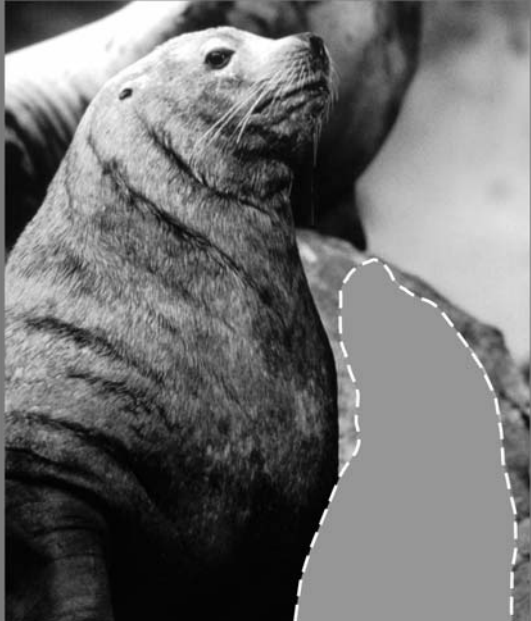# STELLER SEA LION DECLINE:
IS IT FOOD II

Douglas DeMaster and
Shannon Atkinson, Editors

Proceedings of
the Workshop
Is It Food II
Alaska SeaLife Center,
Seward, Alaska
May 2001

Credits

Contents

Summary Statement from Workshop Participants

Is It Food II? Workshop
30-31 May 2001
Alaska SeaLife Center, Seward, Alaska

Convened by Alaska SeaLife Center, National Marine Fisheries Service, and University of Alaska Sea Grant

Twenty-four scientists participated in a two-day workshop at the Alaska SeaLife Center on 30-31 May 2001. The workshop was convened by the Alaska SeaLife Center, National Marine Fisheries Service, and University of Alaska Sea Grant, and was co-chaired by Shannon Atkinson and Douglas DeMaster. Workshop participants presented fourteen talks, followed by a discussion of evidence for and against several hypotheses concerning factors that could be contributing to the decline of the western population of Steller sea lions. The agenda for the workshop is in the appendix at the end of this summary.

Conclusions

Workshop participants generally agreed on the following conclusions:

1. The suite of causes of the steep decline in sea lion abundance in the 1980s is very likely different from the suite of causes of the moderate decline in abundance in the 1990s.

2. Considerable evidence from studies conducted in the 1970s and 1980s supports the hypothesis that sea lions from the western population were nutritionally stressed, and that nutritional stress likely resulted in reductions in the rate of recruitment and the reproductive rate.

3. If the current population of western Steller sea lions of approximately 30,000 to 35,000 animals were stable,approximately 4,700 animals would be lost per year from the population due to natural mortality, which would be offset by recruitment of 1-year-olds into the population. At the observed 5% decline per year in the population at its current size, an additional 1,700 animals are being lost. Fifty to seventy-five percent of this additional mortality is unexplained.

4. While few data from behavioral and physiological research in the 1990s directly support the hypothesis that nutritional stress is a significant factor in contributing to the current decline in the western population of sea lions, nutritional stress cannot be ruled out as a cause of the continued decline. Most of the available data are from adult females and young-of-the-year from the breeding season or young-of-the-year from the later winter. The results to date indicate that animals in the declining population (i.e., the western population) are in better condition on average than animals from the eastern population, which is increasing in size. While these results are inconsistent with the nutritional stress hypothesis, more information on weaned pups and juveniles from other seasons and other areas is needed to resolve uncertainties regarding the importance of nutritional stress. At present, data are inadequate to evaluate the nutritional stress hypothesis as an important factor in understanding the current decline of the western population of Steller sea lions.

5. Additional research is needed to identify condition indices for individual sea lions that are predictive regarding the likelihood that a young-of-the-year animal would survive to maturity and reproduce. At a minimum, condition indices should be correlated with one or more measures of an animal's fitness.

6. Captive feeding studies to date by the North Pacific Universities Marine Mammal Research Consortium and the Alaska SeaLife Center indicate that: (a) developmental and gender related factors cause marked differences in the way the animals respond to changes in their diets, (b) there are strong seasonal effects in the way animals respond to changes in their diet, (c) animals appear healthy after a series of 4-month feeding trials on diets similar to the diets thought to be utilized by animals in the western population and eastern population, (d) fasting animals have been observed to reduce their metabolic rate, and (e) both the caloric density and quality of prey seem to be important in predicting the response of animals to a specific dietary regime.

7. In the wild there are strong differences in the diets of animals from different areas and at different times of the year. These differences in the diet by region are also highly correlated with differences in the regional dynamics of subpopulations of sea lions. In addition, there are strong seasonal differences in the nutritional value of a given prey item. Areal differences occur at a scale of 10-100 km. Seasonal differences in the utilization of migratory species like salmon have been observed. In the Gulf of Alaska and Eastern Bering Sea, pollock is a primary component of the diet throughout the year. In the Aleutian Islands, Atka mackerel and cephalopods are primary components of the diet year-round. Around Kodiak Island, sandlance are an important prey item for Steller sea lions.

8. In the North Pacific (Eastern Bering Sea, Aleutian Islands, and Gulf of Alaska), the biomass of all species of groundfish generally increased throughout the 1980s and remained relatively stable in the 1990s. Annual harvest levels, however, have increased slightly throughout the 1990s, but are still thought to be generally below 20% of exploitable biomass. Target harvest strategies for many species reduce biomass to 40-60% of equilibrium unfished levels, or to levels thought to be more productive without undue risk of overfishing the spawning stock. However, there is significant variance around point estimates of current stock size as well as historical stock size. Removals by commercial fishers are not evenly distributed in time and space, nor with respect to the distribution of the target species itself. Therefore, rates of removal in specific fished locations (many of which are in Steller sea lion critical habitat) are likely to be considerably higher than the target harvest rate of the species in the management area.

9. In the Gulf of Alaska, there has been a dramatic change in the species composition of the nearshore marine community since the 1970s. A nearshore community dominated by shrimp and forage fishes in the 1960s and 1970s was replaced by one dominated by cod, flatfish, and other groundfish in the 1980s and 1990s. This shift in community composition seems to be driven by long-term environmental regime shifts that have repeatedly occurred over thousands of years.

10. More data are needed to evaluate the impact of killer whales on the population dynamics of the western population of Steller sea lions. Currently, there are inadequate data to estimate the number of killer whales west of Kodiak Island, in the Gulf of Alaska, and in the Bering Sea. In addition, to ascertain the impact of predation, information on the frequency at which Steller sea lions are killed by killer whales is needed, as are data on the age and sex composition of the kill. Finally, information is needed on whether killer whale foraging behavior is influenced by the relative availability of different prey items (i.e., functional response in the frequency of occurrence of a particular prey item in the diet). Field studies initiated after October 2000 are designed to provide the information needed to address the issue of whether killer whale predation on sea lions is an important component in the current decline.

11. More data are needed to evaluate the impact of shark predation on the population dynamics of the western population of Steller sea lions. However, to date, there is no evidence that sharks eat Steller sea lions. The following information regarding sleeper sharks is known: (a) sleeper shark abundance in the Gulf of Alaska has increased over the last 5 years, based on International Pacific Halibut Commission catch per unit effort (CPUE) data, observer data from longline vessels, and data from the triennial trawl survey by the National Marine Fisheries Service

(NMFS), (b) the diet of sleeper sharks in Alaska includes fast moving fish species (e.g., salmon, herring) and marine mammals (e.g., harbor seals, unidentified cetaceans), and (c) large sleeper sharks can grow to 25 feet in length and weigh between 6,000 and 8,000 pounds. The following information is needed to ascertain the importance of sleeper shark predation on sea lions to the current decline of sea lions in Alaska: (i) how many sleeper sharks occur in the range of the western population of Steller sea lions, (ii) what fraction of the diet of sleeper sharks is made up of Steller sea lions and what is the age and sex composition of sea lions killed by sleeper sharks, and (iii) do sleeper sharks primarily feed on marine mammal carrion or do they capture and kill free-ranging animals. Field studies initiated after October 2000 are designed to provide the information needed to address the issue of whether sleeper shark predation on sea lions is an important component in causing the current decline.

12. Regarding competition between increasing populations of piscivorous fish and Steller sea lions, one participant raised the issue of whether the spiny dogfish could have become an important competitor in the last 30 years. It was noted that spiny dogfish abundance has increased dramatically in the region from Prince William Sound to southeast Alaska. Additional information on the composition of the diet (e.g., species and size) of spiny dogfish is needed to address this question.

Questionnaire

The following questionnaire was distributed to the workshop participants. The results were as follows:

1. Would you agree with the statement that "nutritional stress is the leading hypothesis regarding the current decline of abundance of the western stock of Steller sea lions"?
   10 (42%) - yes   14 - no

2. Would you agree with the statement that "killer whale predation is the leading hypothesis regarding the current decline of abundance of the western stock of Steller sea lions"?
   1 (4%) - yes   23 - no

3. Would you agree with the statement that "inadequate recruitment is the leading hypothesis regarding the current decline of abundance of the western stock of Steller sea lions"?
   19 (79%) - yes   5 - no

4. Would you agree with the statement that "a regime shift alone could have been responsible for the observed decline in sea lion abundance by over 70%"?
    10 (42%) - yes   14 - no

5. Would you agree with the statement that "competition with fisheries is the leading hypothesis regarding the current decline of abundance of the western stock of Steller sea lions"?
    4 (17%) - yes   20 - no

6. What do you think the western population of sea lions will do over the next 10 years, given no intervention from the National Marine Fisheries Service or Alaska Department of Fish and Game?

    Generally, the answers fell into three categories:

    A. The population will continue to decline - 6 (25%)
    B. The population will level off - 13 (54%)
    C. Impossible to predict with available data - 5 (21%)

Discussion

The following questions were discussed in a plenary session. A summary of answers provided by workshop participants appears below.

1. *Are you aware of any marine mammal populations that have declined continuously for over 30 years and by over 80%, where the decline was not primarily driven by anthropogenic effects?*

    This is a relatively rare phenomenon for marine mammal populations. One recent example is the observed decline of sea otters along the Aleutian Islands in the last 10 years. In addition, some of the archeological records from middens indicate that large scale changes in marine mammal abundance was not uncommon.

2. *What is the evidence supporting the hypothesis that nutritional stress is currently occurring?*

    Data consistent with the nutritional stress hypothesis include: (a) past reports of the observed impact on pinniped survival and reproduction of nutritional stress associated with El Niño events, (b) the existing correlation between differences in the diet of sea lions in subregions of the Gulf of Alaska/Bering Sea–Aleutian islands and differences in the population dynamics of sea lions in these same subregions, (c) the observation that as much as 75% of the sea lion mortality associated with the current decline is unexplained, (d) fisheries data that indicate the local abundance of a target species is significantly reduced over spatial and temporal scales

important to the foraging success of a Steller sea lion, and (e) recognition that the diet of sea lions in the 1990s was different from their diet in the 1970s and that the current diet of sea lions generally has a lower caloric density than it did in the 1970s. Further, the species that comprised much of the diet of sea lions in the 1970s may have been energetically more cost-effective to capture and eat (e.g., shrimp and capelin). It was recognized that (i) nutritional stress could be caused by a lack of forage or a lack of access to adequate forage and (ii) nutritional stress could be caused by environmental factors (e.g., regime shifts) or by human-related factors (e.g., competition with fisheries).

3. *What is the evidence supporting the hypothesis that nutritional stress is currently not affecting Steller sea lions in the winter months, and not affecting juveniles?*

Data are inadequate at present to evaluate this hypothesis.

4. *What is the evidence supporting the hypothesis that sea lions are currently in a "predator pit" that is responsible for the current decline in sea lion abundance?*

The term "predator pit" is often misused. It is best used when referring to a low-density prey equilibrium. The conceptual framework for a low-density prey equilibrium due to top-down forcing requires a complex prey field and one or more predatory species. The predator population or populations are maintained at high levels relative to the density that could be supported by only the prey species said to be in the "pit" by alternate prey species. Under this scenario, the low-density prey species is not driven to extinction by the predator complex because of functional responses in the foraging behavior of the predators, but cannot achieve a high-density equilibrium because predation rates increase with increasing density. While this phenomenon is possible regarding the relationship between Steller sea lions in Alaska and various predatory species (e.g., killer whale and sleeper shark), the data are inadequate at this time to evaluate its likelihood.

