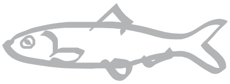
Lowell Wakefield Fisheries Symposium

Forage Fishes in Marine Ecosystems



Proceedings of the
International Symposium on the
Role of Forage Fishes in Marine Ecosystems

Anchorage, Alaska, USA
November 13-16, 1996

Price $40.00

University of Alaska Sea Grant College Program
Report No. 97-01

Elmer E. Rasmuson Library Cataloging-in-Publication Data

International Symposium on the Role of Forage Fishes in Marine Ecosystems (1996 : Anchorage, Alaska)
Forage fishes in marine ecosystems : proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems, November 13-16, 1996, Anchorage, Alaska.

(Lowell Wakefield Fisheries Symposium) (University of Alaska Sea Grant College Program : AK-SG-97-01)

1. Forage fish. 2. Fish populations. I. Alaska Sea Grant College Program. II. Title. III. Series: Lowell Wakefield fisheries symposia series: 14th. IV. Series: Alaska Sea Grant College Program report ; 97-01.

SH327.5157 1996

ISBN 1-56612-049-7

Citation for this volume is: Forage Fishes in Marine Ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No. 97-01. University of Alaska Fairbanks, 1997.

Acknowledgments

This book is the result of work sponsored by the University of Alaska College Program, which is cooperatively supported by the U.S. Department of commerce, NOAA National Sea Grant Office, under grant no. N46RG-0104, project A/75-01; and by the University of Alaska with state funds. The University of Alaska is an affirmative action/equal opportunity institution.

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

Alaska Sea Grant College Program
University of Alaska Fairbanks
P.O. Box 755040
Fairbanks, AK 99775-5040 USA
Fax: 907/474-6285
E-mail: FYPUBS@uaf.edu
http://www.uaf.edu/seagrant

Contents

About the Lowell Wakefield Symposium Series

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

Lowell Wakefield was the founder of the Alaskan king crab industry. He recognized the two major ingredients necessary for the king crab fishery to survive were insuring that a quality product was available to the consumer, and that a viable fishery could be maintained only through sound management practices based on the best scientific data available. Lowell Wakefield and Wakefield Seafoods played important roles in the development and implementation of quality control legislation, in the preparation of fishing regulations for Alaskan waters, and in drafting international agreements for the high seas. Toward the end of his career, Lowell Wakefield joined the faculty of the University of Alaska as an adjunct professor of fisheries where he influenced the early directions of the university's Sea Grant Program. This symposium series is named in honor of Lowell Wakefield and his many contributions to Alaska's fisheries.

About This Symposium

The International Symposium on the Role of Forage Fishes in Marine Ecosystems is the fourteenth Lowell Wakefield symposium. The program concept was suggested by Bob Meyer in mid-1994 when he was with the Anchorage office of the U.S. Minerals Management Service. The meeting was held November 13-16, 1996, in Anchorage, Alaska. The symposium was composed of 75 oral and poster presentations.

The symposium was organized and coordinated by Brenda Baxter, Alaska Sea Grant College Program, with the assistance of the program committee. Committee members are: George Antonelis, U.S. National Marine Fisheries Service; Nic Bax, Division of Fisheries, CSIRO, Australia; Robert Crawford, Sea Fisheries Research Institute, South Africa; Valerie Elliott, U.S. Minerals Management Service; Lew Haldorson, University of Alaska Fairbanks Fisheries Division; Doug Hay, Department of Fisheries and Oceans Canada; Leslie Holland-Bartles, U.S. National Biological Service; George L. Hunt, University California Irvine; Gordon Kruse, Alaska Department of Fish and Game; Daniel Lluch-Belda, Centro de Investigaciones Biologicas del Noroeste, Mexico; Bob Meyer, U.S. Geological

Survey, Biological Research Division; Erlend Moksness, Institute of Marine Research, Norway; A.J. Paul, University of Alaska Fairbanks Institute of Marine Science, committee chair; Stan Senner, *Exxon Valdez* Oil Spill Trustee Council; Rob Stephenson, Department of Fisheries and Oceans Canada; Tokio Wada, National Research Institute of Fisheries Science, Japan; Vidar Wespestad, U.S. National Marine Fisheries Service; and Dave Witherell, North Pacific Fishery Management Council.

Symposium sponsors are: Alaska Department of Fish and Game; *Exxon Valdez* Oil Spill Trustee Council; Institute of Marine Research, Norway; North Pacific Fishery Management Council; U.S. Fish and Wildlife Service; U.S. Minerals Management Service; U.S. National Biological Service; U.S. National Marine Fisheries Service; and Alaska Sea Grant College Program, University of Alaska Fairbanks.

About This Publication

This publication has 56 symposium papers plus a summary of the book. The summary was prepared by Alan M. Springer and Suzann G. Speckman of the University of Alaska Fairbanks Institute of Marine Science. An important part of the summary, and the publication, are the two summary tables. The first table contains references to forage fish species and their role in the marine ecosystem as discussed by the authors in this proceedings book, including page numbers. The second table has references to predators of forage fishes as discussed by the authors in this proceedings book, also with page numbers.

Manuscripts for this book were submitted electronically by authors. The papers have been edited and proofread, but not reviewed for content. The papers by S.M. Ignatyev and S.A. Tsarin were translated from Russian by Ken Coyle, University of Alaska Fairbanks Institute of Marine Science. Editing is by Catherine W. Mecklenburg, Point Stephens Research Associates, Auke Bay, Alaska. Layout, format, and proofing are by Brenda Baxter, Sue Keller, and Carol Kaynor. Cover design is by Susan Gibson and David Brenner.

Forage Fishes in Marine Ecosystems: Introduction to the Symposium

Robert M. Meyer
U.S. Geological Survey, Biological Research Division, Kearneysville, West Virginia

Background

In 1985 the Minerals Management Service hosted a meeting of fisheries scientists to determine if there was sufficient interest and knowledge to justify holding a formal forage fish symposium. Meeting participants agreed that there was sufficient interest and information, so a symposium was organized and held in the fall of 1986 (Allen and Ware 1987). Conference attendees concluded, in part, that in the southeastern Bering Sea the major predator species (walleye pollock) may also be a major prey species, predation is the most important factor controlling abundance of forage fishes, relatively little is known about the biology of forage fishes, and ecosystem models are valuable but need field verification. The appendix contains the results of the conference discussion session and conclusions.

Since the 1986 conference, information from the Department of the Interior-supported Outer Continental Shelf Environmental Assessment Program (OCSEAP) has become widely available as has information from a host of other environmental, marine mammal, fisheries, and pelagic bird assessments and *Exxon Valdez* oil spill research. In addition, computing technology and analytical methodologies have advanced significantly and, similarly, physical oceanographic and ecosystem models have been refined and new ones developed.

As a result, we now have a much better grasp of ecological processes than was heretofore possible. In response to this paradigm shift, several of us in the natural resource management field concluded that the time was ripe for a follow-on forage fish symposium. So, during the spring of 1993, having secured promises of financial support from our parent agencies we contacted Brenda Baxter of Alaska Sea Grant and the 14th symposium in the Wakefield series was launched.

The symposium agenda demonstrates the quality, depth, and breadth of this new research paradigm. No longer are we just counting fishes, reading scales, and trying to guess how many tons of fishes can be harvested next season, we are beginning to address the underlying ecological processes related to forage fishes and the other species and life stages that depend on them.

During the 1986 forage fish conference (Allen and Ware 1987), attendees identified two priority ecological processes—”predator-prey relationships” and “dynamics of coastal fisheries oceanography and the distribution and relative abundance of forage fishes”—that could have been considered in subsequent research and environmental assessments.

During the last half of this century the U.S. Congress has enacted numerous environmental laws, including the Environmental Protection Act, the Marine Mammal Protection Act, the Endangered Species Act, and the Magnuson Fisheries Conservation and Management Act. Ballweber and Jackson in the April 1996 issue of *Fisheries* provided a review of these laws, and Buck (1989/90) reviewed the federal agencies and programs related to fisheries and fish habitat protection.

Environmental and resource management laws and supporting regulations were described by Scalia (1987) and Ballweber and Jackson (1996) as being procedural in nature. Scalia (1987) noted that it is up to the individual agency to determine technical content and adequacy of their assessments. Generally, adequacy relates to insuring that politically sensitive topics are included in environmental assessments. In other words, it is a political process.

Agencies when conducting environmental assessments generally follow the McHarg concept (Bass and Herson 1993) of interdisciplinary ecological planning. This systematic approach involves the overlaying of resource maps (e.g., land use, wildlife, hydrology) to identify areas of potential land use conflict. The overlaying of thematic maps (e.g., a proposed dam and spillway site, location of an anadromous stream, location of an archaeology site) provides a simplistic view of potential conflicts. Although this process can be used to synthesize and portray complex environmental process information, it is seldom used in this manner.

Selection of themes to be included in the analysis is determined by law, regulation, historical precedence, and technical knowledge (agency’s), and through public participation in the scoping process. During the scoping process, an agency seeks input from other agencies and the general public through written requests and through public meetings. Wingate (1996) and the American Fisheries Society’s board of directors hold that it is the role of fisheries scientists to be “fish advocates.”

Delegates to the 1992 World Fisheries Congress concluded that one of the most important issues facing fisheries scientists and managers was public education. The delegates chastised fisheries research and management institutions for failing to translate their findings into understandable concepts and then disseminate the information.

Education of biologists and managers and the general public is critical to the process of bringing issues of concern into the assessment process. A staff biologist can educate her/his managers; they in turn can pass the concern to the appropriate agency during the formal consultation process, or, as a private citizen, you can educate your peers in a political action committee (e.g., conservation organization, industry support group) and have this concern passed on through the scoping process. To illustrate my point, I would like to share the following story told to me by Dr. Gary Hendrix (now retired) concerning the efforts needed to bring an issue to an agency's attention.

