little training and money. There is no systematic study of South American sea lion diet. Most knowledge about diets has been obtained from graduate student research.

New Zealand sea lions

Most studies have been small and undertaken opportunistically by graduate students. They have tended to rely on identifying otoliths and beaks from scats and stomachs (of animals caught incidental to fishing). Blubber biopsies (n = 500-600) from lactating females have been collected and stored in the last 6 years. Work is under way to create a prey library of fatty acid signatures. Proposals are also being developed to measure stable isotopes. No work has been undertaken on using genetics, nor are there any captive New Zealand sea lions available for calibrating and verifying the different techniques.

Australian sea lions

Traditional scat analysis used for other species of sea lions was shown to be unreliable for Australian sea lions by Cheal and Gales in the 1980s. Most hard parts are lost to digestion and ground to a paste. Some do pass, but it is not clear how representative they are. Stomachs of Australian sea lions appear to have more gastroliths than other species, which may help to digest crustaceans. Scats, vomits, and stomachs are being collected from a breeding colony at Seal Bay, while enemas and scats are being used to study the diet of animals at Dangerous Reef. Initial studies are focused on commercial species. Some captive work has been done to examine recovery rates, and research is looking into the use of DNA, stable isotopes, and underwater cameras. Collecting spews is challenging because they tend to be quickly consumed by birds.

Overview of current methodologies

Hard part recovery

Dietary studies of all sea lion species tend to report the percent frequency with which species are recovered from stomachs or scats. This approach tends to report only whether a species was present or absent, and does not make any inference about numbers or sizes of prey contained within the sample.

The next level of analysis is biomass reconstruction, which aims to determine how much an individual or population eats. Population consumption estimates tend to rely on frequency of occurrence data. However, relative volume is needed to understand how much an individual has consumed. Both volume and frequency of occurrence need to be factored when deriving estimates of consumption.

The split sample frequency of occurrence method re-weights the simple frequencies of occurrence to express the proportion of overall diet consisting of any single species. The split sample technique tends to give more weight to species that occur more frequently, and appears to perform better at a population level than at smaller (more individual) scales. Smaller scales need volumetric analysis.

With enough scat or stomach samples, the frequency of occurrence method appears to perform well. However, smaller sample sizes require correction for the variation in digestion and passage of hard parts from different species of prey (which can be done by applying numerical correction factors estimated from captive feeding trials).

Determining diet based on counting the total number of hard parts recovered from any one prey species in a scat or stomach may overestimate the importance of large fish. Bones of a larger fish tend to be more robust and are more likely to survive digestion than the bones of a smaller fish.

The all structures technique is superior to identifying only otoliths. However, it is a technique that requires considerable time and training to develop and apply.

Fatty acids

Identifying diets from the fatty acids found in the blubber of sea lions requires a prey library to account for the dietary sources of fat detected. Running the data through a statistical model (QFASA = quantitative fatty acid signature analysis) allows the biomass of prey eaten by individual sea lions to be estimated. It can also be used to detect transitions in diet (such as switching from milk to fish) as well as regional and seasonal changes in the proportions and types of prey consumed. The technique has been largely developed with phocids. Captive feeding experiments are being conducted with Steller sea lions to determine how well the technique works for sea lions. The captive studies are examining the rate of turnover in fatty acids and how they correspond to changes in quantities and species of prey consumed.

Scat collecting and processing

Computer simulations have been used to estimate the numbers of scats that should be collected to accurately describe sea lion diets using the frequency of occurrence technique. Trites and Joy found that researchers should collect between 59 and 94 scats. A sample of 59 scats ensured identifying species of prey that occur with >5% frequency in the diet, while samples of 94 were needed to detect differences between two populations (with a medium effect size). The rule of thumb being used in British Columbia and Southeast Alaska is to collect 60 scats per site. Ultimately the question of *n* depends on the questions asked, and the level of pooling of sites or periods being used. Prime and Hammond did a similar analysis with biomass reconstructions and concluded that about 100 samples were required. These analyses highlight how easily incorrect conclusions can be drawn about sea lion diets from small sample sizes.

Diets of adult males and females likely differ, and there may also be differences between juvenile and adult diets. Thus, consideration needs to be given when collecting scats about the relative age and sex composition of haul-outs and rookeries. Another factor to consider when making comparisons or conclusions about diet is the time of year. A power analysis on existing data can be performed to determine an optimum sampling design.

Removing hard parts from scats is typically done by spray washing scats through nested sieves. Drawbacks to this method include the smell and mess, as well as the potential to break structures or have them fly out of the sieves. Other techniques that have been explored are cleaning with an elutriator or washing machine. The advantage of the washing machine is that it can process larger numbers of samples and removes the soft parts of the scat more gently. Controlled experiments to test the use of washing machines have shown some loss of structures (particularly pin bones, which cannot be identified to species). The scats are placed in fine mesh paint straining bags, and detergent is added to the water. Different detergents and different wash cycles have been found to produce varying effects. This technique has been primarily used with California sea lions and is being developed for Steller sea lions.