5. *Given the definitions of jeopardy and adverse modification in the Endangered Species Act, is it reasonable to conclude that the groundfish fishery in the Bering Sea and Gulf of Alaska will either jeopardize the continued existence of sea lions or adversely modify their critical habitat?*

To address this question, NMFS will have to establish quantitative or qualitative guidelines on what the following terms mean: (1) reasonable, (2) jeoparμze, and (3) to adversely modify. In addition, NMFS will have to develop explicit classification criteria to allow scientists to understand what recovery means for the western population of Steller sea lions.

Appendix

Agenda

Is It Food? II Workshop
30-31 May 2001

May 30

8:30 a.m.	Introductions
8:45 a.m.	Tom Loughlin, National Marine Mammal Laboratory (NMML): Accounting for losses above replacement
9:15 a.m.	Ken Pitcher, Alaska Department of Fish and Game (ADFG): Food limitation—Clouding the issue
9:45 a.m.	Russ Andrews, University of British Columbia (UBC): At-sea foraging energetics
10:30 a.m.	Randy Davis, Texas A&M University: Maternal attendance, energy transfer to pups, and pup growth on rookeries
11:00 a.m.	Lorrie Rea, ADFG: Condition indices of Steller sea lions
11:30 p.m.	Michael Rehberg, ADFG: Telemetry studies
12:00 p.m.	Mike Castellini, University of Alaska Fairbanks (UAF): Captive studies in Alaska
1:00 p.m.	David Rosen, UBC: Captive studies in Vancouver
1:30 p.m.	Kate Wynne, UAF: Gulf Apex Predator Study
2:00 p.m.	Beth Sinclair (NMML): Recent scat analyses
2:45 p.m.	Lowell Fritz, Alaska Fisheries Science Center (AFSC), Research, ecology, and fisheries management: Status of groundfish stocks in the North Pacific and Bering Sea
3:15 p.m.	Paul Anderson, AFSC Kodiak: Status of fish stocks around Kodiak

May 31

8:15 a.m.	Craig Matkin, North Gulf Oceanic Society (NGOS): Killer whale populations in the Gulf of Alaska
8:45 a.m.	Lee Hulbert, NMFS/Alaska Biological Laboratory: Shark predation on marine mammals
9:15 a.m.	Round robin discussion on the May 30 talks
10:30 a.m.	Discussion of importance of nutritional stress and predation on the status of the western stock of Steller sea lions (Chair: Doug DeMaster)
12:30 p.m.	Summary statement of consensus
1:30 p.m.	Where do we go from here?
3:00 p.m.	Workshop ends

An Accounting of the Sources of Steller Sea Lion Mortality

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May 2001

The western stock of Steller sea lions (*Eumetopias jubatus*) is declining at about 5% per year and total population numbers have dropped by over 80% since the late 1960s (Sease and Loughlin 1999). The magnitude and continuous nature of the decline resulted in this stock being listed as endangered in 1997 by the National Marine Fisheries Service (NMFS). The cause of the decline is not known but likely has changed. During the early phases of the decline incidental catch of sea lions in trawl fisheries and legal shooting were important sources of mortality (Trites and Larkin 1992). After the North Pacific Ocean regime shift in the 1970s, and as U.S. fishery management changed during the mid-1970s and 1980s, the cause of the decline was attributed to nutritional stress resulting from either environmental variability that caused a change in prey base, removal of prey by commercial fisheries, or a combination of these two factors (Loughlin 1998). During the early phases of the decline the cumulative loss of animals from predation, subsistence harvest, and other anthropogenic sources were considered inconsequential. However, as the sea lion population continues to decline, these factors will account for a larger portion of total mortality than before, and thus, estimating the amount of sea lion mortality attributable to nutritional stress or the indirect effects of fisheries may be difficult. Our purpose here is to report our efforts to estimate the number of animals lost to the population each year to each of the possible sources of mortality.

Methods

The present rate of decline in the western stock was estimated by regressing the natural logarithm of the 1991-2000 trend-site non-pup count (NMFS unpubl.) on time. We also calculated the rate of decline by geographic

region in the same way. Estimates of the total number of non-pups in the western stock were calculated by multiplying the number of non-pups counted on trend sites by a correction factor of 1.807 (Loughlin et al. 1992); that factor accounts for animals that were at sea during the survey and for sites that were not surveyed. We approximated the number of sea lion mortalities each year from the western Steller sea lion population using estimates of the total number of non-pups in the population and the observed rate of sea lion decline during 1991-2000, assuming the decline would continue at the same rate.

Based on York's (1994) life table and the assumption that the population was stable, the number of non-pup mortalities would be about 15% per year; this is the level of natural mortality we would expect if the population instantly stabilized. If the population were stable, the number of pups recruited into the non-pup population would equal the number of non-pups lost to natural mortality (e.g., no net gain or loss). In a declining population losses above replacement are "additional" mortality which result from a combination of non-pup and pup mortalities and decreased birth rates, assuming a closed population and no or little emigration, and no density dependence.

Results

During 1991-2000, the western stock of Steller sea lions declined at 5.2% (S.E. = 0.3%) per year. The population declined at statistically significant rates ($P < 0.10$) in all regions except the eastern Aleutian Islands. The greatest rates of declines occurred in the eastern and central Gulf of Alaska and the western Aleutian Islands (all greater than 8.6% per year). Using a published correction factor, we estimated the total population size of the western stock of Steller sea lions to be about 33,000 animals. Based on a published life table and the current rate of decline, we estimate that the total number of mortalities of non-pup Steller sea lions is about 6,383 animals; of those, 4,718 (73%) are mortalities that would have occurred if the population were stable, and 1,666 (27%) are additional mortalities that fuel the decline (Table 1). We tabulated the levels of reported anthropogenic sources of mortality (subsistence, incidental take in fisheries, and research), guessed at another (illegal shooting), then approximated levels of predation (killer whales and sharks). We attempted to partition the various sources of "additional" mortalities as anthropogenic and as additional mortality including some predation. We classified 436 anthropogenic mortalities and 769 anthropogenic plus some predation mortalities as "mortality above replacement" (Table 2); this accounted for 25% and 45 % of the estimated total level of "mortality above replacement." The remaining mortality (75% and 55%, respectively) was not attributed to a specific cause and may be the result of nutritional stress.

Table 1. Projected counts of non-pup Steller sea lions at trend sites and estimates of the total population size for 2001-2020 in Alaska if trends continue as they did in 1991-2000.[a]

	Western Stock—Alaska					Eastern Stock—Alaska		
Year	Count	Estimated population	Additional losses	Stable population	Total mortalities	Count	Estimated population	Gain
2000	18,325	33,116				9,862	17,822	
2001	17,403	31,450	1,666	4,718	6,383	10,032	18,129	307
2002	16,528	29,868	1,582	4,480	6,062	10,204	18,440	312
2003	15,697	28,366	1,502	4,255	5,757	10,380	18,758	317
2004	14,907	26,939	1,427	4,041	5,468	10,558	19,080	323
2005	14,157	25,584	1,355	3,838	5,193	10,740	19,408	328
2006	13,445	24,297	1,287	3,645	4,931	10,925	19,742	334
2007	12,769	23,075	1,222	3,461	4,683	11,112	20,082	340
2008	12,127	21,914	1,161	3,287	4,448	11,304	20,427	345
2009	11,517	20,812	1,102	3,122	4,224	11,498	20,778	351
2010	10,937	19,765	1,047	2,965	4,012	11,696	21,136	357
2011	10,387	18,771	994	2,816	3,810	11,897	21,499	364
2012	9,865	17,827	944	2,674	3,618	12,102	21,869	370
2013	9,368	16,930	897	2,540	3,436	12,310	22,245	376
2014	8,897	16,078	852	2,412	3,263	12,521	22,628	383
2015	8,450	15,270	809	2,290	3,099	12,737	23,017	389
2016	8,025	14,502	768	2,175	2,943	12,956	23,413	396
2017	7,621	13,772	729	2,066	2,795	13,179	23,816	403
2018	7,238	13,080	693	1,962	2,655	13,405	24,225	410
2019	6,874	12,422	658	1,863	2,521	13,636	24,642	417
2020	6,528	11,797	625	1,770	2,394	13,870	25,066	424

[a]For 1991-2000 the annual decrease was 5.03% (S.E. = 0.25%) in the western stock and the annual increase was 1.72% (S.E. = 0.96%) in southeast Alaska (part of the eastern stock). Projected counts were computed from a base of actual counts in 2000.

Table 2. Estimates and source of Steller sea lion mortality during 2001, and that mortality expressed as a percentage of all estimated mortality above replacement (1,666).

Source	Estimated mortality (A)[a]	Estimated mortality (B)[b]	Estimated mortality above replacement (%)
Subsistence harvest	353	353	21.2
Incidental to fishing	30	30	1.8
Illegal shooting	50	50	3.0
Research	3	3	0.2
Predation by killer whales	0	300	0.0/18.0
Predation by sharks	0	33	0.0/2.0
Total	436	769	26.2/46.2

[a]Assumes all predation is in the natural category.

[b]Assumes some portion of predation is "additional" to natural, as explained in text.

Discussion

If our estimations are in the "ball park," then the estimated "additional" mortality that can be accounted for sums to about 436 for identified anthropogenic sources. If we add 333 mortalities attributable to predation by killer whales and sharks that we consider unnatural mortality, then the total "additional" mortality is 769 Steller sea lions annually, or about 45% of the mortality above replacement. We subtracted this sum from the estimated mortality in 2001 (1,666) resulting in about 897 Steller sea lions that may die from an unknown source and possibly attributable to environmental changes, the indirect effect of fisheries, or other factors yet to be recognized. However, if all predation remains in the "natural" mortality category then the anthropogenic source (436 sea lions) represents 25% of the "additional" mortality resulting in 1,230 dead sea lions in the unknown source category.

Our estimates of known removals from the western Steller sea lion population do not fully explain the current decline. It is interesting to ask: if our estimates of mortality are correct, then why are so few dead sea lions observed? More than six thousand dead sea lions per year far exceeds our expectations of mortality based on the number of observed carcasses, yet we believe the values are correct given the present knowledge of Steller sea lion population status and trends. To us the area of possible contention is not the level of mortality but the categorization and magnitude of mortality. As the difficulties of categorizing killer whale mortality exemplify, there are other important interactions among the causes of mortality. For example, if sea lions are nutritionally stressed,

mortality from predation could increase because sea lions spend more time at sea searching for food. Similarly, mortality from disease could increase because of greater nutritional stress or stress from avoiding predators. Also puzzling is the population in southeastern Alaska which continues to increase even though it probably experiences similar types of removals from the same causes (except for subsistence harvests). As the western population continues to decline, mortality attributable to "additional" losses will become smaller and those attributable to known removals, if constant, become more important. Now that the western Steller sea lion population is less than 33,000 animals, known anthropogenic sources of mortality can explain about 25% of the missing sea lions; if those numbers do not change, they would account for more of the missing sea lions in 20 years.

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Nutritional Limitation? An Alternative Hypothesis

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May 2001

Steller sea lions of the western stock in Alaska have declined substantially over the past 25 years or so. Although there is considerable variation in the spatial and temporal patterns of decline we are now at the point where nearly all regions within the western Alaska stock have declined by over 80%. Although not as well documented, we have seen similar declines of harbor seals (*Phoca vitulina*) within this region (Pitcher 1990, Frost et al. 1999).

After reviewing all data available to me I am convinced that the information now available justifies serious consideration of an alternative hypothesis to the current working hypothesis of nutritional limitation. I think that one of the things that has made this whole issue difficult to understand is that the North Pacific Ocean is a dynamic environment and we often try to understand what we are currently observing with data collected in past years under different environmental conditions.