Years ago, Dr. Hendrix was collecting peanut worms on a Miami, Florida tidal flat, while, on the breakwater, a lone patrolman sitting in his cruiser watched the collecting process. After watching awhile, the patrolman left his car, walked through the mud to the collecting site, and inquired as to what Dr. Hendrix was doing. To which he replied, "Collecting peanut worms." The patrolman then asked, "Do you eat them?" The doctor said, "No." The patrolman asked, "Can you sell them?" To which the Doctor replied, "No." The patrolman then asked, "Why are you collecting them?" and Dr. Hendrix responded, "To check on their condition." The patrolman pondered the answer for a few moments than responded in a loud voice, "Who cares!" then turned on his heel, tromped back through the mud to his cruiser, and sped away.

This quip was offered because it underscores the conundrum that we as scientists face. Yes, Dr. Hendrix answered each question truthfully, but his answers did not educate the patrolman.

What do you think the patrolman's reaction would have been if he had said that the worms were being collected to help determine the health of the tide flats and the bay? I suggest that the patrolman's reaction would have been different.

In preparation for this meeting, I reviewed several environmental impact statements dealing with proposed marine activities and was surprised to find that no mention was made of forage fishes or ecological processes. Granted, EISs should not be encyclopedic and should focus on important resources, but why were forage fishes and ecological processes not mentioned?

This observation suggests to me that information generated by the research discussed at this symposium is not being translated into forms that are relevant to resource management biologists, i.e., those doing the environmental assessments, or the general public. In short, we are not communicating our findings and the importance of our findings to our fellow biologists and, more important, it means that we are not getting the information to the concerned public.

As you ponder the material presented during the symposium, I encourage you to ask yourself: Who is going to use this information, how is it going to be used, and how are the findings going to be translated into useful information? In addition, as your proposed project advances through your agency's budgeting process, will your efforts to secure support be enhanced if you can show that you are addressing a priority issue identified by management agencies and an international committee of technical experts and that you are coordinating your research with an international team of experts? For resource managers, this symposium is a good forum for expressing and prioritizing your information needs. You may also wish to consider that science, in general, is going through a time of declining budgets. The U.S. Congress has reduced the nondefense research budget to its lowest level in decades. Why?

Is it because taxpayers no longer see the linkage between our research and their quality of life?

I trust that this symposium is but a step in the process of translating research findings into information useable by resource managers and the general public.

References

Allen, J.M., and R.R. Ware. 1987. Forage fishes of the southeastern Bering Sea: Conference proceedings. OCS Study, MMS 87-0017.

Ballweber, J.A., and D.C. Jackson. 1996. Opportunities to emphasize fisheries concerns in federal agency decision-making: An introduction. Fisheries 21(4):14-19

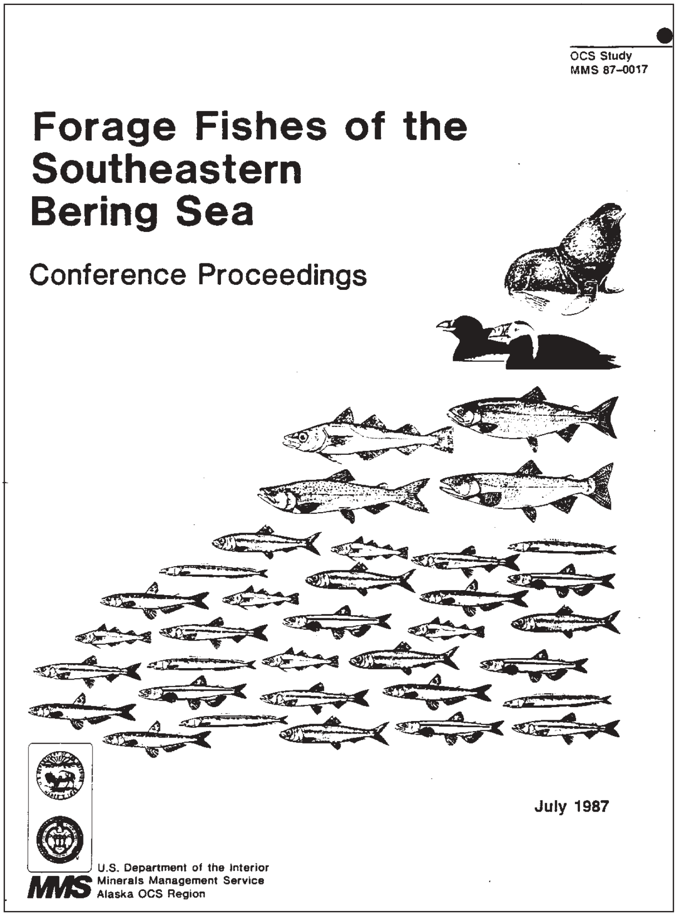
Bass, R.E., and A.I. Herson. 1993. Mastering NEPA: A step-by-step approach. Solano Press, Point Arena, CA.

Buck, E.H. 1989/90. Federal agency programs in living aquatic resources and aquatic habitat protection. Congressional Research Service, Washington, DC.

Scalia, A. 1987. Responsibilities of regulatory agencies under environmental laws. Houston Law Review 24:81-109.

Wingate, P.J. 1996. Advocacy: Using science to save fisheries. Fisheries 21(2):30.

Appendix



OCS Study
MMS 87-0017

Forage Fishes of the Southeastern Bering Sea

Conference Proceedings

July 1987

U.S. Department of the Interior
Minerals Management Service
Alaska OCS Region

Discussion Session from the 1987 Conference

Predator-prey relationships in the southeastern Bering Sea: Ecosystem models are designed to incorporate all available knowledge of an ecosystem into a working model. The model can then be used to examine the causes and magnitudes of population fluctuations, energy flow through the system, and the effects of fishing, industrial, oil and gas, or other activities on species populations. These models attempt to provide structure to our knowledge and show the interrelationship of species and processes in the ecosystem. The models may be altered with the addition of new biological information and, in turn, help to direct biological research. In all cases, the simulation produced requires validation, which is difficult to obtain in open-ocean systems. Ecosystem models may be useful in describing existing information and possible outcomes of present-day processes, but they are often inadequate in precisely forecasting future situations. It is difficult to evaluate the influence of variability, precision, accuracy, and adequacy of the biological parameters on the forecasting potential of such models without dealing with specific species and problems.

In general, conference participants considered the major forage species in the southeastern Bering Sea to include walleye pollock, Pacific herring, rainbow smelt, Pacific sand lance, and capelin, although other species including juvenile salmon and benthic fishes are also important as forage. Major high-level predators in the system include northern fur seals, harbor seals, Steller sea lions, and belukha whales; short-tailed shearwaters, common murres, thick-billed murres, black-legged kittiwakes, and tufted puffins; and fish (e.g., Pacific cod). In the event of a major decrease in the stock size of a specific forage fish species, it was felt that some or most predator species would be able to switch to other forage species; however, the effect of such a change on their biology is unknown without understanding more about the nutritional value of the prey species. The standing stock (total biomass) of predators should not be the only criterion used for judging the importance of predation because seabirds (which have a small standing stock) have greater conversion rates than marine mammals (which have a large standing stock).

Dynamics of coastal fisheries oceanography, and the distribution and relative abundance of forage fish along the north shore of the Alaska Peninsula: The strength of a year class (or cohort) is determined by the degree to which its abundance departs from the average expected abundance of a cohort of a given age. A strong year class is apparent as a peak in the age or size composition of a population that continues to be apparent in successive years (but at successive ages). Year-class strength is affected by physical and biological variables in the environment. Most (about 98%) of the mortality of marine fishes occurs in the egg stage and the life history strategies of the fishes are generally adapted to cope with intense mortality at this period. However, the mortality that occurs during the larval and early juvenile stages is often most crucial in determining the strength of a year class. A change in the mortality rate of 10% or more could have a major effect on a population. Intense mortality on a peak year class could reduce the fishery for several years.

The strength of a year class depends on physical and biological variables. In the southeastern Bering Sea it is thought that predation is the most important factor affecting the year-class strength of forage fishes, although most examples of predation as a controlling force were from studies elsewhere in the world. Predation by marine mammals and seabirds and the effects of commercial fisheries are difficult to separate and are not well documented in Alaska. The effects of predation are primarily local. Other biological parameters are hard to document in the field; for example, the effects of low food supply on forage fishes are uncertain as few starving fish are taken. Many models exist in fisheries oceanography which predict current patterns, temperature regimes, and other variables. Most, however, can only effectively forecast conditions over a short time (e.g., 6 hours for wind direction, 3 days for local transport direction). Variations in extent of ice cover, temperature, and runoff are thought to have little effect on year-class strength, although they could affect the timing of spawning. The best way to forecast year-class strength would be to do prerecruit studies, possibly by examining the stomach contents of predators.

Certain life history traits of pelagic forage fishes make them susceptible to predation or environmental perturbations. Their schooling behavior, which may serve to minimize predation by fishes, may maximize predation by marine mammals. By schooling they are highly and predictively concentrated and hence an easy target for marine mammals, which often follow schools for days. The littoral demersal spawning habits of some species (in particular, Pacific herring) may be affected by unusual beach disturbances, including oil spills. Unfortunately, little is known about the life histories of several species in this region, including capelin, rainbow smelt, and Pacific sand lance.

The ranking of the forage fishes discussed, in terms of their importance as prey, their significance to commercial fisheries, and the knowledge of their life history, is as follows: 1, walleye pollock; 2, Pacific herring; 3, capelin; 4, Pacific sand lance. Squid, although not covered in this conference, may be of equal or greater importance as prey as any of the forage fish species. In terms of sensitivity to environmental perturbation, the forage fish ranking is: 1, Pacific herring; 2, capelin; 3, Pacific sand lance; 4, walleye pollock. Both the Pacific herring and the capelin have specific spawning habitats (intertidal and shallow subtidal zone) that may be sensitive to oil spills and other similar disturbances. The most sensitive area in the region, in terms of potential effects of human activities on forage fishes, is Togiak Bay, an important Pacific herring spawning area. It is followed by Port Moller.