There is increased interest in subsampling scats for analyses of heavy metals or hormone concentrations. These techniques require mixing the sample, which may result in breakage of structures or loss (if removed with a spoon). One method being used to subsample Steller sea lion scats is to suspend the scats in jars with small amounts of water. A small sample of scat can be removed with a pipette with no loss of bones after the scat has settled.

Scats can be weighed, or volume can be taken by measuring the settled level of samples that have been suspended in jars with water. This information may be useful for estimating the volume of prey the scat sample represents. Small scats (with small volumes) should be collected in the field because they contain considerable data. Simulation studies that involved cutting samples into smaller and smaller pieces have shown that small samples are very robust in terms of preserving most information. Bigger samples can provide more information, but the increase in dietary information with increasing size of the individual scat plateaus quickly.

What does a scat represent?

A single scat unlikely represents a single meal. Captive feeding experiments indicate that some bones may pass as much as 7 days following ingestion. However, most scats appear to represent a mixture of prey eaten over the last 18-48 hours. While some fish bones can last days or weeks—and beaks can last longer than one month—the majority do not. Activity, distance traveled, and time spent resting by the sea lion may affect the rates of digestion and recovery of hard parts from scats. DNA of soft parts likely represents 1-2 days of foraging. Thus, a scat does not necessarily represent the last meal.

Most scat studies of sea lions have reported finding tens of species of fish in scats and stomachs that have frequencies of occurrence of <1%. Such infrequently occurring prey may not be important dietary items and may in fact be secondary prey (i.e., they were originally consumed by the species of fish eaten by the sea lion). It may therefore be necessary to only report species that occur with >5% or 10% frequency of occurrence. Moving this line of importance upwards means that fewer samples need to be collected to ensure that important species were not missed. However, increased sample sizes would be needed to detect the presence of the rarer species and assess the effects of sea lion predation on endangered species.

Scat analysis has tended to focus on fish and may overlook detection of cephalopods, crustaceans, birds, etc. The QFASA and DNA techniques can assist with identifying these prey types. QFASA can also identify species consumed in ephemeral spawning areas that are too far for individuals to return to haul outs to defecate. Small cephalopods are known to come through in scats, but not large ones. Beaks can pile up at the pylorus and come through in one pulse, possibly weeks later, resulting in under- or overestimation of the importance of cephalopods. However, eye lenses pass easily and can be good indicator of cephalopod presence in diet.

Some stomachs have been recovered from animals drowned or shot during commercial fishing. Such samples may not represent an average diet and could be biased toward species targeted by fisheries. Secondary prey is another potential bias, but is generally believed to be inconsequential. Stomach stones—present in all species of sea lions—likely also affect the recovery of identifiable hard parts in scats and stomachs.

Where to from here?

Better statistical techniques are required to accurately reconstruct diet. Computer simulations are the most promising way to determine which techniques work and under what circumstances. Data are needed on how sea lions forage in the wild (e.g., do they consume large amounts of small prey versus small amounts of large prey?). Statistical models can also be parameterized with data from captive feeding studies.

QFASA validation has been done using computer simulations that created pseudo-seals eating different amounts of prey. These analyses help to identify which fatty acids are important to model diet. Analysis of blubber samples from captive fed harbor seals has shown QFASA to be good at estimating dominant prey, but poor at estimating the infrequently consumed species. Critter cams have been useful to document feeding behavior of harbor seals, and have supported the results of fatty acid analysis.

DNA analysis of scat (using real time PCR = polymerase chain reaction) appears to perform better if the entire scat is blended. Genetic markers are needed to identify the different species of prey of interest. Captive feeding experiments with Steller sea lions indicate that the DNA method performed well despite varied amounts of different species of prey. Detection of prey improves as more of the each scat is used.

Prey libraries that catalogue bones, DNA and fatty acid signatures are required to effectively use each of the dietary techniques. It is also important to determine the energy content of sea lion prey, as well as mineral and vitamin content. Nutrition received by sea lions from prey has been generally overlooked. At a minimum, prey should be sampled twice per year—once before spawning and 6 months after spawning—because energy content of species in diet changes over the year. Size of prey may also be an important consideration in the ability of sea lions to assimilate energy.

A top priority for dietary studies is the establishment of prey libraries to document size, ontogeny, and temporal and geographic differences of prey. A suggested minimum sample size is 30 of each species, which should be collected at least twice in one year (once before spawning and 6 months later).

Consistency in the application of techniques between labs is another priority. Standardized samples should be shared between labs to ensure that results of different labs are comparable.

Development of new techniques is also to be encouraged. Possibilities include the use of sulfur to distinguish diets from different water sources, or oxygen analysis that may identify diet based on latitude differences. Analysis of micronutrients—minerals and heavy metal elemental signatures—is another possibility. Whiskers also contain a time line of dietary information to be further explored.

Scat analysis is time consuming. A single Steller sea lion scat, for example, can take about 20 minutes for an expert to identify all of the recovered structures. It is therefore important to minimize the cost by optimizing the number of samples that need to be collected to accurately monitor and quantify diets. Other techniques, such as DNA analysis, may ultimately be more cost effective than identifying all bones.