There is substantial evidence that during the 1970s declines of Steller sea lions and harbor seals occurred in conjunction with nutritional stress (Jemison 1997, Calkins et al. 1998, Pitcher et al. 1998). It is probable that changes in prey availability brought on by climate change in the North Pacific Ocean played a significant role in these declines (Springer 1998, Anderson and Piatt 1999) although several aspects of timing of the decline do not fit well, namely that the decline in the eastern Aleutian Islands began before the 1976-1977 shift and that the decline in the northeast Gulf of Alaska may not have started until the late 1980s.

Something appeared to occur around 1989-1990 both in regard to Steller sea lion and harbor seal population dynamics and in regard to the ocean environment. In some areas the decline of Steller sea lions, particularly the eastern Aleutian Islands and the western Gulf of Alaska, and of harbor seals (Tugidak Island) appeared to moderate. It is also my under-

standing that changes in the ocean environment probably also occurred at about this time (Springer 1998). A number of studies evaluating the nutritional status of adult female and neonatal pup sea lions took place during the 1990s. Surprisingly, nearly all results appeared to indicate that the nutritional status of western stock animals was similar or even superior to those in southeast Alaska where the population was increasing. Following is a brief summary of those findings.

- While pup masses at birth were similar between populations, pup growth rates were higher in the west (Brandon 2000).

- Pup masses at one month of age were greater in the west (Merrick et al. 1995, Rea et al. 1998).

- Foraging effort, as defined by foraging trip length and time spent ashore, for females with pups on rookeries was less in the west (Brandon 2000).

- No evidence that pups <1 month of age from the west were nutritionally compromised based on blood chemistry and hematology (Rea et al. 1998).

- Masses of adult females greater in west (Adams 2000) and perhaps fatter in west (M.A. Castellini, Institute of Marine Science, University of Alaska Fairbanks, pers. comm.).

- Behavioral observations of maternal attendance patterns and activity budgets were not consistent with the hypothesis that animals from the western stock were having greater difficulty obtaining prey compared to those from the eastern stock (Milette 1999).

More recent work has focused on growth and body condition of juvenile Steller sea lions. While we are in the early stages of this work and our sample size is small, particularly in the west, we have found nothing to suggest that either growth or body condition is less for western stock animals than it is for juveniles from southeast Alaska. Mass at birth appears similar between pups in southeast Alaska and the west but growth rates appear higher in the west supporting the findings of Brandon (2000). Body composition estimates, if anything, suggest better condition in western stock animals. Data from harbor seals on Tugidak Island in the Gulf of Alaska also suggested improved nutritional status during the 1990s. For example, pupping dates were earlier in the 1990s than in the 1980s. In addition, haulout patterns indicated that animals from the 1990s were able to capture prey more easily than in the 1980s (Jemison 1997).

Comparisons of indices of Steller sea lion abundance and prey abundance suggest that on a per capita basis, prey availability is substantially higher than it was during the late 1970s or is currently in southeast Alaska where the population is increasing.

The question remains: why are Steller sea lion numbers in the western stock continuing to decline if adequate quantities of prey are available and the animals are not nutritionally limited? One possibility is that the combined sources of non-nutritionally linked mortality are high enough, in relation to current population size, to prevent recovery and cause additional declines in some areas. I loosely refer to this as the predator pit hypothesis. Mortality factors may include predation by killer whales and sharks, subsistence harvests, illegal shooting, incidental take in fisheries, rookery trauma, and entanglement in marine debris.

While I suspect that the original decline was largely due to nutritional factors and that the current population may be regulated by non-nutritionally linked mortality factors, there are several research findings that I find bothersome. These issues should not be ignored. These include findings of elevated haptoglobin levels in the west (Zenteno-Savin et al. 1997), elevated PCB and DDT metabolites in Steller sea lions from a portion of western stock range (unpubl. data), elevated mercury in the western stock (L.K. Duffy, Dept. of Chemistry, University of Alaska Fairbanks, unpubl. data), abnormal porphyrin ratios (L.K. Duffy, unpubl. data), and abnormal hemograms (K.B. Beckman, College of Veterinary Medicine, University of Illinois at Urbana Champaign, unpubl. data). These findings are suggestive of stressors such as toxins and diseases but I have no idea of their importance or if they are significantly affecting population dynamics.

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Foraging Behavior and Energetics of Adult Female Steller Sea Lions

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May 2001

The current decline in the population of Steller sea lions (SSL) in western Alaska may be attributable to food shortages in critical areas. Unfortunately, the feeding ecology of SSLs is poorly understood. Population modeling suggests that a decline in juvenile survival is a likely explanation for the recent SSL population decline. Such an increase in juvenile mortality could be due to the inability of mothers to adequately nourish their pups during lactation, or could be due to weaned juveniles not being able to successfully forage on their own. Other pinniped species have been observed to respond to apparent nutritional stress by increasing female foraging trip durations during lactation and/or increasing energy expenditure during foraging.

Studying the foraging behavior and energetics of pups and lactating females should reveal whether SSLs are food stressed in the areas where

their numbers continue to decline. Predictions from such a nutritional stress hypothesis include: (1) lactating female SSLs will increase their foraging effort in the area of population decline, and this may be reflected in increased energy expenditure or a change in diving strategy, such as less time spent resting; (2) foraging trip durations will be longer in the area of decline; (3) and sea lions in the area of decline will travel for a longer period of time or cover greater distance before successfully finding and ingesting prey.

Captive juvenile SSLs at the Vancouver Aquarium were used to develop and validate the use of stomach temperature monitoring in order to determine the timing and quantity of prey ingestion (indicated by precipitous drops in stomach temperature). Estimation of the quantity of ingested prey was complicated by many factors (e.g., body temperature and stomach heat flux changes, movement of the stomach temperature transmitter [STT] within the stomach, diverse prey size and shape, potentially concomitant water ingestion, and insulation of the STT by previously swallowed prey) and suffered a large margin of error. Determination of the timing of ingestion, however, was much more accurate, at least for the first few ingestion events in a bout of feeding. Initial deployments on wild SSLs demonstrated that prey were consumed on all foraging trips. However, long periods of time often elapsed and large distances were covered between successful foraging events. The preliminary work demonstrated that knowing where sea lions traveled and dove does not necessarily allow one to distinguish productive feeding areas from unproductive ones.

In June 1997, we conducted a test of the hypothesis that the current SSL decline is due to nutritional stress. SSLs were studied at two of the central Aleutian Islands, Seguam and Yunaska, and at the Forrester Island rookery complex in southeast Alaska. In the central Aleutians, 5 lactating SSL were captured and instrumented as described above. Four of these were recaptured, but one sea lion had lost her instrument package, resulting in the recovery of three foraging records from this area. Near Forrester Island, 10 lactating SSL were captured and instrumented. Five of these were recaptured and all resulted in successful data recordings. During the research cruise near Forrester Island, real-time satellite tracking data on the at-sea locations of sea lions were relayed to a vessel conducting a fish assessment around Forrester Island, and a similar fish assessment occurred around Seguam Island that summer.

Although a great deal of variability in foraging behavior was observed (both at the individual and rookery level), some basic differences between SSLs from different regions can be identified. Trip durations and the percent time spent at sea were much shorter for SSLs from Seguam Island compared to those from the Forrester Island rookery. Dives at Seguam Island were shorter and shallower, but more frequent than those at Forrester Island The short trips at Seguam Island generally consisted of a single bout of uninterrupted dive cycles while at Forrester Island the trips were broken into dive bouts of varying length separated by periods spent trav-

eling or resting at the surface. However, on average, the percent of a trip spent submerged was not significantly different. Another measure of foraging effort, the vertical travel distance per unit time at sea, was about 1.5 times greater for SSLs at Forrester Island. The at-sea field metabolic rates, however, were similar for both groups. Data on the time and distance elapsed from departure on a foraging trip until commencement of "foraging dives" shows that at both rookeries SSLs appear to begin searching for prey very soon after entering the water. However, the mean time from departure to first prey ingestion, identified by the stomach temperature record, was about five times longer for SSLs at Forrester Island than at Seguam Island. The rough estimation of prey intake rate at Seguam Island was about two times greater than at Forrester Island. Therefore, it would appear that in 1997, adult female SSLs at Seguam Island found suitable prey more quickly, and once they found it were able to ingest it at a much higher rate than SSLs at Forrester Island.

The higher prey capture rate of SSLs at Seguam apparently allows these sea lions to spend shorter periods away from their pups and thereby spend a greater proportion of total time suckling their pups. This may account for the nearly two times greater pup growth rates measured in the central Aleutians compared to Forrester Island (E. Brandon and R.W. Davis, Texas A&M University, Galveston, unpubl. data). The fish abundance assessments conducted at these two rookeries concurrent with the SSL monitoring may provide some insight into the differences in prey capture rate. Catch per unit effort for the fishing vessel at Seguam and another central Aleutians rookery was much higher than that at Forrester Island.

The following factors restrict our ability to make inferences concerning either the past or current SSL population decline, from this limited comparison of the foraging ecology of SSLs in both declining and stable populations: (1) extremely small sample sizes, (2) the possibility of adverse effects of the instruments on foraging behavior and energetics, (3) the difference between the current rate of decline compared to the larger rate from 1979 to 1990, (4) density dependent effects on individual foraging success (reduced population size implies reduced intra-specific competition), (5) and the potential interannual variations in many environmental parameters (e.g., the 1997 El Niño and the anomalous conditions in the Bering Sea that year). However, the direct comparison between two similarly handled groups should allow some general conclusions about SSL foraging behavior to be drawn. From this study it appears that a directly measured difference in prey availability may account for the observed difference in prey capture rate. This greater capture rate by SSLs at Seguam Island may partially explain the greater pup growth rates observed there compared to Forrester Island. The lack of a single highly abundant prey species and the larger SSL population at Forrester Island may result in longer search times for Forrester Island SSL. An important value of this and the related studies to date is that we were able to demonstrate a correlation between prey availability, foraging success, and pup growth, a pa-

rameter that is potentially indicative of future survival and therefore adult female reproductive success.

Acknowledgments

Female Attendance, Lactation, and Pup Growth in Steller Sea Lions

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May 2001

A number of possible causes for the Steller sea lion population decline have been proposed, including redistribution, 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 suspected to be the most significant factor when this research was conducted (1990-1997). If prey (especially high-caloric prey) in the area of Steller sea lion population decline has become less abundant or less diverse, this may negatively affect female provisioning of pups. Possible effects include: (1) increased female foraging trip duration, (2) longer at-sea/onshore attendance cycle, (3) reduced milk production and nutritional quality, (4) slower pup growth, and (5) poor pup body condition. 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. Our null hypotheses for lactating Steller sea lions and their pups during the first six weeks postpartum were: (1) there is no difference

in foraging trip duration or time on shore between populations, (2) there is no difference in the nutritional composition of milk or pup milk intake rates between populations, and (3) there is no difference in the rate of pup growth or pup body condition between populations. Our study sites in Alaska were Lowrie Island (located in the area of stable population) and Marmot, Chirikof, Seguam, and Yunaska islands (located in the area of declining population). Fish Island lies between the areas of declining and stable populations.

Female Attendance

Rationale

Lactating Steller sea lions alternate periods onshore feeding their pups with foraging trips to sea. The average length of a foraging trip is influenced by prey density and distribution and the fasting ability of the pup. Steller sea lion pups do not have large lipid reserves, so their ability to fast is very limited, especially if they are to grow. As a result, female foraging trips are generally short and limited to the area around the rookery. If prey in the area of Steller sea lion population decline has become less abundant or less diverse, this may increase both foraging trip duration and the length of the at-sea/onshore attendance cycle.

Methods

VHF radio transmitters were glued to the hair in the dorsal axillary area of lactating female sea lions. Radio signals from the transmitters were recorded with an automated data logger set to scan each frequency for 20 seconds on a duty cycle of 15 minutes. The presence of a signal indicated that the female was on land or near the water surface, while the lack of a signal indicated that the female was at sea, or a rock or other obstacle blocked the signal. Antennas were positioned to minimize the latter possibility. Transmitter range was estimated in the field to be 2-4 miles. When possible, absence or presence of the females on the rookery was verified by direct observation.

Summary of Results for Female Attendance

1. There was no significant difference among rookeries in the time spent on shore or in the total length of the onshore/at sea cycle, but there was a significant difference among rookeries in time at sea and in the percentage of time at sea.