Conclusions

(1) Major forage fishes in the southeastern Bering Sea, in terms of importance, include walleye pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasi*), capelin (*Mallotus villosus*), Pacific sand lance (*Ammodytes hexapterus*), and rainbow smelt (*Osmerus mordax*). Other schooling species are sometimes important (usually either seasonally or locally) or occur incidentally in the north or south.

(2) Most of these forage fishes school, have relatively short lifespans and short maximum lengths, and are locally very abundant. Most species have demersal eggs, but the walleye pollock has pelagic eggs.

Some species spawn in freshwater streams (e.g., salmon, *Oncorhynchus* spp.; rainbow smelt; eulachon, *Thaleichthys pacificus*), some spawn in shallow water along the beach (Pacific herring, capelin, Pacific sand lance), and the walleye pollock spawns in deep water along the continental shelf.

(3) Forage fishes are prey to marine mammals, seabirds, and larger bony fishes in the southeastern Bering Sea. Major marine mammal predators include northern fur seals (*Callorhinus ursinus*), Steller sea lions (*Eumetopias jubatus*), harbor seals (*Phoca vitulina*), and belukha whales (*Delphinapterus leucas*). Major seabird predators include short-tailed shearwaters (*Puffinus tenuirostris*), black-legged kittiwakes (*Rissa tridactyla*), tufted puffins (*Fratercula cirrhata*), common murres (*Uria aalge*), and thick-billed murres (*U. lomvia*). Major bony fish predators include maturing coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*), Pacific cod (*Gadus macrocephalus*), walleye pollock, and Greenland halibut (*Reinhardtius hippoglossoides*). Demersal eggs of littorally spawning forage fishes could be eaten by yellowfin sole (*Pleuronectes* [= *Limanda*] *aspera*), rock sole (*P.* [= *Lepidopsetta*] *bilineata*), longhead dab (*P.* [= *Limanda*] *proboscidea*), and a variety of invertebrates and shorebirds.

(4) Of the major forage fishes, walleye pollock is one of the most important species in the commercial trawl fishery of the southeastern Bering Sea. The Pacific herring is the target of a purse seine and gillnet fishery for sac roe, and an intertidal fishery for eggs-on-kelp. Capelin could be a target of a commercial fishery in the future. Pacific sand lance and rainbow smelt are not commercially important.

(5) The most important forage fishes for further study include Pacific herring, capelin, and Pacific sand lance. The walleye pollock is relatively well studied compared to these species. The most sensitive species to environmental perturbation are Pacific herring and capelin, both of which have relatively specialized intertidal or shallow subtidal spawning sites.

(6) The most important areas, in terms of being crucial to populations of forage fishes in the Bering Sea, include Togiak Bay and Port Moller, with the former being the most important spawning area for Pacific herring.

(7) Predation is thought to be the most important factor controlling the abundance of forage fishes, with physical variation in the environment playing a relatively minor role. Although mortality is highest in the earliest life history stages (eggs and larvae), variability in mortality among early juveniles (prerecruits) probably is most important in determining year-class strength. A strong year class may carry a population for a number of years. A change in the mortality rate of 10% among small juveniles could have a long-lasting effect on the population. Prerecruit surveys provide the most promise in forecasting stock size for the short term.

(8) Although the role of forage fishes in the ecosystem of the southeastern Bering Sea has been considered in existing ecosystem models for the region, relatively little is known about the biology of most forage fish species (other than walleye pollock) found there. Future studies on forage fishes in the eastern Bering Sea should focus on determining abundance, population dynamics, movements, and trophic relationships, and on describing habitat, environmental requirements, early life history, and spawning location.

(9) Ecosystem models could be substantially improved by field collection of additional information on the biology of forage fish species. With proper field validation and verification, the models could more effectively direct future research.

Prey Resource Partitioning Among Several Species of Forage Fishes in Prince William Sound, Alaska

Mark Willette
Alaska Department of Fish and Game, Cordova, Alaska

Molly Sturdevant
National Marine Fisheries Service, Auke Bay Laboratory, Auke Bay, Alaska

Stephen Jewett
University of Alaska Fairbanks, Institute of Marine Science, Fairbanks, Alaska

Abstract

The goal of this study was to examine prey resource partitioning among forage fish species in Prince William Sound, Alaska. Juvenile walleye pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasi*), pink salmon (*Oncorhynchus gorbuscha*), and chum salmon (*O. keta*) were found to be widely distributed in the upper 20 m of the water column in western Prince William Sound during August and September, 1994. The mean lengths of these fish ranged from 91.3 to 146.1 mm FL. Principal components analysis of diet data identified a prey assemblage associated with prey resource partitioning among these four fish species. Two fish species pairs (pollock and herring, and pink and chum salmon) exhibited a relatively high degree of dietary overlap within each species pair and little overlap between species pairs. The percent dietary overlap was 71% for herring and pollock and 74% for pink and chum salmon. Small calanoid copepods, Malacostraca, and *Pseudocalanus* spp. were important prey items in the diets of pollock and herring, whereas fish larvae and juvenile fish were important in the diets of pink and chum salmon. Diet composition and dietary overlap among pollock, herring, chum salmon, and pink salmon also changed significantly over a diel period. Gelatinous prey such as ctenophores, cnidaria, and *Oikopleura* spp. were important prey items in the diets of juvenile chum salmon.

Introduction

This study was designed to estimate the degree of dietary overlap among forage fish species in Prince William Sound, Alaska. Forage fish are an important food resource for several seabird and mammal species in this region (Kuletz 1983, Sanger 1983). Seabird and mammal species that feed on forage fish have exhibited reductions in population size by more than 50% since the early 1970s. Inter-decadal changes in the food habits of several seabird species in the northern Gulf of Alaska have lead to speculation that the ecosystem has shifted from dominance of pelagic schooling species (e.g., herring, capelin, sand lance) to more demersal species (e.g., Pacific cod, walleye pollock). In Prince William Sound, adult pigeon guillemots delivered substantially fewer sand lance to their chicks in 1994 (8%) compared with 1979 (55%) (Kuletz 1983, Oakley and Kuletz 1993). During the same period, the proportion of the diet composed of gadids increased from approximately 7% (1979-1981) to about 30% in 1994 (Kuletz 1983, Oakley and Kuletz 1993).

Marine ecosystems are characterized by shifts in the dominance of pelagic schooling fish. Dominance shifts between sardine and anchovy have been observed off California (Sharp 1992, Cury et al. 1995), Peru (Pauly and Tsukayama 1987), Japan (Belyaev and Shatilina 1995), and South Africa (Lluch-Belda et al. 1989). In the western English Channel, pilchard replaced herring in the 1930s, and the change was reversed in the 1970s (Cushing 1975). In the Bering Sea, a considerable increase in walleye pollock abundance coincided with a decline in the herring population (Wespestad and Fried 1983). The causes of these dominance shifts is not well understood. In some cases, they are associated with broader changes in ocean temperature and the plankton community (Cushing 1975, Hollowed and Wooster 1992). In Prince William Sound, an outbreak of viral hemorrhagic septicemia virus and later *Ichthyophonus hoferi* coincided with a collapse of the herring population (Marty et al. 1995). During the two years prior to the decline of herring in Prince William Sound, population size was the highest observed since the early 1980s (Donaldson et al. 1995). Mean size-at-age during the autumn prior to the decline was the lowest observed in recent years (Donaldson et al. 1995). These data suggest that competition for food may have been a factor in the decline of the Prince William Sound herring population.

Competition often involves use of preferred food resources or habitats. Prey selection is determined by the relative profitabilities of potential prey (Charnov 1976, Mittelbach 1981). Profitability is a function of the energy content of prey and the time (energy) required to capture and ingest prey. Similarly, habitat choice is determined by the relative profitability associated with each habitat use; although excessive predation risk (Lima and Dill 1990, Milinski 1993) or the presence of a competitor (Fausch and White 1986, Persson 1986, Freeman and Stouder 1989, Klemetsen et al. 1989, Taylor 1991) may cause selection of a less profitable habitat. Selection of suboptimal habitats often leads to reduced growth (Sogard 1994). The degree of dietary overlap among potential competitors must be determined as a first step in evaluating competitive interactions among species.

Methods

A stratified-random sampling design was employed to estimate dietary overlap among several forage fish species. Passages and bays were considered different strata and site was used as the sample unit in the analysis. Samples of forage fish were collected at 31 sites in western Prince William Sound between August 27 and September 9, 1994, using an anchovy seine (240 m long × 20 m deep, 1.5-cm stretch mesh) deployed from a chartered purse seine vessel (Figure 1). At least two net sets were made at each site. Sampling was generally conducted between 0600 hours and noon and between 1800 and midnight. A randomly selected sample of 10-15 individuals (whole fish) were preserved in 10% buffered formaldehyde solution from each species at each site. Quantitative zooplankton samples were collected at each site to evaluate prey size selection. Replicate zooplankton samples were collected with a ring-net (0.5-m diameter, 102-micron mesh) towed vertically from 25 m depth to the surface. Replicate samples were combined in a single sample bottle and preserved in 10% buffered formaldehyde solution.

In the laboratory, stomach content analyses were conducted after a minimum of 30 days to stabilize shrinkage. Whole fish were blotted dry, weighed to the nearest 0.01 g and measured (fork length) to the nearest 0.5 mm. Fish showing evidence of regurgitation were not analyzed. The foregut was excised, blotted dry, and weighed full to an accuracy of 1.0 mg. The contents were then removed, and the stomach lining was blotted and weighed again. Total stomach contents wet weight was estimated by subtraction. Prey items in the gut were teased apart and identified to the lowest possible taxonomic level and enumerated. Standard subsampling techniques were employed when stomach contents were too large to count every prey (Kask and Sibert 1976). Total biomass in each taxonomic group was estimated by the product of average body blotted-dry weight and abundance. Literature values for average blotted-dry wet weight of each species or developmental stage were used when available (Coyle et al. 1990). When literature values were not available, unpublished data were used (Pers. comm., R.T. Cooney, University of Alaska Fairbanks, Fairbanks, Alaska 99775) or at least 50 intact specimens were taken from stomach or zooplankton samples and weighed to the nearest 0.1 mg.