Further work is needed using computer simulations to develop better techniques to reconstruct diets. This requires the skills of statisticians and biologists, as well as data from controlled feeding experiments and field studies of foraging sea lions.

Many questions remain about the timing and process of weaning in sea lions. Application of fatty acid and stable isotope analysis are promising techniques to resolve such questions and will undoubtedly be given greater attention in the future.

Considerable attention is currently given to estimating the biomass of prey consumed by sea lions. Yet the most important variable may well be energy content and nutrition derived from different species, and their interaction with seasons. Further research into these and other questions is needed to obtain a fuller understanding of the diets and needs of sea lions within the ecosystem.

Workshop participants

Participants in the Assessing the Diets of Sea Lions workshop were Naomi Bargman, Carrie Beck, Pádraig Duignan, Pat Gearin, Simon Goldsworthy, Charles Hu, Juan Jose, Bec McIntosh, Peter Olesiuk, Lorrie Rea, Fredorico Riet Sapriza, Diego Rodríguez, Dom Tollit, Andrew Trites, JJ Vollenweider, Brad Warren, Nick Wolfe, and Jamie Womble. This summary was prepared by Andrew Trites, Naomi Bargman, and Bec McIntosh.

Participants

Juan Jose Alava
University of South Carolina
School of the Environment
Columbia SC 29205
jalva@environ.sc.edu

Carlos Alvarez-Flores
NOAA Fisheries
Alaska Fisheries Science Center
7600 Sand Point Way NE Bldg. 4
Seattle WA 98115
carlos.alvarez@noaa.gov

Russel D. Andrews
Alaska SeaLife Center
PO Box 1329
Seward AK 99664-1329
russ_andrews@alaskasealife.org

John P.Y. Arnould
Deakin University
School of Biological and Chemical Sciences
221 Burwood Hwy
Burwood VIC 3125
Australia
jarnould@deakin.edu.au

Shannon Atkinson
Alaska SeaLife Center
PO Box 1329
Seward AK 99664
Shannon_Atkinson@alaskasealife.org

David Aurioles-Gamboa
University of California
Long Marine Lab
100 Shaffer Rd.
Santa Cruz CA 95060
daurioles@hotmail.com

Stephen Ban
University of British Columbia
Marine Mammal Research Unit
6248 Biological Sciences Rd.
Vancouver BC V6T 1Z4
Canada
ban@zoology.ubc.ca

Carrie A. Beck
Alaska Dept. of Fish and Game
525 W. 67th St.
Anchorage AK 99518
charlotte_beck@fishgame.state.ak.us

Kimberlee B. Beckmen
Alaska Dept. of Fish and Game
Div. of Wildlife Conservation
1300 College Rd.
Fairbanks AK 99701
kimberlee_beckmen@fishgame.state.ak.us

John L. Bengtson
NOAA Fisheries
National Marine Mammal Lab
7600 Sand Point Way NE
Seattle WA 98115
john.bengtson@noaa.gov

Mary Bozza
Alaska SeaLife Center
PO Box 1329
Seward AK 99664
Mary_Bozza@alaskasealife.org

Melinda Braun
Wildlife Computers
16150 NE 85th St. #226
Redmond WA 98052
tags@wildlifecomputers.com

Paul A. Breen
National Institute of Water and Atmospheric Research (NIWA)
Box 14901
Wellington 6003
New Zealand
p.breen@niwa.cri.nz

Reid Brewer
University of Alaska Fairbanks
Marine Advisory Program
PO Box 526
Unalaska AK 99685
brewer@ims.uaf.edu

Holly Briggs
Texas A&M University
Dept. of Marine Biology
5007 Avenue U
Galveston TX 77551
hbriggs@pxe.org

Melanie N. Brown
NOAA Fisheries
Alaska Region, Sustainable Fisheries Div.
709 W. 9th St.
Juneau AK 99801
melanie.brown@noaa.gov

Kathy A. Burek
Alaska Veterinary Pathology Services
PO Box 773072
Eagle River AK 99577
fnkab1@uaf.edu

Vladimir Burkanov
Natural Resources Consultants Inc.
NOAA NMFS
7600 Sand Point Way NE Bldg. 4
Seattle WA 98119
vladimir.burkanov@noaa.gov

Jennifer M. Burns
University of Alaska Anchorage
Biological Sciences Dept.
3211 Providence Dr.
Anchorage AK 99508
jburns@uaa.alaska.edu

Don Calkins
Alaska SeaLife Center
PO Box 1329
Seward AK 99664
don_calkins@alaskasealife.org

Katherine A. Call
NOAA Fisheries
National Marine Mammal Lab
7600 Sand Point Way NE Bldg. 4
Seattle WA 98115
kate.call@noaa.gov

Richard Campbell
West Australia Marine Research Labs
Dept. of Fisheries
PO Box 20
North Beach 6020
Australia
rcampbell@fish.wa.gov.au

Shane Capron
NOAA Fisheries
Office of Protected Resources
222 W. 7th Ave. #43
Anchorage AK 99513
shane.capron@noaa.gov