2. Trips to sea ranged in length from an average of 7.1 to 25.6 hr.

3. Time onshore ranged from an average of 20.7 to 25.2 hr.

4. Females spent 24-51% of their time at sea, and 49-76% of their time on the rookeries.

5. Females in the Aleutian Islands made significantly shorter trips to sea than females on Lowrie Island.

6. Females on both the Aleutian Islands and Chirikof Island spent a significantly smaller percentage of time at sea than did females on Lowrie Island.

7. Females on the Aleutian Islands also spent a significantly smaller percentage of time at sea than did females on Fish Island.

8. The pattern of arrivals and departures from foraging trips showed no clear pattern on Lowrie Island.

9. Females on Chirikof Island and the Aleutian Islands tended to arrive in the morning and depart in the evening.

Milk Composition and Consumption

Rationale

The energy available to the pup during lactation is a function of both milk composition and milk yield (volume). If a lactating female is unable to consume sufficient prey to meet the demands of milk synthesis, body fat and protein reserves will be mobilized to satisfy the nutritional requirements. Female Steller sea lions do not accumulate large adipose tissue reserves prior to parturition, so the ability of a nutritionally stressed female to synthesize milk from body reserves is limited. As a result, access to adequate prey (i.e., energy) during lactation is crucial for milk production and pup growth.

Methods

Milk samples were collected from anesthetized females and analyzed for water, protein, and lipid content. Milk energy content was calculated from the lipid and protein content. Pups were captured, weighed, bled, and injected with deuterium oxide. Ten to 14 days later, they were recaptured, bled, and re-injected with deuterium oxide. Total water intake was calculated from the decline in the blood concentration of deuterium oxide. Milk and energy intake were calculated from water intake, the water and energy content of milk, and metabolic water production.

Summary of Results for Milk Composition and Consumption

1. The proximate composition of milk did not differ significantly among rookeries. Milk averaged 62% water, 22% lipid, 9% protein, and 2% ash. Energy content averaged 10.2 kJ ml^{-1}.

2. There were no significant differences among rookeries for water (64 ml kg^{-1} d^{-1}), milk (72 ml kg^{-1} d^{-1}), or energy (741 kJ kg^{-1} d^{-1}) intake rates.

3. Water, milk, and energy intake rates did not differ between male and female pups when these rates were expressed on a body weight basis. Only milk yield was expected to change with food stress, not the milk quality.

4. The average predicted maintenance requirement for milk energy was 390 kJ kg^{-1} d^{-1}.

Neonatal Growth

Rationale

Sea lion pups depend completely on milk for neonatal growth. Studies of other otariid species 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) and a reduced growth rate. This may have lifelong consequences because neonatal growth is an important factor in determining adult size and survival.

Methods

Body mass (BM), standard length (SL), and body composition were measured for pups 1-5 days old. Water labeled with a stable isotope of hydrogen (deuterium) was used to estimate total body water, lean mass, and total body lipid. Pups were recaptured at two- to three-week intervals over a six-week period, weighed, and measured. Isotope-ratio mass spectrometry was used to determine serum deuterium concentration and estimate total body water (TBW). Lean body mass (LBM) was estimated from TBW. Total body lipid (TBL) was calculated as the difference between BM and LBM.

Summary of Results for Pup Growth and Body Condition

1. Average BM at birth did not differ by rookery. However, male pups (22.4 kg) were significantly larger than female pups (18.7 kg) at birth.

2. There was no significant difference by rookery or sex in total body water (TBW), lean body mass (LBM), or total body lipid (TBL) of newborn pups. Average TBW was 72.1% of BM, resulting in an LBM of 96.6% and a TBL of 3.4% of BM.

3. Male and female pups on the same rookery grew at the same rate during the first six weeks postpartum.

4. BM increased at a faster rate for pups on the Aleutian Islands and Chirikof Island than for pups on Lowrie Island.

Conclusions

In comparing the areas of stable and declining populations, we observed no differences in (1) milk composition, (2) milk consumption, and (3) pup body mass and body composition at birth. Females in the area of population decline made shorter foraging trips and spent a smaller percentage of the attendance cycle at sea; the pups of these females spent less time fasting between maternal visits and therefore grew faster despite similar milk intake rates. Our results show no evidence of nutritional stress in lactating females and their pups in the area of population decline during the first six weeks postpartum. However, lactation in this species may last 12 months or longer, and milk intake increases with pup age and mass. Without data on female attendance, milk production, and pup growth throughout lactation, we cannot say whether food availability during the entire pre-weaning period is a factor in the population decline.

Indices of Condition in Steller Sea Lions (*Eumetopias jubatus*)

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May 2001

Several studies have utilized traditional indices of body morphology to describe the condition of Steller sea lions throughout their range. Two studies have shown that pups less than 5 weeks of age in the western portion of their range (area of decline) have higher body mass than those in the area of stable population (Merrick et al. 1995, Rea et al. 1998). Similarly adult females in the western population have been found to be "rounder, longer and heavier than their Southeast Alaska counterparts with lower percent body water, reflecting higher body fat content" (M. Castellini, Univ. of Alaska Fairbanks, Feb. 1999, pers. comm.). Although standard morphometric indices such as standard length and axillary girth have been shown to be predictive of total body mass (Castellini and Calkins 1993), these parameters have been shown to be poor indicators of blubber thickness in Steller sea lion pups (Trites and Jonker 2000). Condition and density indices were unable to distinguish between starveling and average pups (Rea 1995) and LMD-index (using standard length, mass, and dorsal blubber depth measures) explained only 58% of the variability in sculp mass in animals collected between 1975 and 1989 ($n = 523$; Pitcher et al. 2000). Density index, calculated as $[\text{mass}/(SL \times AG^2)] \times 10^6$, was not significantly correlated with total percent body fat measured by deuterium dilution technique in 140 juvenile animals aged 2 months to 5 years ($r^2 = 0.01$, Fig. 1).

Percent body fat content has been shown to significantly decrease during food limitation in 7 to 14 day captive fasting studies (0.8 ± 0.4 % decrease in lipid per day as a percent of original body mass, $n = 16$). Thus the estimation of total body water (TBW) and the subsequent calculation of total body fat is currently considered the best index of body condition. This technique requires a minimum animal handling time of 2 hours for equilibration of the injected labeled water; thus it has often proven to be the limiting factor in the number of free-ranging animals studied during
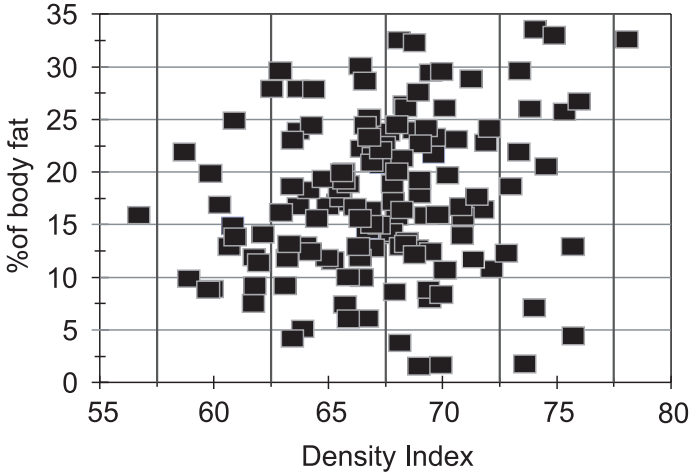
Figure 1. Density index, calculated as [mass/(SL × AG²)] × 10⁶, versus percent body fat content (as determined by deuterium dilution) for Steller sea lions between 2 months and 5 years of age (r² = 0.01, n = 140).

field investigations. Research has been under way to validate the use of bioelectrical impedance analysis (BIA) as an index of body condition in Steller sea lions as it is an instantaneous measure of TBW. Preliminary data show that TBW determined by BIA is highly correlated with TBW as estimated by the longer deuterium dilution technique (actual TBW = 0.985* [predicted]; forced through zero; $r^2 = 0.89$; $P < 0.0001$; Castellini 2001). This regression is particularly strong for small body sizes (up to 150 kg), although there is increased noise in this relationship in animals above 150 kg.

Percent body fat data (estimated by deuterium dilution) is currently available for 119 sea lions, ranging from 2 to 26 months of age (southeast Alaska $n = 74$; Prince William Sound $n = 45$). An additional 50 samples are under analysis (Kodiak Island area $n = 13$; southeast Alaska $n = 37$). Given our attempt to distribute sampling coverage throughout the year to investigate several aspects of development of juvenile Steller sea lions, sample sizes at any particular age are not yet sufficiently large to make reliable regional or gender based comparisons. Body fat content within each age group sampled is highly variable, particularly after 10 months of age. I would caution that percent body fat alone, without consideration of the weaning status of that particular sea lion, could be a misleading indicator of fitness. Phocid seals have been documented to decrease body fat content by 15% over a 2 week captive period of feeding on fish following a sustained post-weaning fast by significantly increasing lean body mass growth relative to adipose tissue growth (Rea 1990).

Figure 2.   Weight percent of 20:1-11 fatty acid in blubber lipids of Steller sea lion juveniles 2-26 months of age, captured in southeast Alaska (gray bars) and Prince William Sound (black bars).

Preliminary data on fatty acid signatures show close correspondence between the lipid profiles of milk collected from the stomach of one 7-month-old sea lion and blubber collected from that animal ($n = 1$) suggesting that blubber profiles will prove to be a representative composite of diet in Steller sea lions. Two fatty acids which are indicative of prey are not readily transferred into milk in phocids (20:1w-11 and 22:1w-11 fatty acids, Fig. 2). Relatively high levels of these "prey" fatty acids were seen in 10.5- ($n = 12$) and 22.5- ($n = 3$) month-old sea lions captured in Prince William Sound. This could indicate either that Prince William Sound animals are relying more heavily on fish than 9- or 19-month-old sea lions in southeast Alaska, or that milk ingested by the Prince William Sound animals had a higher content of these fatty acids. Additional milk and collected blubber biopsy samples are currently being analyzed from both areas. If Prince William Sound milk samples prove similar in composition to that from southeast Alaska, these two fatty acids may provide evidence to identify juveniles that are at least supplementing their diet with fish. It will be important to look at individual patterns of fatty acid distribution, along with body composition, to be able to achieve our goal of identifying sea lions that are nutritionally independent.

Nutritional blood chemistry parameters such as ketone body (B-hydroxybutyrate or B-HBA) and blood urea nitrogen (BUN) concentrations have been shown to change significantly in response to food limitation in fasting studies on 6 week old pups (Rea et al. 2000). Similar changes in B-HBA have not been demonstrated by fasting juvenile sea lions over the age of 1.5 years. Thus, B-HBA has proven to be a useful tool in determining the proportion of handled pups at a site that are currently fasting. Published blood chemistry data have demonstrated that a higher proportion of pups studied in the 1990s in southeast Alaska showed B-HBA levels indicative of fasting than those pups sampled in the area of decline (Rea et al. 1998). These data are supported by observations of longer at-sea foraging times in southeast Alaska during the time of the study; thus pups were left alone fasting on the rookery for longer periods. Similarly, significantly higher B-HBA levels were measured in sea lion pups captured on Ugamak Island in 1997 (compared to 4 previous years of capture) coinciding with anomalous warm oceanographic conditions and low relative acoustic biomass signals at that location.

Plasma levels of the hormone leptin have been shown to be related to body and metabolic condition in several mammal species. Preliminary data on Steller sea lions have shown leptin concentrations to change during periods of food limitation with levels increasing in juvenile female sea lions ($n = 2$) during captive fasting experiments, and decreasing in similar fasting studies on male sea lions ($n = 3$). Plasma leptin levels were not highly correlated with total body fat content; however, ongoing research in this area will further consider the role of other factors now recognized to influence leptin secretion in other mammals, such as nutritional state (fasting/feeding), season, reproductive hormone levels, and circadian rhythm in this relationship. There is promise that when leptin is measured in concert with other hormonal indicators (e.g. thyroid hormones), an informative profile of metabolic condition can be developed.