Zooplankton samples were first scanned whole to enumerate large or rare organisms. A Hansen-stempel pipette (1-, 5-, or 10-ml capacity) or Folsom plankton splitter were used to collect random subsamples. Each sample was diluted to achieve a total count of 300 organisms in

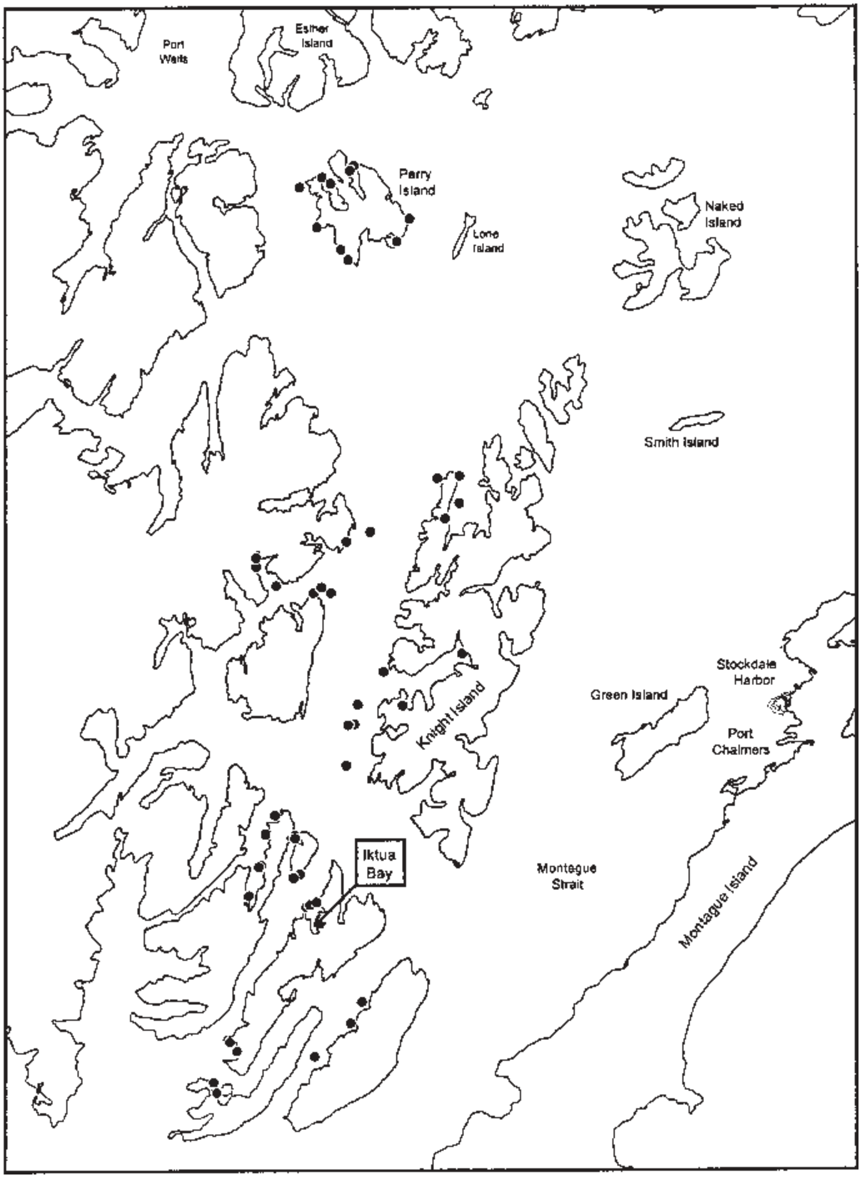


Figure 1. Study sites sampled in western Prince William Sound, August-September 1994. A diel study was conducted at Iktua Bay.

each subsample. Zooplankton were identified to the lowest practical taxonomic level and enumerated. Total abundance of organisms in each sample was estimated by the product of the subsample count and the subsample fraction. Total biomass in each taxonomic group was estimated by the product of average body blotted-dry weight and abundance. For pollock, herring, pink salmon, and chum salmon, chi-square analysis was used to evaluate selection of prey in three prey body-weight groups (<1 mg, 1-2.7 mg, >2.7 mg). The frequency of occurrence of prey in fish diets and ring net samples for all sites combined was calculated for the three prey body-weight groups. The body-weight frequency of zooplankton at all sites combined was used to determine appropriate body-weight groups.

A summary of the diet of pollock, herring, pink salmon, and chum salmon was prepared by summing percent total prey biomass, frequency of occurrence, and abundance over broad taxonomic groups (e.g., amphipods, euphausiids, larvaceans). Prey taxa that composed less than 1% of total biomass were pooled into a general “other” prey category. Plots of the index of relative importance were then constructed (Pinkus et al. 1971).

Principal components analysis was used to describe common modes of variability in the diet composition of all fish species combined (Gauch 1982). The dependent variables in the analysis were the mean proportion of total stomach biomass in each prey taxonomic group for each fish species and site. Data were only used for fish species with a minimum sample size of five at each site. The principal components were derived from the covariance matrix of the prey diet data. The sampling errors associated with each principal component were estimated as described by North et al. (1982) assuming independence among sites.

Analyses of variance (ANOVA) were conducted to test for differences in diet composition among fish species. Separate ANOVAs were conducted using the scores from each significant principal component as the dependent variable. Pairwise comparisons were used to test for differences in diet composition between specific fish species. Hierarchical agglomerative cluster analysis (Euclidean metric, complete linkage) was used to classify fish species by diet composition and to indicate the degree of similarity or dissimilarity between species (Gauch 1982).

An index of percent dietary overlap (P_{jk}) was used to describe the degree of diet similarity between pairs of fish species:

$$P_{jk} = \left[\sum_i \min(P_{ij}, P_{ik}) \right] \times 100 \qquad (1)$$

where p_{ij} is the proportion of total biomass in prey taxon i in fish species j and p_{ik} is the proportion of total biomass in prey taxon i in fish species k (Krebs 1989). This index ranges from 0 to 100, representing no and complete dietary overlap, respectively. Site was used as the sample unit in the analysis.

Diel changes in diet composition and dietary overlap were evaluated from fish samples collected at Iktua Bay (shallow bay habitat) in southwest Prince William Sound. Samples were collected every 4 hours over a 24-hour period and processed as previously described. Principal components analysis was used to describe common modes of variability in the diet composition of all fish species combined as previously described (Gauch 1982). ANOVA was used to test for diel changes in dietary overlap among fish species. Separate ANOVAs were conducted using the scores from each significant principal component as the dependent variable. A factorial model (with interaction) was used with fish species and time of day as class variables.

Results

The percent frequency of occurrence in net sets was greatest for pollock, herring, pink salmon, and chum salmon (Table 1). Mean lengths for all species ranged from 85.8 to 212.5 mm. The percent frequency of co-occurrence was also greatest for pollock, herring, pink salmon, and chum salmon (Table 2).

Fish (mostly larvae) were significant components of the diets of pink and chum salmon (Figure 2). The diets of pink and chum salmon differed in the amounts of large copepods and Malacostraca consumed. Gelatinous prey (larvaceans, ctenophores, and cnidaria) composed 12.7% of the diet of chum salmon by weight (Figure 2). Small copepods, large copepods, and Malacostraca were important in the diets of pollock and herring (Figure 2). However, the amounts of small and large copepods consumed were somewhat different between pollock and herring.

Principal components analysis of the fish diet composition data indicated two significant ($\alpha = 0.05$) principal components (Figure 3). The first and second principal components described 17% and 13% of the total variance, respectively. Results from ANOVA indicated that the scores from the first principal component were significantly different among fish species ($P < 0.0001$), but the scores from the second principal component were not different ($P = 0.4854$) among fish species.

The eigenvectors from the first principal component revealed two prey assemblages (Table 3). Mean scores were positive and significantly different from zero for pollock (0.46, $P = 0.0428$) and herring (0.32, $P = 0.0872$), and negative and significantly different from zero for Pacific tomcod (–1.49, $P = 0.0170$), pink salmon (–1.10, $P = 0.0058$), and chum salmon (–0.45, $P = 0.0346$). Pairwise comparisons indicated that the mean scores were not significantly different between pollock and herring ($P = 0.6262$) and between tomcod, pink salmon, and chum salmon ($P > 0.1000$). In addition, mean scores for pollock and herring were significantly different ($P < 0.0010$) from mean scores for tomcod, pink

Table 1. Mean catch per net set and mean length of the dominant fish species captured in western Prince William Sound, August-September 1994.