Michael Castellini
University of Alaska Fairbanks
Institute of Marine Science
Fairbanks AK 99775-1090
mikec@alaskasealife.org

Aurelie Castinel
New Zealand Wildlife Health Centre
Massey University
Inst. of Veterinary, Animal and Biomedical Sciences
Palmerstown North
Manawatu PB11-222
New Zealand
A.Castinel@massey.ac.nz

B. Louise Chilvers
Dept. of Conservation
Science and Research Unit
PO Box 10-420
Wellington
New Zealand
lchilvers@doc.govt.nz

Dennis Christen
Alaska SeaLife Center
PO Box 1329
Seward AK 99664-1329
dennis_christen@alaskasealife.org

Andrea P. Coombs
University of British Columbia
Marine Mammal Research Unit
6248 Biological Sciences Dr.
Vancouver BC V6T 1Z4
coombs@zoology.ubc.ca

Leslie Cornick
Alaska Pacific University
Environmental Science
4101 University Dr.
Anchorage AK 99508

Daniel P. Costa
University of California Santa Cruz
Long Marine Lab
100 Shaffer Rd.
Santa Cruz CA 95060
costa@ucsc.edu

Jen Dailer
Alaska SeaLife Center
PO Box 1329
Seward AK 99664-1329
jen_dailer@alaskasealife.org

Randall W. Davis
Texas A&M University
Dept. of Marine Biology
5007 Avenue U
Galveston TX 77551
davisr@tamug.tamu.edu

Pieter A.P. deHart
University of Alaska Fairbanks
SFOS, Institute of Marine Science
PO Box 757220
Fairbanks AK 99775-7220
pdehart@ims.uaf.edu

Robert L. DeLong
NOAA Fisheries
National Marine Mammal Lab
7600 Sand Point Way NE Bldg. 4
Seattle WA 98115
robert.delong@noaa.gov

Doug DeMaster
NOAA Fisheries
Alaska Fisheries Science Center
7600 Sand Point Way NE Bin C15700
Seattle WA 98115-0070
Douglas.Demaster@noaa.gov

Heather Down
Alaska SeaLife Center
PO Box 1329
Seward AK 99664-1329
heather_down@alaskasealife.org

Padraig J. Duignan
Massey University
New Zealand Wildlife Health Centre
Inst. of Veterinary, Animal and Biomedical Sciences
Palmerstown North
Manawatu PB 11222
NEW ZEALAND
P.J.Duignan@massey.ac.nz

Brian S. Fadely
NOAA Fisheries
National Marine Mammal Lab
7600 Sand Point Way NE
Seattle WA 98115
brian.fadely@noaa.gov

Gavin Fay
University of Washington
School of Aquatic and Fishery Sciences
PO Box 355020
Seattle WA 98195-5020
gfay@u.washington.edu

Shannon L. Fowler
University of California Santa Cruz
Center for Ocean Health
100 Shaffer Rd.
Santa Cruz CA 95060
fowler@biology.ucsc.edu

Alejandro Frid
Simon Fraser University
Dept. of Biological Sciences
8888 University Dr.
Burnaby BC V5A 1S6
Canada
ilexp@yknet.yk.ca

Lowell Fritz
NOAA Fisheries
National Marine Mammal Lab
7600 Sand Point Way NE
Seattle WA 98115
lowell.fritz@noaa.gov

Patrick J. Gearin
NOAA Fisheries
National Marine Mammal Lab
7600 Sand Point Way NE
Seattle WA 98115
pat.gearin@noaa.gov

Tom Gelatt
NOAA National Marine Fisheries Service
Alaska Fisheries Science Center
7600 Sand Point Way NE
Seattle WA 98115
tom.gelatt@noaa.gov

Scott M. Gende
National Park Service
Glacier Bay Field Station
3100 National Park Rd.
Juneau AK 99801
Scott_Gende@nps.gov

Leah R. Gerber
Arizona State University
School of Life Sciences
PO Box 874501
Tempe AZ 85287-4501
leah.gerber@asu.edu

Jenelle Gilding
Alaska SeaLife Center
PO Box 1329
Seward AK 99664-1329
jenelle_gilding@alaskasealife.org

Nathan Glassey
Ministry of Fisheries New Zealand
Private Bag 14
Nelson
New Zealand
glasseyn@fish.govt.nz

Tracey Goldstein
Alaska SeaLife Center
PO Box 1329
Seward AK 99664-1329
tracey_goldstein@alaskasealife.org

Simon Goldsworthy
South Australian Research and Development Inst. (SARDI)
Aquatic Sciences
Henley Beach SA 5022
Australia
goldsworthy.simon@saugov.sa.gov.au

Manuela Gonzalez-Suarez
Arizona State University
School of Life Sciences
PO Box 874601
Tempe AZ 85287-4601
manuela.gonzalez@asu.edu

Sylvie Guénette
University of British Columbia
Fisheries Centre
2259 Lower Mall
Vancouver BC V6T 1Z4
Canada
s.guenette@fisheries.ubc.ca