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Overview of Recent Steller Sea Lion Telemetry Work in Alaska

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May 2001

Steller sea lions in the endangered western stock of Alaska have declined by more than 80% since the 1970s (Loughlin et al. 1992, Sease and Loughlin 1999). Nutritional stress has been the leading hypothesis for the decline of the Steller sea lion population. The reproductive success of adult females and survival of juveniles to maturity are important factors in the population dynamics of Steller sea lions (York 1994). To gain a better understanding of movements, foraging behavior, dive ontogeny, and resource selection, location-, haulout-, and dive-reporting satellite data recorders (SDRs) and location-only Argos platform transmitter terminals (PTTs) have been deployed on adult females with dependent young and juvenile (<3 years-of-age) Steller sea lions. Between 1989 and 2001, 179 instruments were deployed on Steller sea lions in Alaska by the Alaska Department of Fish and Game (ADFG) and National Marine Mammal Laboratory (NMML) (Table 1, Fig. 1). Of those, 94 instruments were deployed in the western stock and 85 instruments were deployed in the eastern stock.

Initial satellite telemetry efforts focused on adult female foraging capabilities and the movements of adult females with dependent pups on the rookery. Adult females were captured on the haulout by darting with Telazol, and instruments attached to the pelage using fast-setting epoxy and nylon mesh. Fifty-four instruments were deployed on adult females from 1990 to 1993. Results from these studies have been previously reported by Merrick et al. (1994) and Merrick and Loughlin (1997). An analysis of the foraging ecology of adult females with dependent pups is in preparation (R. Andrews, University of British Columbia, Vancouver, pers. comm.)

Table 1. Stock (Western and Eastern divided at Cape Suckling) region, capture period, sex, approximate age class, and number of satellite data recorders (SDRs) deployed on Steller sea lions in Alaska, with mean deployment duration and range of SDRs.

Stock/region	Capture period	Pups/Juveniles M	Pups/Juveniles F	Adults F	Total no. SDRs deployed	Mean deployment duration/range (days)
Western stock						
NMML						
Central Aleutians	Jul 90, Feb 00	1	3	5	9	43(0-104)
Eastern Aleutians	Jun 90, Jul/Nov 91	4	3	8	15	38(1-67)
GOA-W	Jul 91,93; Mar 96	1	1	6	8	28(0-52)
GOA-C (Kodiak region)[b]	Jun/Dec 90, Jun 91, Feb/Jul 92, Feb 93, Dec 94, Jan 96	7	3	21	31	45(0-174)[a]
Total		13	10	40	63	
ADFG						
GOA-C (Kodiak)	Mar 01	10	3		13	[a]
GOA-E	Jan 93		1	1		114
GOA-E	Jan 95		1	1		129(113-145)
GOA-E	Jun 95		1	0	1	11
PWS	Apr 00	4	4		8	42.5(10-78)
PWS	Apr 00	0	2		2	64(54-74)
PWS	Aug 00	1	3		4	67.8(51-103)
Total		17	13	1	31	
Eastern stock						
SE-N	Nov 98	5	5		10	44.6(12-119)
SE-N	Jan 00	2	5		7	81.6(60-138)
SE-N	Jan 00	2	1		3	146.7(120-181)
SE-N	May 01	2	2		4	[a]
SE-N	May 01	1	1		2	[a]
SE-C	Mar 98	7	5		12	81.7(30-143)
SE-C	Aug 99	4	6		10	5.6(3-13)
SE-C	Sept 00	3	2		5	106(82-114)
SE-C	May 01	5	3		8	[a]
SE-S	May/Jul 92	0	1	5	6	40(28-84)
SE-S	Jun/Jul 93			7	7	28(21-36)[c]
SE-S	July 98	3	7		10	21.1(11-34)[c]
SE-S (NMML)	Jul 91			1	1	<1
Total		34	38	13	85	

[a]Data collection still in progress as of 31 May 2001.

[b]10 instruments deployed by NMML in Unimak Pass during March 2001 are not included in this table.

[c]Feeding trips for summer-captured adult females with pups are being analyzed for Andrews et al. (in prep). Locations outside feeding trips not used.

PWS = Prince William Sound, GOA-C = Central Gulf of Alaska, GOA-E = Eastern Gulf of Alaska, SE = Southeast Alaska, N = North, C = Central, S = south. Pups/Juveniles are <36 months of age.
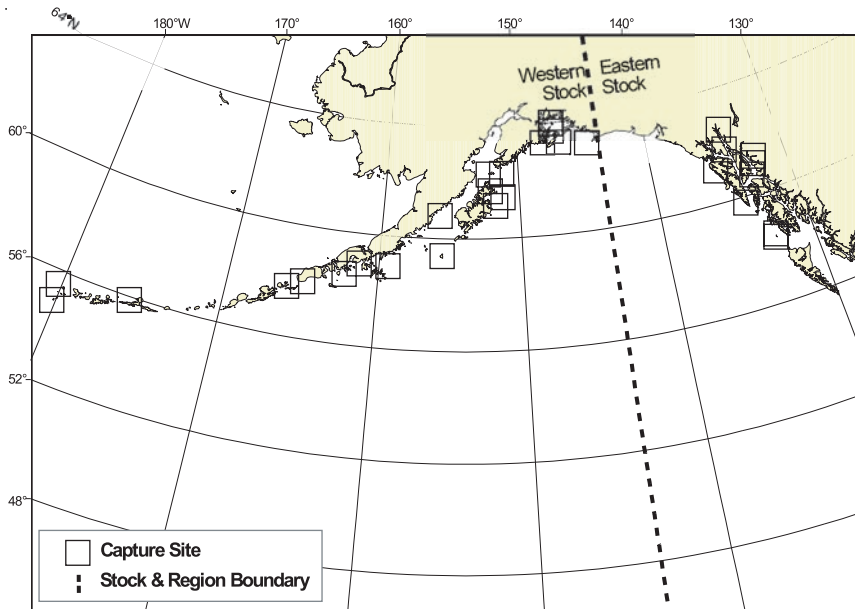
Figure 1.   Steller sea lion haulouts and rookeries at which SDRs and PTTs have been deployed by ADFG and NMML.

Reduced juvenile survivorship is believed to be one of the primary factors contributing to the decline of the Steller sea lion (York 1994). After emphasis shifted from adult to juvenile survival, we deployed SDRs on juveniles to better describe the early life history of Steller sea lions. This information will yield a more complete picture of the diving capabilities of juveniles and how they compare to adult female sea lions. With this information, we may better understand the limitations in dive behavior of juveniles, describe their usage of at-sea habitat near haulouts, identify the transition between the behavior of nutritionally dependent pups to independently foraging juveniles, and understand how diving ability may affect their ability to obtain prey.

We used two different methods to capture juvenile Steller sea lions: capturing animals on land, and capturing animals using the underwater technique developed by D. McAllister and W. Cunningham (ADFG unpubl. data). As of May 2001, 125 SDRs have been deployed on juvenile animals (Table 1, Fig. 1). Of those, 53 (30 on males, 23 on females) were deployed in the western stock and 72 (34 on males, 38 on females) were deployed in the eastern stock. SDR deployment duration ranged from 0 to 181 days. Earlier juvenile telemetry results have been reported by Merrick and Loughlin (1997). Results of more recent studies are in preparation (dive

development, M. Rehberg; movement and resource selection, K. Raum-Suryan; and integrated movement and diving behavior, T. Loughlin, NMFS NMML, Seattle, Washington, pers. comm.).

SDR instrumentation of juveniles continues, and the future goals of juvenile satellite telemetry work are to integrate the dive and location information with concurrent studies by other researchers, such as forage fish distribution and biomass studies (Gulf Apex Predator-Prey study and Southeast Alaska Predator-Prey study, K. Wynne (University of Alaska Fairbanks) and M. Sigler, National Marine Fisheries Service, Juneau, Alaska, pers. comm., forage information from scat collections, and nutritional status (M. Rehberg, unpubl. data).

ADFG and NMML had slightly different goals for pre-2001 juvenile deployments. ADFG, studying diving ontogeny during the first 2 years of life, programmed its instruments with a day-on/day-off duty cycle to extend SDR life as long as possible. NMML, studying the use of habitat near western stock haulouts, did not use a daily duty cycle, which resulted in a more continuous set of location data. Since January 2000 ADFG and NMML have programmed their SDRs to collect dive and haulout data in a compatible fashion, which will permit better comparisons between the eastern and western Steller sea lion stocks.

The most recently deployed SDRs (since March 2001) have increased battery capacity at least double that of earlier units, allowing longer, non-duty-cycled deployments and greater data transmission rates. Programming changes devised by NMML have increased the quantity and diurnal spread of location and dive data reported (although data completeness continues to vary by individual). Attachment techniques developed by ADFG have increased the duration of instrument attachment to 8 months (although antenna durability remains an issue). Our future goals include testing improved instrumentation and instrument placement locations on sea lions, which should allow collection of more detailed location, dive, and haulout information.

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Captive Studies with Steller Sea Lions at the Alaska SeaLife Center

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May 2001

Captive studies on Steller sea lions at the Alaska SeaLife Center (ASLC) were initiated in 1998 and consisted of multiple, simultaneous studies on a range of topics that dealt with both nutrition and non–food related project areas. Most of these studies were funded to outside (non-ASLC) scientists. Work not directly associated with food and nutrition included metal chemistry, immune function, organochlorine chemistry, reproductive chemistry, and dive instrumentation development. In addition, a series of projects were directly relevant to the "Is It Food" issue. These included studies on fasting biochemistry, body condition, and optimal foraging theory. A large, multi-year feeding regime trial designed by ASLC was also initiated and continues at present.

Fasting Biology

The fasting biochemistry study was run by Lorrie Rea through the University of Central Florida. She examined the biochemical and physiological reactions in sea lions to medium length fasting periods (about 10-14 days). Since seasonal fasting is a normal component of the sea lion annual cycle, Rea was interested in examining how sea lions reacted to fasting during the time of year when they should be adapted to this behavior (breeding season), vs. fasting during the time of year when they would ordinarily be feeding. This work was directly related to the issue of how sea lions would react to limited food intake during winter in the field. These experiments determined that sea lions are able to enter a "fasting adapted" metabolic state all times of the year, but that the ability to maintain this conservative state may be limited during the nonbreeding season. Furthermore, smaller animals may be limited in their fasting ability even within the breeding season. She concluded that most sea lions could easily adapt to

reduced food sources during summer months, but may be more severely impacted by low food availability during the rest of the year.

Body Condition

The development of photogrammetric methods for determining body mass and condition was a project run by Markus Horning from Texas A&M University. Along with M.S. student Jason Waite, they were able to develop methods to use 3-D digital photographs to determine the body volume and mass of sea lions. This work forms the basis of continued work by Horning to develop remote, visual body condition monitoring methods for sea lions. In addition, the Horning laboratory worked on the development of an attached recording device that could monitor the bio-impedance of a free-swimming sea lion in order to track body condition. While the device recorded valid impedance data, it was not compatible with long-term deployment on the animals due to tissue reactions to the electrodes.

Optimal Foraging Theory

This project, also by Horning at Texas A&M, examined how sea lions would balance time spent underwater with the quantity of food presented to them through underwater feeding tubes. This project was a primary component of the PhD. work for Leslie Cornick and will be completed in the summer of 2001. This research established an experimental relationship between simulated prey density and dive behavior, an important verification of foraging theory predictions. One of the primary goals of the work in summer 2001 is to show if an increase in the cost of swimming has similar effects to a decrease in prey accessibility. If this can be shown, then research teams can monitor the response of free-ranging animals to experimental changes in cost of swimming, and use the response of the free-ranging animals to this manipulation to predict their response to changes in a reduction in prey accessibility. This will be a very important element in the development of a comprehensive, energetics-based model.

Feeding Regime Study

The largest study relevant to testing the nutritional stress hypothesis is the ongoing feeding regime program. This study was initiated to test the hypothesis that different types of prey would impact the body condition and health of Steller sea lions. The conceptual design of the study is to test the sea lions on three different prey regimes representing diets consumed by sea lions before the decline began (1970s diet), during the period of significant decline (1980s), and a diet representative of southeast Alaska, where the sea lion population is stable.

Several design criteria were essential to a robust interpretation of the feeding study:

1. The animals were to stay on any particular diet long enough to eliminate behavioral or short-term responses to dietary shifting.