	Frequency of occurrence (%)	Mean catch	Coefficient of variation	Mean length (mm, FL)
Pacific herring (*Clupea pallasi*)	77	476.1	2.9	118.2
Walleye pollock (*Theragra chalcogramma*)	70	761.5	3.9	91.3
Chum salmon (*Oncorhynchus keta*)	47	5.8	2.1	146.1
Pink salmon (*Oncorhynchus gorbuscha*)	34	2.5	3.5	141.5
Pacific tomcod (*Microgadus proximus*)	13	6.1	7.8	106.2
Sockeye salmon (*Oncorhynchus nerka*)	6	0.1	5.5	212.5
Pacific cod (*Gadus macrocephalus*)	5	3.0	5.6	88.5
Capelin (*Mallotus villosus*)	4	0.1	5.0	78.3
Pacific sand lance (*Ammodytes hexapterus*)	4	14.3	8.3	85.8

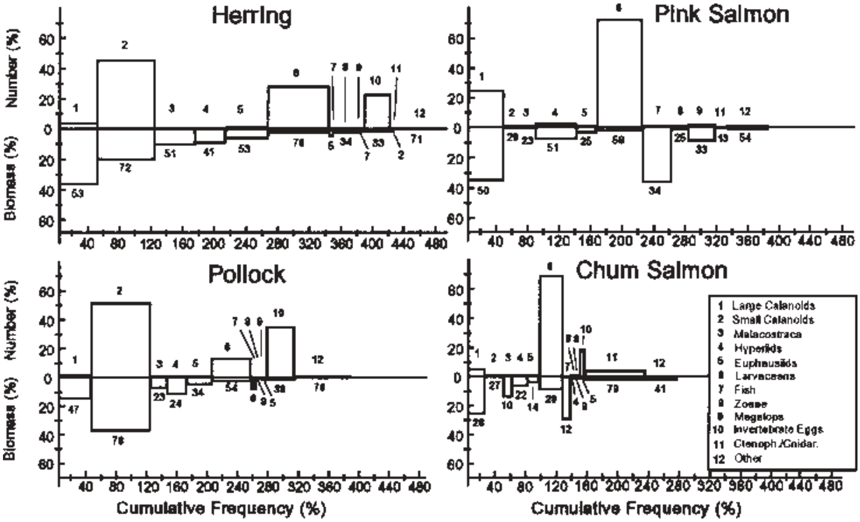


Figure 2. Prey composition of juvenile forage species in August-September 1994 in Prince William Sound. Prey taxa listed in key are shown in order from left to right along x-axis and index numbers for each prey taxa are indicated above each bar. Height of bar above the line indicates percent number; height of bar below the line indicates percent frequency of occurrence (frequency indicated below each bar).

Table 2. Percent frequency of co-occurrence for fish species pairs captured in western Prince William Sound, August-September 1994.

	Walleye pollock	Chum salmon	Pink salmon	Pacific tomcod	Sockeye salmon	Pacific cod	Capelin	Pacific sand lance
Pacific herring	57	36	27	11	4	4	4	4
Walleye pollock		33	23	10	0	7	4	4
Chum salmon			27	4	6	4	1	1
Pink salmon				3	3	4	0	0
Pacific tomcod					0	3	1	1
Sockeye salmon						0	0	0
Pacific cod							0	0
Capelin								0

Net set was used as the sample unit in the analysis.

Table 3. Prey species and associated eigenvectors for the first principal component describing diet composition of the dominant fish species captured in western Prince William Sound, August-September 1994.

Taxonomic group	Eigenvector	Taxonomic group	Eigenvector
Fish larvae	–0.832	Small copepod	0.329
Juvenile fish	–0.124	Malacostraca	0.277
Mallotus villosus	–0.055	*Pseudocalanus* sp.	0.250
Oikopleura sp.	–0.053	Large copepod	0.166
Barnacle cirri	–0.034	*Pseudocalanus* - AF[a]	0.045
Parathemisto sp.	–0.026	*Thysannoessa* sp.	0.036
Cyphocaris sp.	–0.025	Invertebrate egg	0.035
Epilabidocera longipedata	–0.021	*Calanus marshallae*	0.025
Ctenophore (<2 mm)	–0.020	*Hyperia* sp.	0.021

[a] adult female

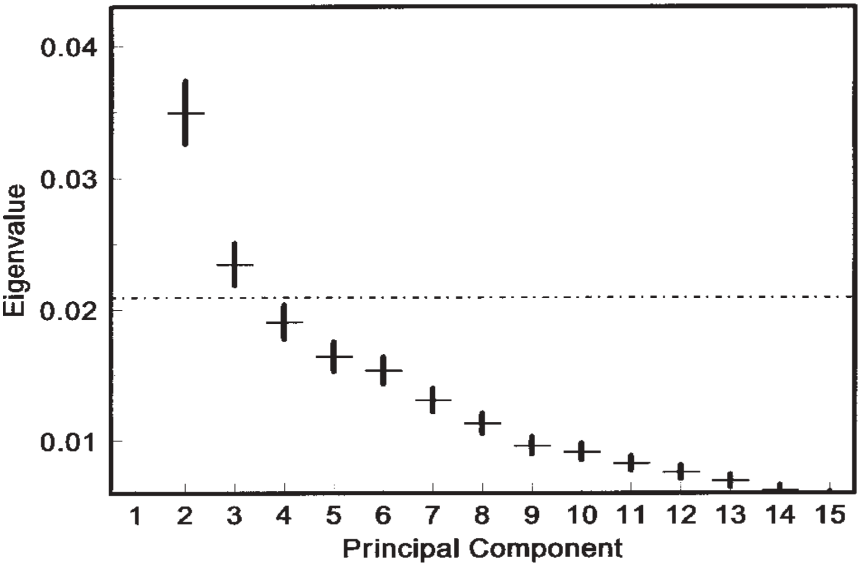


Figure 3. Eigenvalues obtained from a principal components analysis of fish diet composition data from western Prince William Sound, August-September 1994. Bars represent the 95% confidence intervals on the eigenvalues. The dashed line separates the statistically significant eigenvalues.

salmon, and chum salmon. Results from a cluster analysis indicated the greatest diet similarity between herring and pollock, pink and chum salmon, and sand lance and capelin (Figure 4). Percent dietary overlap was 71% between herring and pollock and 74% between pink and chum salmon (Table 4). Percent dietary overlap was greater at sympatric than allopatric sites for all species pairs except pink salmon and tomcod and chum salmon and tomcod (Table 4).

Analysis of prey size selection indicated a relatively high frequency of occurrence of zooplankton and fish prey less than 1 mg wet weight (Figure 5). Chi-square tests indicated significant differences ($P = 0.0010$) between the size frequency distributions of zooplankton and the prey of pollock, herring, pink salmon, and chum salmon. Examination of the percent difference in these frequencies between zooplankton and fish prey indicated that pollock, herring, pink salmon, and chum salmon preferred relatively large prey organisms and avoided smaller prey (Figure 6).

Results from a diel feeding study indicated a pattern of dietary overlap among pollock, herring, chum salmon, and pink salmon similar to that previously described. Principal components analysis of the fish diet composition data from the diel study indicated one significant ($\alpha = 0.05$) principal component describing 15% of the total variance. The eigenvectors were positive for small copepods (0.65), *Pseudocalanus* sp. (0.42), and *Oikopleura* sp. (0.30), and negative for euphausiids (–0.29), fish larvae (–0.27), and gelatinous prey (–0.16). Results from ANOVA indicated that the scores from the first principal component were significantly different among fish species ($P < 0.0001$) and time periods ($P = 0.0214$). The interaction term in the model was marginally significant at $P = 0.0947$. Pairwise comparisons indicated that the mean scores for pink salmon and chum salmon were significantly different ($P < 0.0001$) from herring and pollock. Changes in the mean scores over the diel study indicated that the diets of herring and pink salmon were strongly associated with the prey assemblage described by the first principal component in the afternoon (Figure 7A). This association decreased at night (2200-0700 hours). Stomach fullness was also greatest in the afternoon and decreased at night (Figure 7B).

Discussion

The relatively high dietary overlap between pollock and herring and between pink and chum salmon found in the present study indicates that competition for food resources may occur within these species pairs when food abundance is low or fish population density is high. However, further analyses of dietary overlap are needed to establish the level of intra- and interannual variation in dietary overlap within each of these species pairs. In the present study, small copepods and *Pseudocalanus* spp. were important prey items in the diets of pollock

Table 4. Percent dietary overlap between dominant fish species captured in western Prince William Sound, August-September 1994. For each fish species pair, the first value is for sympatric sites, and the second value is for allopatric sites.

	Walleye pollock	Pink salmon	Chum salmon	Pacific tomcod
Pacific herring	71	36	44	57
	27	24	26	32
Walleye pollock		20	40	54
		12	08	19
Pink salmon			74	32
			—	55
Chum salmon				35
				55

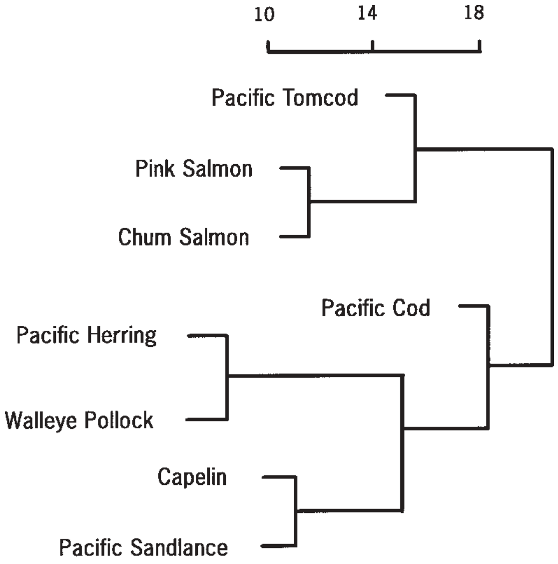


Figure 4. Dendrograms obtained from a cluster analysis of fish diet composition data from western Prince William Sound, August-September 1994. The scale indicates Euclidean distances between fish species pairs.

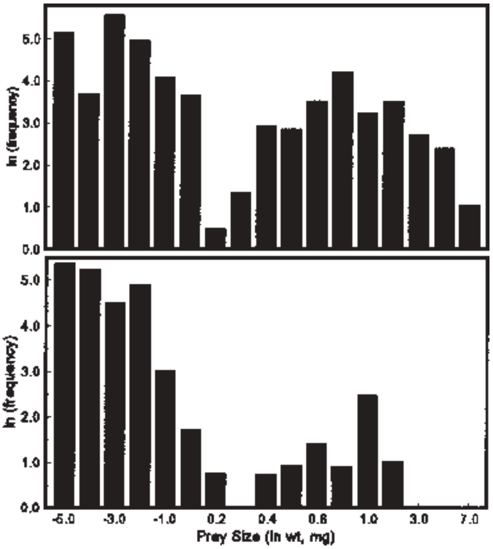


Figure 5. Size frequency distribution of (top) prey of walleye pollock, Pacific herring, pink salmon, and chum salmon combined, and (bottom) size frequency distribution of zooplankton in western Prince William Sound, August-September 1994.