Gordon D. Hastie
University of British Columbia
Marine Mammal Research Unit
6248 Biological Sciences Rd.
Vancouver BC V6T 1Z4
Canada
hastie@zoology.ubc.ca

Kelly Hastings
Alaska Dept. of Fish and Game
Div. of Wildlife Conservation
333 Raspberry Rd.
Anchorage AK 99518
kelly_hastings@fishgame.state.ak.us

Kaoru Hattori
Hokkaido National Fisheries Research Inst.
Fisheries Oceanography Division
Laboratory of Higher Trophic Levels
Kushiro 085-0802
Japan
khattori@affrc.go.jp

Catherine Hegwer
Aleutians East Borough
301 Research Court
Kodiak AK 99615
cathyhegwer@ak.us

Ronald Heintz
NOAA Fisheries
Auke Bay Lab
11305 Glacier Hwy
Juneau AK 99801-8626
Ron.Heintz@noaa.gov

Daniel R. Hennen
Montana State University
203 N. Wallace
Bozeman MT 59715
hennen@rapid.msu.montana.edu

Claudia J. Hernandez Camacho
Centro Interdisciplinario de Ciencias Marinas-IPN
Departmento de Pesquerias y Biologia Marina
La Paz, Baja California Sur 23096
Mexico
jcamacho@ipn.mx

Sheila J. Heymans
University of British Columbia
Marine Mammal Research Unit
6248 Biological Sciences Rd.
Vancouver BC V6T 1Z4
Canada
s.heymans@fisheries.ubc.ca

Roger Hill
Wildlife Computers
16150 NE 85th St. #226
Redmond WA 98052
tags@wildlifecomputers.com

Sue Hills
University of Alaska Fairbanks
Institute of Marine Science
Fairbanks AK 99775-7220
shills@ims.uaf.edu

Gina Himes Boor
Montana State University
1104 S. Spruce Dr.
Bozeman MT 59715
gkhimesboor@montana.edu

Sarah Hinckley
NOAA Fisheries
Alaska Fisheries Science Center
7600 Sand Point Way NE Bldg. 4
Seattle WA 98115-0070
sarah.hinckley@noaa.gov

Laura K. Hoberecht
University of Washington
School of Aquatic and Fishery Sciences
Box 355020
Seattle WA 98195
llitzky@u.washington.edu

David Holley
Alaska SeaLife Center
PO Box 1329
Seward AK 99664
david.holley@alaskasealife.org

Lisa A. Hoopes
Texas A&M University
Dept. of Biology
4000 Central Florida Blvd.
Orlando FL 32765
lhoopes@mail.ucf.edu

Hiroshi Hoshino
Hokkaido University
Graduate School of Fisheries Sciences
Kita 20 Nishi 2 Kaeisou 17
Sapporo Hokkaido 0010020
Japan
selchie@fish.hokudai.ac.jp

Luis A. Hückstädt
Universidad de Concepcion
Departmento de Oceanografia
Casilla 160-C
Chile
lhuckst@udec.cl

Kohji Iida
Hokkaido University
Graduate School of Fisheries Sciences
3-1-1, Minato-cho
Hakodate Hokkaido 041-8611
Japan
iidacs@fish.hokudai.ac.jp

Takeomi Isono
Econixe Co. Ltd.
Atsubetsu-ku
Shimonopporo Technopark 1-2-14
Sapporo Hokkaido 004-0015
Japan
t-isono@econixe.co.jp

Lianna Jack
The Alaska Sea Otter and Steller Sea Lion Commission
6239 B St. # 204
Anchorage AK 99518
ljack@gci.net

Lauri Jemison
Alaska Dept. of Fish and Game
Div. of Wildlife Conservation
525 W. 67th Ave.
Anchorage AK 99518
lauri_jemison@fishgame.state.ak.us

Caroline Jezierski
University of Alaska Fairbanks
School of Fisheries and Ocean Sciences
Fairbanks AK 99775-7220
jezierski@sfos.uaf.edu

Scott W. Johnson
NOAA Fisheries
Auke Bay Lab
11305 Glacier Hwy
Juneau AK 99801
scott.johnson@noaa.gov

Peter Jones
National Marine Fisheries Service
NOAA/OMI
PO Box 21668
Juneau AK 99802

Ruth Joy
University of British Columbia
Marine Mammal Research Unit
6248 Biological Sciences Dr.
Vancouver BC V6T 1Z4
Canada
joy@zoology.ubc.ca

Jennifer Katalinich
Oregon State University
1280 Mildred Lane SE
Salem OR 97306
jtjornehoj@yahoo.com

Edward O. Keith
Nova Southeastern University
Oceanographic Center
8000 N. Ocean Dr.
Dania Beach FL 33004
edwardok@nsu.nova.edu

James C. King
Alaska Dept. of Fish and Game
525 West 67th Ave.
Anchorage AK 99518
Jamie_King@fishgame.state.ak.us

Mark King
The Alaska Sea Otter and Steller Sea Lion Commission
PO Box 965
Cordova AK 99574
asoc@alaska.net