2. Each sea lion would act as its own control.

3. The impact of seasonal changes in metabolism needed to be quantified.

Three different periods in the annual cycles of sea lions were defined:

1. The reproductive period (February-May).

2. The post-reproductive/molting period (July-November).

3. The winter fattening period (November-March).

Given these caveats, a three year, repeated measures–crossover experimental design was created. In this design, each sea lion consumes each diet (A, B, C) during each of the three seasons. For example, when the experiment is finished, the female "Kiska" will have consumed diet 1 during the spring, summer, and fall-winter periods, and likewise with diets 2 and 3. This will provide a seasonal correction for any particular diet. In the final matrix, diets can be compared across season for each animal.

The study is scheduled to be completed in spring 2002; therefore, not all comparisons of season and diet can be made as of this writing. However, several patterns appear to be emerging:

1. Under some seasonal conditions, the animals appear to defend body mass regardless of diet. They seem to do so by adjusting the volume of food consumed.

2. The male sea lion and one of the females hold body composition (percent lean or fat tissue) relatively stable regardless of season or diet. The second female shows more flexibility in body composition.

3. The sea lions have maintained excellent health and blood chemistry, regardless of diet.

These preliminary results suggest that Steller sea lions have a tremendous ability to compensate for dietary shifts through behavior (consuming more or less), physiology (defense of body mass and perhaps body condition), and biochemistry (maintenance of metabolic status). Studies designed to identify and quantify the regulation of the metabolic pathways associated with this apparent adaptive ability are currently being reviewed and may be implemented in the future.

The four projects on captive sea lions at the ASLC have shown that laboratory controlled experiments can be valuable in interpreting data from field studies. These projects have demonstrated the biochemical

background to fasting, developed the core concepts for remote monitoring of body condition, tested models for assessing foraging theory, and allowed for testing hypotheses on the nutritional quality of different diets.

What Is It about Food? Examining Possible Mechanisms with Captive Steller Sea Lions

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May 2001

Overview

Changes in the quality or quantity of food can have a dramatic effect on the population status of wild animals. Unfortunately, it is difficult to assess (or define) whether nutritional stress is a contributing factor to the decline of any particular species. The "nutritional quality" of a diet to an animal is a complex matter to assess given the range of components that can influence its value. The effects of different diets on animal health are equally complex, and are particularly difficult to assess in large, wild animals.

Research by the North Pacific Universities Marine Mammal Research Consortium with captive Steller sea lions is evaluating the possible mechanisms by which dietary changes might adversely affect the nutritional or health status of individual animals, and ultimately the population as a whole. The research investigates the three potential proximate mechanisms by which changes in diet might impact Steller sea lions: a decrease in energy intake, a decrease in the intake of some essential element, and the over-consumption of an element detrimental to sea lion health.

Energy Intake

To examine the hypothesis that population changes are the result of decreases in relative energy intake, our research evaluates both the potential energetic value of prey items (energy intake), and the energy requirements of sea lions (energy output).

The first step in determining potential limitations in energy intake is to quantify sea lion diet. Although analysis of fish remains in scat samples

is an accepted technique for diet determination, we have been developing correction factors for these diet reconstructions, and quantifying the time period that these samples represent. We are also participating in a study to test the efficacy of fatty acid signatures to identify prey intake over longer time periods.

Experiments to determine the heat increment of feeding (HIF) and fecal energy loss (FE) enable us to calculate the net (biologically useful) energy value of common prey. These studies are necessary to accurately convert between energetic demand and food consumption estimates. The results suggest that sea lions would have to consume substantially more pollock (35-80%) and squid (107-145%) to achieve the same energy intake of a herring diet (Rosen and Trites 1999, 2000a,b). The differences can be further magnified by the need to ingest larger meals of low-energy prey, which further decreases digestive efficiency (Rosen and Trites 1997). The significant range of these estimates results primarily from variation in prey energy content. Proximate composition analyses of common prey items have revealed that the gross energy content of potential prey items changes temporally, geographically, and by age/sex class (C. Azano, U.B.C., unpubl. data).

Ad libitum feeding trials are used to investigate potential controls and limitations in food intake, particularly in younger animals given the allometries between body mass, energetic needs, and digestive capacity. In several studies, young sea lions did not increase their food intake sufficiently on (short-term) low energy diets to maintain energy intake and body mass (Rosen and Trites 1999, 2000a). We suspect that physical or chemical satiation may be limiting the sea lions' capacity for energetic compensation through increased food intake. Studies continue into the factors limiting food and energy intake, including satiation and feeding opportunities.

A computer model of Steller sea lion bioenergetics has helped to understand the relationship between energy intake and expenditures. The model integrates diet information with empirically derived data on the costs of particular parameters of the sea lion's energy budget (Winship et al. 2002). Experiments with captive sea lions have provided data on the costs (including variation and interaction) associated with standard metabolism, swimming, foraging, and thermoregulation. These studies have also been instrumental in testing and developing techniques for measuring energy expenditure in wild sea lions (e.g., heart rate).

Metabolic studies with fasted or food-restricted sea lions have documented the degree to which bioenergetic adaptations (e.g., metabolic depression, changes in activity) can compensate for decreased energy intake. When fasted or on a low-energy diet, the sea lions displayed a decrease in metabolism proportional to changes in body mass (Rosen and Trites, in press), typical of a "fasting response." While this metabolic depression was significant (<30%), it was not sufficient to preclude loss of body mass. In contrast, the sea lions exhibited a "foraging response," characterized by

increased activity and no metabolic depression, during food restriction trials. We are investigating further the criteria that trigger these alternate energetic strategies.

Intake of Essential or Detrimental Elements

One aspect of the nutritional stress hypothesis suggests that sea lion health is being negatively affected because sea lion diet does not provide adequate levels of unspecified essential elements. An alternate hypothesis proposes that the diet is providing too much of an element that is detrimental to sea lion health. We have begun to investigate both of these possibilities by evaluating the composition of key prey items, and by documenting the effect of different prey items on animal health. Both avenues are key to the investigation: chemical analyses of prey can help suggest which physiological effects to monitor, and vice versa.

Given that a major difference between potential prey items is their lipid content, we have been specifically investigating the effects of a low-fat diet on sea lion condition and health. Initial results suggest that when sea lions are maintained on isocaloric pollock and herring diets for 6 weeks, they display similar changes in body mass. However, body lipid stores decrease faster when sea lions are on a (low fat) pollock-only diet, although additional factors (e.g., season, gender) may control body lipid levels.

Numerous chemical analyses can be performed on prey samples. We have concentrated our efforts on those elements we feel are most likely to impact Steller sea lions, including essential fatty acids and key vitamin complexes. The impact of these prey items has primarily been investigated through blood samples taken from sea lions while they were on different diets. For example, we are currently investigating whether a diet high in gadid species results in hematological abnormalities, as demonstrated with other mammals.

Given the constraints of studying long-lived species, we have used an alternate mammalian model to document the long-term effects of different diets on key life history parameters. Initial experiments have used rats on normal and lipid-enhanced pollock and herring based diets. Results confirm the need for increased pollock intake, but also suggest that increased intake of pollock oil may negatively impact certain life history parameters (e.g., low birth weights) (C. Donnelly, U.B.C., unpubl. data).

Initial Conclusions

- The gross energy content of specific prey items can vary widely. Our experiments have affirmed that accurate calculations of the net energy of these prey items are essential to determining their biological energy value and for accurate estimates of prey requirements.

- Ingested food mass may be limiting the degree to which sea lions, particularly younger animals, can compensate for lower energy-den-

sity prey by increasing food intake. The frequency of feeding opportunities may also limit total food intake.

- Steller sea lions can alter their energy budgets to compensate for decreased energy intake, but the extent and duration of this ability is limited. There is also a clear differentiation between a physiological "foraging" response and a "fasting" response.

- There are preliminary indications that the nutritional quality of particular prey may be negatively impacting Steller sea lion health. Initial results from sea lion and alternate models suggest both short-term (hematological changes, lipid stores) and long-term (reproductive success) effects.

- In evaluating the link between diet changes and sea lion population declines, it is imperative to evaluate whether potential energetic or nutritional deficiencies incurred by an individual ultimately impact the life history parameters of the population.

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Is It Food *Now*? Gulf Apex Predator-Prey Study

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May 2001

The University of Alaska Fairbanks Gulf Apex Predator-Prey (GAP) Program is composed of vertically integrated, trophic studies designed to explore the interrelationships between Steller sea lions and their prey, predators, and competitors in the Kodiak area. This multidisciplinary program involves individual but coordinated studies that overlap in space and time in a geographically focused area. Ultimately, results from these and related studies will be incorporated into a model of the seasonal trophic interactions, dynamics, and energy flow in the Gulf of Alaska. This discussion summarizes our efforts to assess prey use by Steller sea lions.

Key to the GAP approach is the documentation of seasonal prey species composition, distribution, and abundance on the east side of Kodiak Island through repetitive hydro-acoustic and (midwater and bottom) trawl surveys. Surveys are centered within Steller sea lion critical habitat surrounding Long Island (in Chiniak Bay) and conducted in March, May, and November. From each survey, we estimate seasonal prey biomass (number and kilograms per kilometer), document seasonal species composition and distribution, collect samples for seasonal prey quality analyses, and collect seasonal zooplankton and CTD data. Surveys were completed in this area in March, May, and November 2000, and May 2001; funding has been secured for November 2001 and March 2002. An extended acoustic/midwater trawl survey will be conducted in July 2001 to determine if the study area is representative of waters east of Kodiak.

We collect fecal samples (scats) throughout the year (1-4 collections per year) from Long Island and eight other sea lion haulouts to assess seasonal prey use by Steller sea lions in the Kodiak area. Prey remains are recovered from each scat, identified to lowest possible taxon, and the frequency of occurrence of each prey species is tallied in each sample. Although it is not possible to determine the volume of specific prey con-

Table 1. **The most frequently occurring prey recovered from 295 Steller sea lion scats collected from Kodiak haulouts between September 1999 and August 2000.**

Prey	% of scats containing prey
Sandlance	49
Arrowtooth flounder	37
Pacific cod	33
Walleye pollock	31
Irish lords/sculpins	21
Salmon	17
Capelin	16
Flounder/sole	12
Snailfish	11

sumed in such analyses, scats provide an accessible long-term index of the relative annual, seasonal, and regional importance of prey in the diets of sea lions using Kodiak area haulouts.

To date, we have collected 1,200 scats from nine Kodiak area haulouts, of which 295 (from ten collections on six haulouts) have been analyzed. Our preliminary results suggest that Steller sea lions in the Kodiak area are currently exploiting a variety of prey species, with as many as ten species being recovered from more than 10% of scats in each collection. Based on the number of species recovered from individual scats analyzed to date, it appears individual sea lions may consume a variety of prey daily. While 68 (23%) of 295 scats analyzed to date contained a single species (15 capelin, 14 arrowtooth flounder [ATF]) and 70 contained only two species, 44 (15%) scats contained remains from five or more prey species.

Sandlance is the most frequently occurring prey recovered from 295 Kodiak scats analyzed to date (Table 1). The frequency of occurrence of prey species varies both regionally (between haulouts) and seasonally (between months or seasons) within the study area. The relative frequency of prey occurrence in Long Island scats shifts between monthly samples, with sandlance, arrowtooth flounder, and salmon ranking first in different collections (Fig 1). Scats collected from Long Island will be used to compare seasonal prey use by sea lions to the quality and availability (species composition, abundance, distribution) of prey within 20 nautical miles of the haulout, as determined by the GAP seasonal acoustic and trawl surveys.
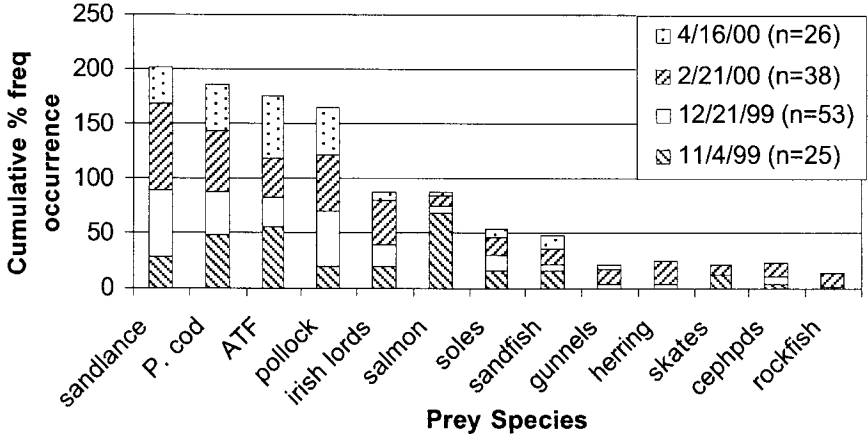
Figure 1. Prey found in >10% of Steller sea lion scats from 4 collections on Long Island between November 1999 and May 2000 (n = 138) (ATF = arrowtooth flounder, cephpds = cephalopods).