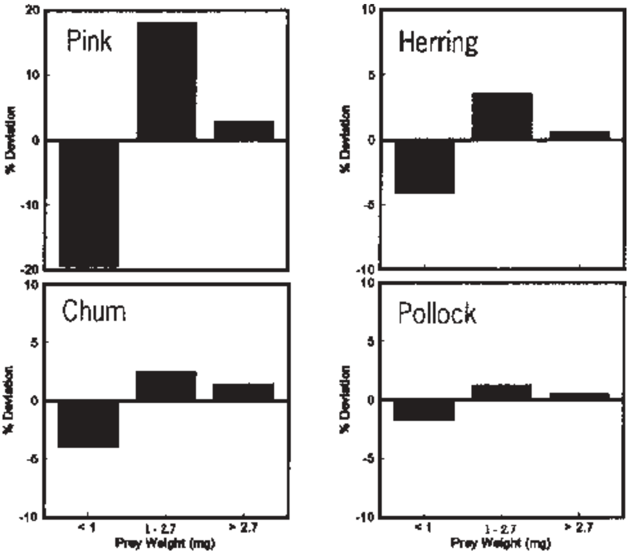


Figure 6. Percent difference between the frequency of occurrence of zooplankton and of prey in three size groups for walleye pollock, Pacific herring, pink salmon, and chum salmon in western Prince William Sound, August-September 1994.

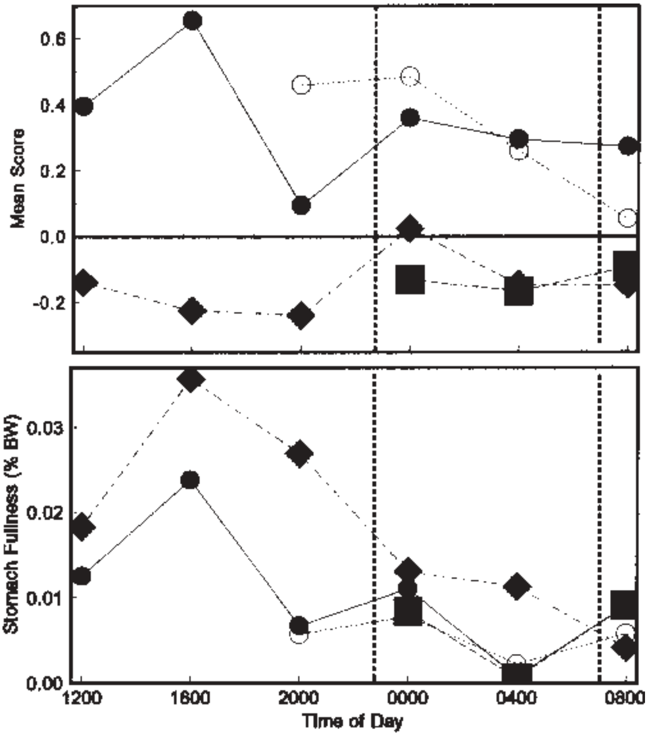


Figure 7. Diel changes in (top) diet composition as described by the first principal component scores and (bottom) stomach fullness for walleye pollock (open circle), Pacific herring (solid circle), pink salmon (diamond), and chum salmon (square) at Iktua Bay in western Prince William Sound, September 1994. Vertical lines indicate times of sunset and sunrise.

and herring. It is likely that many of the organisms in the “small calanoid copepod” category were *Pseudocalanus* spp. that were too digested to identify. Several studies from various parts of the world have documented the apparent preference for *Pseudocalanus* spp. among pollock (Kamba 1977, Cooney et al. 1980, Lee 1985, Grover 1990, Grover 1991) and herring (Hinrichs 1985, Evtyukhova et al. 1986).

Similarity between the diets of pink and chum salmon has been documented at other life stages. During the fry stage (<60 mm), both species have been found to consume harpacticoid copepods, calanoid copepods, amphipods, euphausiids, chaetognaths, and fish larvae (Andriyashev 1970, Okada and Taniguchi 1971, Healey 1980, Shershnev et al. 1982, Simenstad and Salo 1982). Despite these similarities, chum salmon fry tend to feed more heavily on epibenthic species such as harpacticoid copepods and gammarid amphipods (Simenstad and Salo 1982). Pearcy et al. (1988) estimated a 38% dietary overlap between immature pink and chum salmon in the North Pacific.

In the present study, gelatinous zooplankton were a significant component of the diet of juvenile chum salmon. Healey (1991) documented consumption of gelatinous zooplankton among juvenile chum salmon in Hecate Strait; however, in the Bering Sea, fish larvae (*Mallotus, Ammodytes*, and *Clupea*) and euphausiids were the principal prey of juvenile chum salmon (Hartt et al. 1970). Pearcy et al. (1988) also documented a high occurrence of gelatinous zooplankton in the diet of immature chum salmon in the North Pacific. Isotopic studies later supported the conclusion that gelatinous zooplankton compose a large portion of the diet of immature chum salmon in the North Pacific (Welch and Parsons 1993). Further studies are needed to determine the importance of this component of the plankton in the diet of juvenile chum salmon.

In the present study, diel changes in diet composition and overlap were observed. Diel changes in trophic interactions between planktivorous fish and their prey have been widely documented in fresh water (Hall et al. 1979, Bohl 1980, Forsyth et al. 1990, Kwak et al. 1992, Johnson and Dropkin 1993, Johnson and Dropkin 1995) but much less so in the ocean (Robb 1981). Such changes are often associated with vertical migrations of predators or prey and appear to be largely driven by light level and its effect on prey visibility and predation risk (Clark and Levy 1988). Patterns of diel feeding may be determined by the relative densities of prey and predators at different times in various habitats (Clark and Levy 1988). Frost and Bollens (1992) observed highly variable diel vertical migratory behavior among *Pseudocalanus newmani* in a Pacific coast embayment. In the present study, an apparent increase in dietary overlap at night may have resulted from our inability to distinguish prey species that were highly digested. However, it is also possible that filter feeding may have continued at night. This feeding strategy would likely lead to greater dietary overlap. Laboratory studies have documented that juvenile herring filter feed at night (Batty et al. 1986).

Acknowledgments

We thank the staff of the Alaska Department of Fish and Game, National Marine Fisheries Service, University of Alaska Fairbanks, and the charter vessel crews who assisted in the collection and processing of samples for this study. Their hard work and dedication under difficult work schedules made this study possible. We also thank the Prince William Sound Aquaculture Corporation for kindly providing logistical support for our field sampling program.

References

Andriyashev, A.P. 1970. Feeding of pacific salmon juveniles in the Sea of Okhotsk. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 78:105-115. (Transl. from Russian: Fish. Res. Board Can. Transl. Ser. 2441.)

Batty, R.S., J.H.S. Blaxter, and D.A. Libby. 1986. Herring (*Clupea harengus*) filter feeding in the dark. Mar. Biol. 91(3):371-375.

Belyaev, V.A., and T.A. Shatilina. 1995. Variations in abundance of pelagic fishes in the Kuroshio Zone as related to climatic changes. In: R.J. Beamish (ed.), Climate change and northern fish populations. Can. Spec. Publ. Fish. Aquat. Sci. 121:553-559.

Bohl, E. 1980. Diel pattern of pelagic distribution and feeding in planktivorous fish. Oceologia 44:368-375.

Charnov, E. 1976. Optimal foraging: Attack strategy of a mantid. Am. Nat. 110:141-151.

Clark, C.W., and D.A. Levy. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. Am. Nat. 131(2):271-290.

Cooney, R.T., M.E. Clarke, and P. Walline. 1980. Food dependencies for larval, post-larval, and juvenile walleye pollock, *Theragra chalcogramma*, in the southern Bering Sea. In: PROBES: Processes and resources of the Bering Sea shelf. Prog. Rep. vol. 2, pp. 169-189. Inst. Mar. Sci., Univ. Alaska, Fairbanks, Alaska 99775.

Coyle, K.O., A.J. Paul, and D.A. Ziemann. 1990. Copepod populations during the spring bloom in an Alaskan subarctic embayment. J. Plankton Res. 12(4):759-797.

Cury, P., C. Roy, R. Mendelssohn, A. Bakun, D.M. Husby, and R.H. Parrish. 1995. Moderate is better: Exploring nonlinear climatic effects on the Californian northern anchovy (*Engraulis mordax*). In: R.J. Beamish (ed.), Climate change and northern fish populations. Can. Spec. Publ. Fish. Aquat. Sci. 121:417-424.

Cushing, D.H. 1975. Marine ecology and fisheries. Cambridge University Press, Cambridge, England.

Donaldson, W., S. Morstad, D. Sharp, J. Wilcock, and S. Sharr. 1995. Prince William Sound management area 1993 annual finfish management report. Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Central Region, 333 Raspberry Rd., Anchorage, Alaska 99518.

Evtyukhova, B.K., E.A. Ojaveer, A.K. Naglis, T.L. Raid, R.Y. Line, M.V. Kaleis, E.A. Yula, and A.Y. Lumberg. 1986. Some peculiarities in herring stock dynamics, structure and state in the northeastern Baltic and the Gulf of Finland in connection with environmental factors. Fisheries Research by the GDR and the USSR in the Baltic Sea 24(2):12-15.

Fausch, K.D., and R.J. White. 1986. Competition among juveniles of coho salmon, brook trout, and brown trout in a laboratory stream, and implications for Great Lakes tributaries. Trans. Am. Fish. Soc. 115:363-381.

Forsyth, D.J., M.R. James, and M. Cryer. 1990. Alteration of seasonal and diel patterns in vertical migration of zooplankton by *Anabaena* and planktivorous fish. Arch. Hydrobiol. 117(4):385-404.

Freeman, M.C., and D.J. Stouder. 1989. Intraspecific interactions influence size specific depth distribution in *Cottus bairdi*. Environ. Biol. Fishes 24:231-236

Frost, B.W., and S.M. Bollens. 1992. Variability of diel vertical migration in the marine planktonic copepod *Pseudocalanus newmani* in relation to its predators. Can. J. Fish. Aquat. Sci. 49:1137-1141.