Laura Kucey
University of British Columbia
Marine Mammal Research Unit
6248 Biological Sciences Rd.
Vancouver BC V6T 1Z4
Canada
kucey@zoology.ubc.ca

Carey E. Kuhn
University of California
Dept. of Ecology and Evolutionary Biology
100 Shaffer Rd.
Santa Cruz CA 95060
kuhn@biology.ucsc.edu

Jeffrey L. Laake
NOAA Fisheries
National Marine Mammal Lab
7600 Sand Point Way NE Bldg. 4
Seattle WA 98115
jeff.laake@noaa.gov

Vanessa Labrada Martagon
Centro Interdisciplinario de Ciencias Marinas (CICIMAR)
Av. IPN s/n, AP592
Col. Playa Palo de Santa Rita
Mexico
vlabradam@ipn.mx

Lisa Laceby
Lotek Wireless Inc.
115 Pony Dr.
Newmarket ON L3Y 7B5
Canada
llaceby@lotek.com

Michelle E. Lander
National Marine Mammal Lab
NOAA NMFS
7600 Sand Point Way NE Bldg. 4
Seattle WA 98115
michelle.lander@noaa.gov

Mary-Anne Lea
University of British Columbia
The Behaviour@Sea Project, Marine
Mammal Research Unit
6248 Biological Sciences Rd.
Vancouver BC V6T 1Z4
Canada
lea@zoology.ubc.ca

Nikolai Liebsch
IFM-Geomar
Duesternbrooker Weg 20
Kiel 24105 Schleswig Holstein
Germany
Nliebsch@ifm-geomar.de

Elizabeth A. Logerwell
NOAA Fisheries
Alaska Fisheries Science Center
7600 Sand Point Way NE, F/AKC2
Seattle WA 98115-6349
libby.logerwell@noaa.gov

Eugene T. Lyons
University of Kentucky
Dept. of Veterinary Science
Gluck Equine Research Center
Lexington KY 40546-0099
elyons1@uky.edu

Daniela Maldini
Alaska SeaLife Center
PO Box 1329
Seward AK 99664-1329
daniela_maldini@alaskasealife.org

Evgeny G. Mamaev
Vyatka State Agricultural Academy
133, Octyabrskiy Prospekt
Kirov 610017
Russia
emamaev.lionsea.kirov.ru

John Maniscalco
Alaska SeaLife Center
PO Box 1329
Seward AK 99664-1329
john_maniscalco@alaskasealife.org

Kendall Mashburn
Alaska SeaLife Center
PO Box 1329
Seward AK 99664
kendall_mashburn@alaskasealife.org

Ole Mathisen
University of Alaska Fairbanks
School of Fisheries and Ocean Sciences
1632 San Juan Dr.
Friday Harbor WA 98250
randim@rockisland.com

Rob Mattlin
New Zealand Ministry of Fisheries
256 Lambton Bay
PO Box 1020
Wellington
New Zealand
robert.mattlin@fish.govt.nz

Lori Mazzuca
NOAA Fisheries
Alaska SeaLife Center
PO Box 1329
Seward AK 99664
lori.mazzuca@noaa.gov

Dennis McAllister
Alaska Dept. of Fish and Game
PO Box 122
Sitka AK 99835
dennis.mcallister@fishgame.state.ak.us

Rebecca McIntosh
La Trobe University
Sea Mammal Ecology Group
Zoology Dept.
Victoria 3086
Australia
r.mcintosh@zoo.latrobe.edu.au

Sharon R. Melin
NOAA Fisheries
National Marine Mammal Lab
7600 Sand Point Way NE, Bldg. 4
Seattle WA 98115
sharon.melin@noaa.gov

Jo Ann Mellish
Alaska SeaLife Center
PO Box 1329
Seward AK 99664-1329
joann_mellish@alaskasealife.org

Yoko Mitani
Texas A&M University
5007 Avenue U
Galveston TX 77551
cantonp@tamug.edu

Patricia Morris
University of California Santa Cruz
233 Northrop Pl.
Santa Cruz CA 95060
pamorris@ucsc.edu

Heather Mostman
University of California Santa Cruz
Center for Ocean Health, Long Marine Lab
100 Shaffer Rd.
Santa Cruz CA 95060
mostman@biology.ucsc.edu

Elizabeth Moundalexis
Alaska SeaLife Center
PO Box 1329
Seward AK 99664-1329
elizabeth_moundalexis@alaskasealife.org

Gabriele Müller
Leibniz-Institut fur Meereswissenschaften
Gebaude Westufer, FB3, Marine Zoologie
Dussternbrooker Weg 20
Kiel 24105
Germany
gmueller@ifm.uni-kiel.de

Matthew Myers
Alaska SeaLife Center
PO Box 1329
Seward AK 99664
matthew_myers@alaskasealife.org

Bonita Nelson
NOAA Fisheries
Auke Bay Lab
11305 Glacier Hwy
Juneau AK 99801
bonita.nelson@noaa.gov