Seasonal Diet Trends among the Western Stock of Steller Sea Lions (*Eumetopias jubatus*)

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May 2001

This study is based on scat (fecal) material collected throughout the 1990s on rookeries and haulouts across the range of the U.S. western stock of Steller sea lions. It is the first study to evaluate long-term regional trends in Steller sea lion diet and document long-term diet trends during winter months, a time considered to be important for juvenile survival.

Steller sea lion scats were collected (1990-1998) from 31 rookeries (May-September) and 31 haulouts (December-April) across the U.S. range of the western stock resulting in a sample of 3,762 scats with identifiable prey remains. Fish (bones, scales, otoliths) and cephalopod (beaks) remains were identified using reference collection specimens, and the relative "importance" of each prey species was based on their frequency of occurrence (FO). Frequency of occurrence is calculated by dividing the number of scats in which a prey item occurred by the total number of scats that contained identifiable prey. Frequency of occurrence values combined across years, seasons, and sites depict walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*) as the two dominant prey species, followed by Pacific salmon (Salmonidae) and Pacific cod (*Gadus macrocephalus*). Other primary prey species consistently occurring at frequencies of 5% or greater included arrowtooth flounder (*Atheresthes stomias*), Pacific herring (*Clupea pallasii*), Pacific sandlance (*Ammodytes hexapterus*), Irish lord (*Hemilepidotus* sp.), and cephalopods (squid and octopus). Additional species that occurred among the top three prey items on select islands included: snailfish (Liparididae), rock green-

ling (*Hexagrammos lagocephalus*), kelp greenling *(Hexagrammos decagrammus*), sandfish (*Trichodon trichodon*), rock sole (*Lepidopsetta bilineata*), northern smoothtongue (*Leuroglossus schmidti*), skate (Rajidae), and smelt (Osmeridae).

Sites where the frequency of occurrence of prey species were most similar were identified using principal components and agglomerative hierarchical cluster analysis, resulting in regions of diet similarity. These newly defined diet regions were used to compare regional and seasonal differences in prey. The diet divisions closely parallel those defined as metapopulations based on patterns in population decline by York et al. (1996). To be consistent, the regional names defined by York et al. (1996) are used here.

Chi-square analysis demonstrated significantly ($P = 0.01$) strong seasonal patterns in diet within each of the defined diet regions (island groupings as defined by cluster analysis). Pacific cod FO was significantly larger in winter in every region. Salmon FO was significantly lower during winter in the western Gulf of Alaska through the eastern Aleutian Islands, and higher in winter throughout the central and western Aleutian Islands. In the western Gulf of Alaska, where arrowtooth flounder is most abundant in scats and well represented year-round, its FO was significantly lower in winter. Atka mackerel was significantly lower in the winter in the central and western Aleutians where it is the dominant prey species year-round. Forage fishes (herring and Pacific sand lance) are significantly different between seasons; however, there is no general trend among the regions. Walleye pollock is an important prey year-round in all regions up to the central Aleutian Islands where it is replaced by Atka mackerel. Likewise, cephalopod FO was not significantly different between seasons in any region. Irish lord FO was generally higher in winter than in summer and though rarely occurring during summer and not included in Chi-square analysis, sandfish and snailfish have relatively high occurrences during the winter across all regions.

Based on the prey matrix described here and in earlier studies (Fiscus and Baines 1966, Pitcher 1981, Calkins 1998) Steller sea lions feed throughout the water column in the epipelagic (herring), demersal (arrowtooth flounder), and semi-demersal (pollock, Atka mackerel) zones. While the size of prey consumed undoubtedly varies with the age and sex of the sea lion sampled, the remains of primary prey represented in this study are largely from adult-sized fish (T. Zeppelin, unpubl. data.). The seasonal and regional patterns in prey consumption by Steller sea lions presented in this study, along with known distributions of their primary prey, indicate that Steller sea lions target prey when they are densely schooled in spawning aggregation near shore (over or near the continental shelf) or along oceanographic boundary zones. This is true in summer when collected scats are primarily from adult females, and in winter when scats are presumably from some increased proportion of juveniles and adult males as well as females.

Based on the close parallel of these data with those of metapopulation patterns of decline (York et al. 1996), we suggest that regional diet patterns reflect regional foraging strategies learned at or near the natal rookery site on seasonally dense prey patches characteristic of that area. These data do not reflect Steller sea lion diet during periods when they are foraging at distant pelagic feeding sites, nor do they reflect diet outside the range of the U.S. western stock.

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Status of Demersal and Epibenthic Species in the Kodiak Island and Gulf of Alaska Region

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May 2001

Trophic Changes

The Gulf of Alaska (GOA) marine ecosystem undergoes extreme changes in trophic structure which have become known as regime shifts (Piatt and Anderson 1996, Anderson and Piatt 1999, Anderson 2000). The extent and degree of these changes are documented and will become important in determining future strategies for management of the marine ecosystem. Analysis of over 50 years of small-mesh trawl data is a first step in gaining an appreciation for the rapid and abrupt changes that have occurred in the marine species complex in the last five decades. The data from small-mesh shrimp trawl cruises provides an opportunity to review changes in the composition of forage species and other epi-benthic fish and invertebrates that occurred through time in the GOA from the early 1950s to the present. Yet the state of scientific knowledge is inadequate to explain the mechanisms at work that drive changes in this system. The following report is a compendium of what the data tells us is important in the demersal and epibenthic portion of the GOA marine ecosystem and offers some possible mechanisms that control trophic structure. Unfortunately the data needed to fully understand the dynamics of this abundant system have not been collected consistently in the past and our hope is that we can make a compelling case for collecting this information in the future.

Historically, there is evidence of major abundance changes in the fish/ crustacean community in the western GOA. Fluctuation in Pacific cod availability on a generational scale was reported for coastal Aleutian Native communities. Similarly, landings from the nearshore Shumagin Islands

cod fishery showed definite periods of high and low catches with the fishery peaking in late 1870s. King crab commercial catches in the GOA show two major peaks of landings, one in the mid-1960s and another in 1978-1980. All of the area was closed to fishing in response to low population levels in 1983 and has yet to reopen. By the 1960s there was evidence of high pandalid shrimp abundance in these same areas. One of the highest densities of pandalid shrimp known in the world was to spur the development of a major shrimp fishery. By the late 1970s the shrimp population density had declined radically and was accompanied by a closure of the shrimp fishery and the return of cod to inshore areas. Finally, catches of almost all salmon stocks of Alaskan origin suddenly increased to unprecedented levels in the 1980s. These changes, witnessed over the last century, imply dynamic fluctuations in abundance of commercially fished species. Managers, fishermen, and processors should be aware of these dynamics and their impacts on the ecology and economy.

Indicator Species

In a complex natural ecosystem, it is difficult (if not impossible) to measure the complete set of factors that provides a unified picture of the state of the ecosystem. Indicator species may provide a good sense of the ecosystem's status in some global way. Indicator species can either be indicative of some environmental condition or correlated with concurrent changes in other species (Thorson 1957, Dufrêne and Legendre 1997). Pandalid shrimp occupy a central position in the trophic structure of the northeast Pacific where they constitute the main prey of many species and in turn prey on the zooplankton community. They also occupy all depths of the water column from benthos to near surface. Therefore shrimp are good candidates for indicators of possible environmental change because they integrate changes that occur throughout the water column.

The absence of one or more species that were present previously at the same site is more indicative of environmental effect than absence of a single species. It is clearly necessary to know which species should be found at the site or in the system under prevailing environmental regimes.

In the case of the trawl survey data we analyze species group abundance against environmental variables. Canonical correlation analysis was used to measure the association between abundance of three major species groups (pandalid shrimps, gadids including walleye pollock [*Theragra chalcogramma*] and Pacific cod [*Gadus macrocephalus*]), and pleuronectid flatfish and environmental parameters. These groups together represented more than 90% of catch weights from shrimp surveys. The relation of shrimp and environmental parameters was investigated with correlation using Pearson Product Moment Correlation and Spearman's Rank Correlation taking into account any ties.

The abundance of the three species groups and the set of environment variables were correlated at 95%, as indicated by the first canonical

variate. The correlation was slightly improved (96%) when the species were lagged: shrimp and flatfish at one year, gadids at three years. In the canonical correlation, gadids were almost as important as shrimp, perhaps yielding this species as another indicator. The correlations for shrimp abundance relative to water column temperature are significantly different ($P < 0.001$) from zero, indicating that there is a trend between the variables. The correlation of shrimp catch per unit effort (CPUE) and water column temperature anomaly (GAK250) was $r = -0.71$. The correlation between proportion of shrimp in survey catches and water column temperature anomaly was $r = -0.72$. That is, as water temperature increased, shrimp abundance and the proportion of the catch composed of shrimp tended to decline.

The results reported in this study suggest that shrimp react very quickly to warming climate trends and are a useful indicator of impending changes in the ecosystem that require longer time periods to fully manifest themselves. When the climate reverts to colder temperatures the low shrimp population may not react as quickly due to its low reproductive potential. In the case of near extinctions such as *P. goniurus,* rebuilding may take a considerable amount of time. The present high biomass of fish in the GOA probably precludes rapid rebuilding of shrimp stocks.

It is noteworthy that the GOA and the northeast Pacific are predicted to soon revert to the cold regime. Pandalid shrimp appear to be useful as indicators of a cold to warm regime changes, so it is unlikely that shrimp population changes will reflect this latest cooling trend for some time. However, there is some evidence that Pacific cod have the ability to react quickly to nearshore cooling of the water column. Recent data analysis suggest that cod are redistributing away from nearshore bay habitat in the Kodiak region. Cod are probably good indicators when reverting to cold from warm regime conditions.

In addition to the main indicator species of cod and shrimp, several noncommercial species of different orders were apparently impacted by the environmental changes. Among noncommercial species the most significant change since the early 1970s has been the decline of *Lumpenella longirostris*, long-snout prickleback. Catches of pricklebacks averaged 2 to 3 kg km^{-1} in the early 1970s. However, since 1981 catches have remained at relatively low levels averaging substantially less than 1 kg km^{-1}. All pricklebacks combined averaged 0.9 kg km^{-1} in the period 1972-1999, and have remained stable at 0.3 kg km^{-1} in the 1994-1999 period. *Eumicrotremus orbis*, spiny lumpsucker, has completely disappeared from catches in recent years. In the early 1970s this fish was locally abundant in some of the bays along the Alaska Peninsula. This species, while relatively low in total biomass during the early 1970s, is now almost extinct in the nearshore region of the GOA. Highest catch rates of spiny lumpsucker occurred in 1963 and 1964; no records of this species in this trawl series has been recorded since 1988. Clearly there is some concern that this species may now be functionally extinct in our survey area.

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Killer Whales and Predation on Steller Sea Lions

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The western stock of Steller sea lions has declined from over 140,000 individuals in the 1960s to possibly fewer than 40,000 individuals in 2000. The primary hypotheses put forth by the National Marine Fisheries Service (NMFS) explaining this decline centers around food limitation. One alternative hypothesis that has recently received attention is that the decline or lack of recovery is due to the effects of predation by killer whales or sharks. Reports of large numbers of killer whales surrounding longline and trawl fishing vessels in western Alaska suggest that there are many killer whales in the region.

In order to assess the impact of killer whale predation on this population decline, we need the following information:

1. Number of Steller sea lions.

2. Intrinsic growth rate of Steller sea lion population.

3. Number of killer whales that prey on Steller sea lions.

4. Percentage of the killer whale diet that consists of Steller sea lions and age class of sea lion that is consumed.

Table 1.   Killer whale population estimates for Alaska, British Columbia, and Washington.