Gauch, H.G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, Massachusetts.

Grover, J.J. 1990. Feeding ecology of late-larval and early-juvenile walleye pollock, *Theragra chalcogramma*, from the Gulf of Alaska in 1987. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 88:463-470.

Grover, J.J. 1991. Trophic relationship of age-0 and age-1 walleye pollock *Theragra chalcogramma* collected together in the eastern Bering Sea. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 89:719-722.

Hall, D.J., E.E. Werner, J.F. Gilliam, G.G. Mittelbach, D. Howard, and C.G. Doner. 1979. Diel foraging behavior and prey selection in the golden shiner (*Notemigonus crysoleucas*). J. Fish. Res. Board Can. 36:1029-1039.

Hartt, A.C., M.B. Dell, and L.S. Smith. 1970. Tagging and sampling. In: Investigations by the United States for the International North Pacific Fisheries Commission: 1968. Int. North Pac. Fish. Comm. Annu. Rep. 1968:68-79.

Healey, M.C. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia. In: W.J. McNeil and D.C. Himsworth (eds.), Salmon ecosystems of the North Pacific. Oregon State University Press, Corvallis, Oregon, pp. 203-229.

Healey, M.C. 1991. Diets and feeding rates of juvenile pink, chum, and sockeye salmon in Hecate Strait, British Columbia. Trans. Am. Fish. Soc. 120:303-318.

Hinrichs, R. 1985. Quantity and composition of food of herring and sprat in the Baltic Sea from 1980-1981. Fisch. Forsch. 23(1):70-81.

Hollowed, A.B., and W.S. Wooster. 1992. Variability of winter ocean conditions and strong year classes of northeast Pacific groundfish. In: R.R. Dickson, P. Maelkki, G. Radach, R. Saetre, and M.P. Sissenwine (eds.), Hydrobiological variability in the ICES area, 1980-1989. ICES Mar. Sci. Symp. 195:433-444.

Johnson, J.H., and D.S. Dropkin. 1993. Diel variation in diet composition of a riverine fish community. Hydrobiologia 271:149-158.

Johnson, J.H., and D.S. Dropkin. 1995. Diel feeding chronology of six fish species in the Juniata River, Pennsylvania. J. Freshwater Ecol. 10(1):11-18.

Kamba, M. 1977. Feeding habits and vertical distribution of walleye pollock, *Theragra chalcogramma*, in early life stage in Uchiura Bay, Hokkaido. Res. Inst. North Pac. Fish., Hokkaido Univ., Spec. Vol. pp. 175-197.

Kask, B., and J. Sibert. 1976. A laboratory method for the analysis of fish stomach contents. In: C.A. Simenstad and S.J. Lipovosky (eds.), Fish food habit studies. Washington Sea Grant Program, University of Washington, Seattle, Washington, pp. 193.

Klemetsen, A., P.A. Amundsen, H. Muladal, S. Rubach, and J.I. Solbakken. 1989. Habitat shifts in a dense, resident Arctic charr *Salvelinus alpinus* population. Physiol. Ecol. Jpn. 1:187-200.

Krebs, C.J. 1989. Ecological methodology. Harper and Row, New York.

Kuletz, K.J. 1983. Mechanisms and consequences of foraging behavior in a population of breeding pigeon guillemots. M.S. thesis, University of California, Irvine. 79 pp.

Kwak, T.J., M.J. Wiley, L.L. Osborne, R.W. Larimore. 1992. Application of diel feeding chronology to habitat suitability analysis of warmwater stream fishes. Can. J. Fish. Aquat. Sci. 49:1417-1430.

Lee, S.S. 1985. A comparison of the food habits of juvenile Pacific cod and walleye pollock in the southeast Bering Sea. M.S. thesis, University of Alaska Fairbanks. 130 pp.

Lima, S.L., and L.M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Can. J. Zool. 68:619-640.

Lluch-Belda, D., R.J.M. Crawford, T. Kawasaki, A.D. MacCall, R.H. Parrish, R.A. Schwartzlose, and P.E. Smith. 1989. World-wide fluctuations of sardine and anchovy stocks: The regime problem. S. Afr. J. Mar. Sci. 8:195-205.

Marty, G.D., E.F. Freiberg, T.R. Meyers, J. Wilcock, C.R. Davis, T.B. Farver, and D.E. Hinton. 1995. *Ichtyophonus hoferi*, viral hemorrhagic septicemia virus, and other causes of morbidity in Pacific herring spawning in Prince William Sound in 1994, *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 94320S), *Exxon Valdez* Oil Spill Trustee Council, Restoration Office, 645 G Street, Suite 401, Anchorage, Alaska 99501-3451.

Milinski, M. 1993. Predation risk and feeding behaviour. In: T.J. Pitcher (ed.), Behaviour of teleost fishes. Chapman and Hall, London, pp. 285-305.

Mittelbach, G.G. 1981. Foraging efficiency and body size: A study of optimal diet and habitat use by bluegills. Ecology 62:1370-1386.

North, G.R., T.L. Bell, R.F. Cahalan, and F.J. Moeng. 1982. Sampling errors in the estimation of empirical orthogonal functions. Mon. Wea. Rev. 110:699-706.

Oakley, K.L., and K.J. Kuletz. 1993. Population, reproduction and foraging ecology of pigeon guillemots at Naked Island, Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill. *Exxon Valdez* Oil Spill Restoration Project Annual Report (Bird Study no. 9), *Exxon Valdez* Oil Spill Trustee Council, Restoration Office, 645 G Street, Suite 401, Anchorage, Alaska 99501-3451.

Okada, S., and A. Taniguchi. 1971. Size relationship between salmon juveniles in shore waters and their prey animals. Bull. Fac. Fish. Hokkaido Univ. 22:30-36.

Pauly, D., and I. Tsukayama. 1987. The Peruvian anchoveta and its upwelling ecosystem: Three decades of change. ICLARM (Int. Cent. Living Aquat. Resour. Manage.) Stud. Rev. 15, 351 pp.

Pearcy, W.G., R.D. Brodeur, J.M. Shenker, W.W. Smoker, and Y. Endo. 1988. Food habits of Pacific salmon and steelhead trout, midwater trawl catches and oceanographic conditions in the Gulf of Alaska, 1980-1985. Bull. Ocean Res. Inst. 26(II):29-78.

Persson, L. 1986. Effects of reduced interspecific competition on resource utilization in perch (*Perca fluviatilis*). Ecology 67:335-364.

Pinkus, L., M.S. Oliphant, and I.L.K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Fish Game Fish Bull. 152:1-83.

Robb, A.P. 1981. Observations on the food and diel feeding behaviour of pelagic 0-group gadoids in the northern North Sea. J. Fish Biol. 18:183-194.

Sanger, G.A. 1983. Diets and food web relationships of seabirds in the Gulf of Alaska and adjacent marine regions. Outer Continental Shelf Environmental Assessment Program, Final Reports of Principal Investigators 45:631-771.

Sharp, G.D. 1992. Fishery catch records, El Niño/Southern Oscillation, and longer-term climate change as inferred from fish remains in marine sediments. In: H.F. Diaz and V. Markgraf (eds.), El Niño. Cambridge University Press, Cambridge, England, pp. 379-417.

Shershnev, A.P., V.M. Chuypakhin, and V.A. Rudnev. 1982. Ecology of juvenile pink salmon, *Oncorhynchus gorbuscha* (Salmonidae), from Sakhalin and Iturup islands during the marine period of life. J. Ichthyol. 22:90-97.

Simenstad, C.A., and E. Salo. 1982. Foraging success as a determinant of estuarine and nearshore carrying capacity of juvenile chum salmon (*Oncorhynchus keta*) in Hood Canal, Washington. In: B.R. Melteff and R.A. Neve (eds.), Proceedings of the North Pacific Aquaculture Symposium. Alaska Sea Grant College Program, University of Alaska, AK-SG-82-02, pp. 21-37.

Sogard, S.M. 1994. Use of suboptimal foraging habitats by fishes: Consequences to growth and survival. In: D.J. Stouder, K.L. Fresh, and R.J. Feller (eds.), Theory and application in fish feeding ecology. University of South Carolina Press, Columbia, South Carolina, pp. 103-132.

Taylor, E.B. 1991. Behavioural interaction and habitat use in juvenile chinook, *Oncorhynchus tshawytscha*, and coho, *O. kisutch*, salmon. Anim. Behav. 42:729-744.

Welsh, D.W., and T.R. Parsons. 1993. δ^{13}-δ^{15} values as indicators of trophic position and competitive overlap for Pacific salmon (*Oncorhynchus* spp.). Fish. Oceanogr. 2(1):11-23.

Wespestad, V.G., and S.M. Fried. 1983. Review of the biology and abundance trends of Pacific herring (*Clupea harengus pallasi*). In: W.S. Wooster (ed.), From year to year. Washington Sea Grant Program, University of Washington, WSG-WO 83-3, pp. 17-29.

Pelagic Fishes and Their Macroplankton Prey: Swimming Speeds

Sergey M. Ignatyev
National Ukrainian Academy of Sciences, Institute of Biology of Southern Seas, Sevastopol, Ukraine

Abstract

The escape response is an important consideration in estimating food accessibility in predator-prey relationships. In tropical pelagic systems, prey accessibility is especially sensitive to the swimming speeds of macroplankton (Crustacea, Cephalopoda, Chaetognatha) and micronekton (Myctophidae and other small pelagic fishes and squids), when the predators and prey are similar in size. This study is based on visual observations and filming of the swimming speeds of macroplankton (euphausiids, decapods and their larvae, chaetognaths, small pelagic fishes and squids—18 species in all); observations of swimming both in aquaria aboard ship and under natural conditions; and on analysis of literature data. Speeds of actively swimming pelagic animals 10-50 mm in length are 2-35 cm/s. The average swimming speeds are 2-20 body lengths/s. When the swimming speeds of potential prey and their predators are similar, predation losses on prey populations are low. Motile macroplankton make up less than 12% of the diet of fishes of a similar size. However, large fish with fast swimming speeds successfully feed on motile macroplankton.