Peter Nilsson
Alaska SeaLife Center
PO Box 1329
Seward AK 99664-1329
peter_nilsson@alaskasealife.org

Sarah Norberg
Alaska SeaLife Center
PO Box 1329
Seward AK 99664-1329
sarah_norberg@alakasealife.org

Patrick O'Flaherty
Lotek Wireless, Inc.
114 Cabot St.
St. John's NFLD
Canada
poflaherty@lotek.com

Peter Olesiuk
Fisheries and Oceans Canada
Pacific Biological Station
3190 Hammond Bay Rd.
Nanaimo BC V9R 5K6
Canada
OlesiukP@pac.dfo-mpo.gc.ca

Kathryn Ono
University of New England
Marine Science Center
11 Hills Beach Rd.
Biddeford ME 04005
kono@une.edu

Anthony J. Orr
NOAA Fisheries
National Marine Mammal Lab
7600 Sand Point Way NE
Seattle WA 98115
tony.orr@noaa.gov

Tae-Geon Park
Hokkaido University
Graduate School of Fisheries Sciences
3-1-1, Minato
Hakodate Hokkaido 041-8611
Japan
parktg@echo.fish.hokudai.ac.jp

Cecilia Pedernera
Ciudad Universitaria, Delegacion Coyoacan
Facultad de Medecina Veterinaria
UNAM, Mexico
CP 04510 DF
Mexico
pedrom@servidor.unam.mx

Mike Pendergast
Alaska SeaLife Center
PO Box 1329
Seward AK 99664-1329
mike_pendergast@alaskasealife.org

Grey W. Pendleton
Alaska Dept. of Fish and Game
Wildlife Conservation
PO Box 240020
Douglas AK 99824-0020
grey_pendleton@fishgame.state.ak.us

Kenneth W. Pitcher
Alaska Dept. of Fish and Game
Div. of Wildlife Conservation
525 W. 67th Ave.
Anchorage AK 99518
ken_pitcher@fishgame.state.ak.us

Heidi Jennifer Porras Peters
Centro Interdisciplinario de Ciencias Marinas (CICIMAR)
S/N, Col. Playa de Santa Rita
La Paz, Baja California Sur
Mexico
jenniferpp@lycos.com

Shilpa Rajkumar
University of Wollongong
Centre for Marine Policy
Northfields Avenue
Wollongong NSW 2522
Australia
shilpa@uow.edu.au

Kimberly L. Raum-Suryan
Hatfield Marine Science Center
2030 SE Marine Science Dr.
Newport OR 97365
kraumsuryan@charter.net

Lorrie Rea
Alaska Dept. of Fish and Game
University of Alaska Fairbanks
Fairbanks AK 99775-7220
lorrie_rea@fishgame.state.ak.us

Michael J. Rehberg
University of Alaska Anchorage
Dept. of Biological Sciences
3211 Providence Dr.
Anchorage AK 99508
michael_rehberg@uaa.alaska.edu

Julie P. Richmond
Alaska Dept. of Fish and Game
525 West 67th Ave.
Anchorage AK 99518
julie_richmond@fishgame.state.ak.us

Frederico G. Riet Sapriza
Massey University
Inst. of Veterinary, Animal and Biomedical Sciences
Palmerstown North
Manawatu PB11-222
New Zealand
F.sapriza@massey.ac.nz

Diego Rodríguez
Universidad Nacional del Mar del Plata
CONICET
Casilla de Correos 43
Mar del Plata 7600 Buenos Aires
Argentina
dhrodri@mdp.edu.ar

David A. Rosen
University of British Columbia
Marine Mammal Research Unit
6248 Biological Sciences Rd.
Vancouver BC V6T 1Z4
Canada
rosen@zoology.ubc.ca

Danielle Savarese
Alaska Native Harbor Seal Commission
800 E. Dimond Blvd. # 3590
Anchorage AK 99515
danielle.savarese@harborsealcommission.org

Lawrence Schaufler
NOAA Fisheries
Auke Bay Lab
11305 Glacier Hwy
Juneau AK 99801
Lawrence.Schaufler@noaa.gov

Wendy Schrader
Alaska SeaLife Center
PO Box 1329
Seward AK 99664-1329
wendy_schrader@alaskasealife.org

Michael Sigler
NOAA Fisheries
Auke Bay Lab
11305 Glacier Hwy
Juneau AK 99801
mike.sigler@noaa.gov

Robert J. Small
Alaska Dept. of Fish and Game
1255 West 8th St.
Juneau AK 99802
bob_small@fishgame.state.ak.us

Nathan J. Soboleff
University of Alaska Fairbanks
Juneau Center, SFOS
11120 Glacier Hwy
Juneau AK 99801
ftnjs@uaf.edu

Karim H. Soto
University of British Columbia
Marine Mammal Research Unit
6248 Biological Sciences Rd.
Vancouver BC V6T 1Z4
Canada
soto@zoology.ubc.ca

Gregory Spencer
Alaska SeaLife Center
PO Box 1329
Seward AK 99664-1329

Vicki K. Stegall
University of Alaska Fairbanks
Alaska Dept. of Fish and Game
Steller Sea Lion Program
Fairbanks AK 99775-7220
vicki_stegall@fishgame.state.ak.us