Region	Resident	Transient	Total	Reference
Southeast Alaska, B.C., Washington	405 (65%)	219 (35%)	624[a]	Ford and Ellis 1999, Ford et al. 2000, Matkin et al. 1999
PWS/Kenai Fjords	352 (87%)	54 (13%)	406	Matkin et al. 1999
Western Alaska	238 (88%)	33 (12%)	271	Dahlheim 1994, NMFS NMML Database
Total	995 (76%)	306 (24%)	1,301[a]	

[a]Does not include 200+ genetically unique "offshore whales."

There are good data from adult and pup counts on trend sites (haulouts and rookeries) to establish minimum numbers of Steller sea lions both in the eastern population (about 30,000) and in the western population (about 39,000) (Ferrero et al. 2001). A.W. Trites (University of British Columbia, Vancouver, pers. comm.) estimated an intrinsic rate of increase of 4% for Steller sea lions in both the eastern and western populations. However, in the 1980s the population was estimated to have declined at an annual rate of 15%, while in the 1990s the population was estimated to have declined at an annual rate of 5%.

In the eastern North Pacific, from Puget Sound to Kenai Fjords, two ecotypes of killer whales have been identified. These are residents (fish eaters) and transients (marine mammal eaters). They are genetically separable using mtDNA sequencing of the d loop region and nuclear DNA microsatellite techniques. They do not associate or interbreed. It appears that a similar division exists in western Alaska; however, separation of ecotypes in this region has been based only on visual inspection of photographs of individually identifiable animals.

Genetic separation using mtDNA has determined two haplotypes of resident whales, northern resident and southern resident. Although both haplotypes exist in the Prince William Sound/Kenai Fjords region as separate acoustic clans, there is male mediated gene flow between them. Several haplotypes of transient killer whales have been identified in Alaska, including the unique AT1 transient population, the Gulf of Alaska transients, and the West Coast transients. The AT1 transients appear limited to the Prince William Sound/Kenai Fjords region and have declined from 22 whales in 1988 to10 whales in 2001. The Gulf of Alaska transients are of unknown population size but have been photographed from Prince William Sound west to the waters around Kodiak Island. We suspect their

**Table 2.   Marine mammals and predation by West Coast tran-
sient killer whales in British Columbia, 1973-1996.[a]**

Prey species	Kill	Harassment	Total	(% of total)
Harbor seal	72	8	80	(49)
Harbor porpoise	16	0	16	(10)
Steller sea lion	8	12	20	(12)
Dall's porpoise	7	11	18	(11)
California sea lion	4	4	8	(5)
White-sided dolphin	1	3	4	(2)
Gray whale	0	2	2	(1)
Minke whale	0	1	1	(1)
River otter	0	3	3	(1)
Unidentified mammal	14	0	14	(8)

Also observed were 27 attacks on seabirds.
[a]From Ford et al. 1998.

range extends to the west beyond Kodiak. Accurate determination of the size of the transient population in the waters west of Kenai Fjords is necessary to assess the impact of killer whale predation on Steller sea lions.

There are more residents than transients, particularly in the range of the western Steller sea lion (Table 1). In British Columbia and southeastern Alaska, where harbor seal and Steller sea lion populations have been stable or increasing, the percentage of transients is much higher than in Prince William Sound/Kenai Fjords or from preliminary data from western Alaska.

Based on population numbers from Prince William Sound/Kenai Fjords and the preliminary data from western Alaska, we developed a point estimate of 125 marine mammal–eating transient killer whales occupying the range of the western Alaska population of Steller sea lions. The actual figure may range higher or lower than this.

Stomach contents from six Alaska killer whales contained harbor seals (in 5 stomachs), Dall's porpoise (in 2 stomachs), Steller sea lions (in 2 stomachs), and beluga (in 1 stomach). One stomach was empty. The percentage of the killer whale diet that consists of Steller sea lions has been examined during feeding habit studies of killer whales conducted in British Columbia and in Prince William Sound. (Tables 2 and 3) The percentage of the predation and harassment events that involved Steller sea lions were 12% in British Columbia and 19% in Prince William Sound. The actual percentages of predation were undoubtedly lower since a majority of the interactions in British Columbia and all of the interactions in Prince William Sound were harassments where no positive evidence of a kill was observed or collected. In addition, feeding habit studies in Prince William Sound

Table 3.   Marine mammals and predation by AT1 and Gulf of Alaska transients in Prince William Sound, 1988-1996.[a]

Prey species	Kill	Harassment	Total	(% of Total)
Harbor seal	10	12	22	(30)
Dall's porpoise	12	6	18	(23)
Steller sea lion	0	14	14	(19)
Harbor porpoise	2	0	2	(3)
Humpback whale	0	6	6	(8)
Sea otter	0	3	3	(4)
River otter	0	1	1	(1)
Unidentified mammal	7	0	7	(9)
Salmon	0	1	1	(1)

Also observed was 1 attack on seabirds.

[a]From Saulitis et al. 2000.

Table 4.   Killer whale predation estimates for western Alaska.

	High	Low	Best	Historical
Killer whale food needs (kg day^{-1})	72	59	59	59
Total number of killer whales	175	125	125	125
Avg. weight sea lion taken (kg)	160	300	160	160
% Sea lion in killer whale diet	0.20	0.05	0.125	0.125
No. sea lions eaten by killer whales	5,908	449	2,103	2,103
Total number of sea lions	38,000	38,000	38,000	100,000
Total sea lion deaths[a]	7,600	7,600	7,600	20,000
% Deaths due to killer whales	77	6	27	10

[a]Crude death rate estimated at 0.20.

indicate that some transient populations or individuals specialize on particular prey items. The AT1 transient population preyed primarily on harbor seals and Dall's porpoises, while most Steller sea lion harassments in Prince William Sound were by specific individuals in the Gulf of Alaska killer whale transient population. Only stomachs from Gulf of Alaska transients contained Steller sea lion remains. We currently estimate a range of percent sea lion in the killer whale diet of 5-20 with a point estimate of 12.5.

The food requirements for a wild killer whale were determined using estimates of caloric requirements (cal kg^{-1} day^{-1}) from three sources (Baird 1994, Barrett-Lennard et al. 1995, Estes et al. 1998). Their estimates ranged from 50 to 62 cal kg^{-1} day^{-1}. For an average killer whale of 3,500 kg (from captive data) eating pinnipeds with an average caloric value of 3,000 cal gm^{-1} (Perez 1990), this suggests a requirement of 59-72 kg day^{-1} of prey. Estimates were made using several combinations of derived estimates for the predation parameters that simulated high, low, and best guess estimates as well as an estimate of historical predation (Table 4). A more complex model is under construction by author L. Barrett Lennard.

The results of these calculations demonstrate the need for more reliable data, particularly refinement of our estimates of killer whale population size and the percentage of sea lion in the killer whale diet. Also needed is better information on the size of sea lions typically consumed. Until these data are available, we cannot rule out the possibility that killer whale predation may be a factor in the continuing decline and lack of recovery of Steller sea lions. However, it is unlikely that they played a role in the initial decline of the western population of Steller sea lions.

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Pacific Sleeper Shark Predation on Steller Sea Lions

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May 2001

Steller sea lion (*Eumetopias jubatus*) abundance has declined since at least 1965 in Alaska from Prince William Sound westward (Frost et al. 1994, Calkins et al. 1999, Frost et al. 1999). The extent of this decline led the National Marine Fisheries Service (NMFS) to list the Steller sea lion as threatened range-wide under the Endangered Species Act (ESA) in April 1990. The decline has continued for the western stock in Alaska, which was declared endangered in 1997. The eastern stock remains listed as threatened.

The cause of the sea lion decline is unknown. Several hypotheses have been proposed including fisheries competition, environmental change, predation, anthropogenic effects of disturbance/intentional mortality/ harvests, disease, and pollution. One or more of these factors may have caused the decline. The purpose of our study is to determine whether sleeper sharks prey on Steller sea lions and if they do, estimate the predation rate.

Pacific sleeper sharks (*Somniosus pacificus*) and the Atlantic congener, Greenland sleeper sharks (*Somniosus microcephalus*) consume marine mammals. A whole seal was found in a Greenland shark stomach (Bigelow and Schroeder 1948). The genital zone and complete fetus of a female southern right whale dolphin (*Lissodelphis peronii*) was found in the stomach of a Pacific sleeper shark caught in Chilean waters (Crovetto et al. 1992). Portions of at least three harbor seals were found in the stomach of a 3.45 m female sleeper shark caught in Kachemak Bay, Alaska (Bright 1959). Seven of thirty-three sleeper shark stomachs collected in Prince William Sound in August 2000 contained cetacean tissue, and one contained fresh harbor seal tissue (L. Hulbert, unpubl. data). Other biologists working in Alaska waters have reported identifying harbor seal tissue in stomach contents of sleeper sharks (William Bechtol, Alaska Department of Fish and Game, Homer, 2001, pers. comm.; Jim Taggart, USGS Biological Resources Division, Juneau, Alaska, 2000, pers. comm.; and Craig Matkin,

North Gulf Oceanic Society, Homer, Alaska, 2000, pers. comm.). Yang and Page (1998) found no marine mammal tissue in 13 sleeper sharks collected near Kodiak Island, Alaska. It is unknown whether sleeper sharks actively prey on live, free swimming marine mammals, or are scavengers of marine mammal carrion.

Predation of juvenile Steller sea lions is a difficult event to measure, as the potential predators are not commercial species that are routinely observed or sampled. Predation events may be opportunistic, dispersed offshore, difficult to observe, and affected by prey limitation (low numbers of prey for sea lions probably increase foraging time and exposure to predation). Evidence of shark predation on Steller sea lions would identify a source of Steller sea lion mortality.

A three-phase approach will be implemented in this study. The objective of phase I is to determine if sleeper sharks prey on live Steller sea lions. Phase II will estimate the proportion of sleeper sharks preying on Steller sea lions, and phase III will assess the status of the population of Pacific sleeper shark in the regions occupied by Steller sea lions.

Phase I: Sleeper Shark Diet, and Habitat Overlap Studies

Our approach is to capture sleeper sharks around Steller sea lion rookeries during times of pup vulnerability to sleeper shark predation. This study will use stomach content samples, including microsatellite DNA identification of questionable prey items, forensic methods to determine whether the prey was live or scavenged, and fatty acid analysis of sleeper shark tissue from sleeper sharks caught on longlines near Steller sea lion rookeries. Cruise operations are planned for August 2001 and May 2002, two periods of high pup vulnerability. In August pups are vulnerable to predation as they begin entering the water. Another vulnerable period for pups is the weaning period, March to May. Lucas and Stobo (2000) found that most Sable Island harbor seal pup mortality due to sharks occurred during the pupping and weaning period (midsummer). Sampling effort will be focused near three sea lion rookeries in the central Gulf of Alaska: Outer Island, Sugarloaf Island, and Marmot Island. The three largest rookeries in the central Gulf of Alaska are located on these islands and large numbers of sleeper sharks are commonly caught near these islands during the International Pacific Halibut Commission's (IPHC) halibut survey.

The objective of shark habitat utilization tagging studies in 2001-2002 is to determine if the habitat of sleeper sharks and sea lions overlap. Our approach is to measure the vertical migration behavior of sleeper sharks by tagging, and compare it to the diving behavior of Steller sea lions while at sea. Currently, three sleeper sharks are tagged with satellite pop-up tags (tagged in 2000); we plan to tag nine more in 2001. Sharks will be tagged during the cruises described in the previous section.

Phase II: Predation Rate

If Steller sea lion tissue is found in sleeper shark stomachs during the August 2001 cruise, then we plan to expand sampling of sleeper shark stomachs in 2002 to estimate the proportion of sleeper sharks preying on Steller sea lions. Representative samples of sleeper shark stomachs will be requested to be collected during International Pacific Halibut Commission, NMFS, and Alaska Department of Fish and Game longline surveys.

Phase III: Shark Stock Assessment

We plan to begin conducting sleeper shark stock assessments in 2003, probably in cooperation with the Alaska Fisheries Science Center's Resource Ecology and Fisheries Management (REFM) Division scientists.

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