Jeremy T. Sterling
NOAA Fisheries
National Marine Mammal Lab
7600 Sand Point Way NE
Seattle WA 98115
jeremy.sterling@noaa.gov

Beth Stewert
Aleutians East Borough
Natural Resources Director
2767 John St.
Juneau AK 99801
beths@acsalaska.net

Diana Szteren
Centro Interdisciplinario de Ciencias Marinas (CICIMAR)
Av. Instituto Politecnico Nacional s/n
Col. Playa Palo de Santa Rita
La Paz Baja, California Sur
23096 Mexico
dszteren@ipn.mx

Rebecca Taylor
Montana State University
Ecology Dept.
Bozeman MT 59717
rtaylor@montana.edu

John Thedinga
NOAA Fisheries
Auke Bay Lab
11305 Glacier Hwy
Juneau AK 99801
john.thedinga@noaa.gov

Gary L. Thomas
University of Miami
Rosenstiel School of Marine and Atmospheric Sciences
4600 Rickenbacker Causeway
Miami FL 33149
gthomas@rsmas.miami.edu

David Thompson
University of St. Andrews
Sea Mammal Research Unit
Gatty Marine Lab
St. Andrews Fife KY16 8LB
UK
dt2@st-and.ac.uk

Richard E. Thorne
Prince William Sound Science Center
PO Box 705
Cordova AK 99574
thorne@pwssc.gen.ak.us

Dominic J. Tollit
University of British Columbia
Marine Mammal Research Unit
6248 Biological Sciences Rd.
Vancouver BC V6T 1Z4
Canada
tollit@zoology.ubc.ca

Andrew Trites
University of British Columbia
Marine Mammal Research Unit
6248 Biological Sciences Rd.
Vancouver BC V6T 1Z4
Canada
trites@zoology.ubc.ca

Delphine Verrier
Alaska SeaLife Center
PO Box 1329
Seward AK 99664-1329

Stella Villegas
University of California Santa Cruz
775A Brommer St.
Santa Cruz CA 95062
stella@biology.ucsc.edu

Johanna J. Vollenweider
NOAA Fisheries
Auke Bay Lab
11305 Glacier Hwy
Juneau AK 99801
johanna.vollenweider@noaa.gov
Marc Webber
US Fish and Wildlife Service
Marine Mammals Management
1011 E. Tudor Rd., MS-341
Anchorage AK 99503
marc_webber@fws.gov

Michael J. Weise
University of California Santa Cruz
Dept. of Ecology and Evolutionary Biology
100 Shaffer Rd.
Santa Cruz CA 95060
weise@biology.ucsc.edu

Terrie M. Williams
University of California Santa Cruz
Center for Ocean Health, Long Marine Lab
100 Shaffer Rd.
Santa Cruz CA 95060
williams@biology.ucsc.edu

Donna Willoya
The Alaska Sea Otter and Steller Sea Lion Commission
6239 B St. # 204
Anchorage AK 99518
dwilloya@gci.net

Ben Wilson
University of British Columbia
The Behaviour@Sea Project
Marine Mammal Research Unit
6248 Biological Sciences Rd.
Vancouver BC V6T 1Z4
Canada
bwilson@zoology.ubc.ca

Betsy Wilson
Alaska Dept. of Fish and Game
Steller Sea Lion Program
PO Box 538
Haines AK 99827
betswil@hotmail.com

Bill Wilson
North Pacific Fishery Management Council
Protected Resources Coordinator
605 W. 4th Ave. # 306
Anchorage AK 99501-2252
Bill.wilson@noaa.gov

Arliss J. Winship
University of British Columbia
Marine Mammal Research Unit
6248 Biological Sciences Rd.
Vancouver BC V6T 1Z4
Canada
winship@zoology.ubc.ca

Sandra S. Wise
University of Southern Maine
Wise Laboratory of Environmental and Genetic Toxicology
96 Falmouth St., 178 Science Bldg.
Portland ME 04104-9300
swise@usm.maine.edu

Nicholas Wolf
University of California, CSTAR
Dept. of Applied Mathematics and Statistics
Jack Baskin School of Engineering
Santa Cruz CA 95064
nwolf@u.washington.edu

Jamie N. Womble
NOAA Fisheries
Auke Bay Lab
11305 Glacier Hwy
Juneau AK 99801
jamie.womble@noaa.gov

Kate Wynne
University of Alaska Fairbanks
Marine Advisory Program
118 Trident Way
Kodiak AK 99615
ffkmw@uaf.edu

Carlos Francisco Yaipen-Llanos
Organization for Research and Conservation of Animals, Marine Mammals (ORCCAMM)
Cerro Hermoso L-16
San Ignacio de Monterrico
Lima 33
Peru
orcarlos@orccamm.org

Orio Yamamura
Hokkaido National Fisheries Research Institute
Katsurakoi 116
Kushiro 085-0802
Japan
orioy@affrc.go.jp

Index