Introduction

Motility is an important factor linking the components of marine ecosystems. Matter and energy exchange through the food web is facilitated by motility in marine organisms. Therefore quantitative data on swimming speeds should be incorporated in all ecosystem models, especially in predator-prey models. Swimming is especially important in the pelagic environment, where cover is absent and the only way for predators to capture prey is through swimming. Therefore, quantitative measures of the swimming speed of predators and their prey are necessary for assessing their role in marine ecosystems.

We will consider the predator-prey system involving actively swimming organisms: macroplanktonic animals and pelagic fishes and squids. This system is unique in that predators and prey are similar in size, i.e., within 1-5 cm of each other. Research by the Institute of Biology of Southern Seas (IBSS) (Greze 1983, Chesalin 1994, Ignatyev 1995, Zuev et al. 1996) has shown that actively swimming macroplankton (euphausiids and pelagic shrimps) play an important role in the diet of micronektonic predators (squids and mesopelagic fishes). They make up 12-80% of the diet of these predators. Micronektonic predators in turn are food for larger pelagic fishes and squids. Therefore, the ability of predators and their potential forage to swim at high speed is an important factor in their interactions. We studied active swimming types and speeds of macroplanktonic and nektonic organisms, which form a major component of the multifaceted marine pelagic food web.

Materials and Methods

Two methods of observation are used to study swimming speeds in pelagic animals: visual and instrumental (Komarov 1976). Visual methods include direct observation in aquaria, underwater, or by other means, of the movement of organisms, frequently without application of recording devices. The second type commonly includes movie films, videos, or photographs of the swimming animals. Acoustic methods are also included in the second group. They are based on the fact that the sound scattering layers (SSL) are composed of animals and the vertical movement of the SSL coincides with vertical migration of the sound-scattering organisms (mainly fishes and macroplanktonic crustaceans). Therefore, hydroacoustic observations can be used to study movement by the sound-scattering animals (Ignatyev 1988). However, the SSL consist of various systematic groups and the migration behavior (ethology) of the various groups must be accounted for. Therefore, the hydroacoustic data must be accompanied by the more complicated methods of direct observation.

We used movie- and video-filming as a more objective method to study active swimming by macroplankton and micronekton. The study animals were caught by pelagic trawls in tropical waters of the Atlantic and Indian oceans (cruises from 1984 to 1991). We studied four species of euphausiids, ten species of pelagic shrimps, and three species of micronektonic fishes. We also used visual observations of pelagic animals from ship board and from a submersible. In comparing results, it is important to keep in mind that while the swimming speeds of fish have been studied fairly extensively (Aleev 1976, Komarov 1976), speeds of large pelagic crustaceans and other macroplankton have not. We therefore also present literature data on the speeds of actively swimming macroplanktonic organisms, which were measured by different methods (Table 1), and compare the results (Table 2).

Discussion

The higher macroplanktonic crustaceans (euphausiids and decapods), which are a substantial portion (12-63%) of the diet of pelagic fishes, move using two types of swimming appendages: the pleopods and the caudal appendages (telson and uropods). These two types of appendages permit two types of movement by the higher crustaceans: (1) pleopod swimming, which is the main type of long-distance swimming used for migrations; and (2) swimming using the caudal appendages, which is the fastest type of swimming and is used only for escape.

The available data (Tables 1 and 2) show that macroplanktonic crustaceans, which include a uniform size group (1-5 cm), are characterized by similar absolute and relative speeds for identical swimming methods. Swimming speeds are 0.5-42 cm/s (0.2-10 body lengths/s) using pleopod swimming, and 20-200 cm/s (10-27 body lengths/s) using caudal swimming.

While different swimming behaviors result from different swimming appendages in the crustaceans, fish have only one undulating swimming appendage (Aleev 1976). Therefore, a large variety of terms are used by authors to describe swimming (Komarov 1976). However, several basic swimming behaviors can be discerned: quiet swimming or migration (at average speeds), swimming for foraging, and swimming for escape. These swimming types have been verified by much data, including observations from submersibles.

There are many measurements of swimming speeds of migrating fish (Aleev 1976, Komarov 1976). We can also study them acoustically (measuring migration speeds of the SSL) (Ignatyev 1988). The migrational swimming speeds of fish are at the lower range, 1-5 body lengths/s. There are various types of foraging swimming behavior: filter feeding, and active and passive predation. The range of speeds of foraging fish fluctuates widely from minimal to maximal values.

There are few direct measurements of swimming speeds of small pelagic fishes and squids from the oceanic SSL due to the difficulty of capturing and maintaining the study animals. In the majority of cases, extreme or average values are reported. According to data from a movie camera, Stromateidae, small pelagic fishes, swim at speeds of 1.2-3.8 cm/s (Ponomareva and Suslyaev 1980). Myctophids of the genera *Diaphus* and *Myctophum* swim at speeds of 2.5-30 cm/s (Gorelova 1977, this study). Submersible observations on myctophids in the tropical Atlantic have produced active swimming speeds of 6-10 cm/s (Roger 1977). Analogous results (up to 20-27 cm/s in the horizontal direction) were obtained on discrete scatters (presumably myctophids) using a submersible acoustic array (Farmer and Grawford 1976). The above

Table 1. Swimming speeds of pelagic organisms.

Organisms	Swimming speeds (V, cm/s)	Authors	Method of observation
Crustacea, Euphausiacea			
Euphausiid furcilia	0.3-1.2 [Pl] (3.0) [Tail]	Pogodin 1980	Ship board
Adult euphausiids	0.8-20.5 (8.0) [Pl] 18.2-0.0 [Tail]	Bainbridge 1952 Blaxter & Currie 1967 Lomakina 1978 Pogodin 1980 Ponomareva 1963 Roger 1977 Vinogradov 1968	Ship board Submersible
Meganyctiphanes norvegica	(7.5) [Pl]	Bainbridge 1952 Hardy & Bainbridge 1954 Mauchline 1980 Ponomareva 1963	Ship board Submersible
Thysanopoda tricuspidata	(3.5) [Pl] 1.5-10.0 (5.2) [Pl] 16.5-30.0 (23.2) [Tail]	Hardy & Bainbridge 1954 This study	Submersible Movie film
Thysanopoda monacantha	2.0 -17.5 (8.4) [Pl] 4.0-26.6 (12.5) [Tail]	This study	Movie film
Thysanopoda acutifrons	(3.5) [Pl]	Bainbridge 1952 Hardy & Bainbridge 1954	Ship board Submersible
Thysanoessa inermis	1.3-4.2 [Pl]	Bainbridge 1952 Hardy & Bainbridge 1954	Ship board Submersible
Thysanoessa raschii	0.5-2.2 [Pl]	Harding 1977	Ship board
Euphausia sp.	2.8-5.7 [Pl]	Vinogradov 1968	Ship board
Euphausia diomedeae	1.0-15.0 (7.5) [Pl] 19.2-25.0 (22.7) [Tail]	Ponomareva & Suslyaev 1980 This study	Movie film
Euphausia triacantha	2.0-17.6 (8.5) [Pl] 18.2-27.0 (23.3) [Tail]	This study	Movie film
Euphausia pacifica	3.0-12.0 [Pl]	Ignatyev 1984 Klyashtorin & Yarshombek 1973 Torres & Childress 1983	Movie film Ship board
Euphausia tenera	0.4-2.3 [Pl]	Ponomareva & Suslyaev 1980	Movie film
Euphausia superba	3.0-40.0 (25.0) [Pl] 100-150 [Tail]	Kils 1979 Semenov 1969	Movie film Ship board
Crustacea, Decapoda			
Decapoda larvae	0.8-2.0	Myleikovsky 1973	Ship board
Sergia lucens zoeae	0.2-0.3	Hammer 1977 Myleikovsky 1973	Ship board
Brachyura zoeae	0.8-2.2	Bainbridge 1952 Hardy & Bainbridge 1954	Ship board Submersible
Panulirus japonicis phyllosoma	0.4-3.0	Saisho 1966	Ship board
Panulirus longipes larvae	9.0-33.0 (15.0) [Pl] 40.0-46.0 [Tail]	Phillips & Olsen 1975	Ship board
Natantia	(27.5) [Pl]	Konstantinov 1979	Ship board
Sergestidae	0.5-2.0 [Pl]	Ponomareva & Suslyaev 1980 This study	Movie film

Table 1. Cont'd.

Organisms	Swimming speeds (V, cm/s)	Authors	Method of observation
Sergestes (Sergestes) lucens	0.5-5.7 [Pl]	Hammer 1977	Photograph Ship board
Sergestes (Sergestes) sp.	2.5-9.7 [Pl] 20.0-46.0 [Tail]	This study	Movie film
Lucifer sp.	0.5-2.7 [Pl]	This study	Movie film
Acanthephyra sp.	2.5-32.2 (16.0) [Pl] 40.0-65.0 (50.0) [Tail]	This study	Movie film
Systellaspis sp.	19.2-35.6 [Pl] 47.0-76.0 [Tail]	This study	Movie film
Oplophorus typus	12.5-27.2 (17.6) [Pl] 42.0-75.0 (50.0) [Tail]	This study	Movie film
Oplophorus spinicauda	2.5-22.2 (9.6) [Pl] 30.0-47.0 [Tail]	This study	Movie film
Stylopandalus richardi	2.2-15.0 (9.0) [Pl]	This study	Movie film
Mollusca, Cephalopoda			
Stenoteuthis pteropus			
L = 1-5 cm	1.5-70.0 (30.0)	Zuev et al. 1985	Ship board
L = >10 cm	30-120	Zuev et al. 1985	Ship board
Chaetognatha			
Flaccisagitta sp.	2.0-6.0 (4.0)	This study	Ship board
Sagitta setosa	6.2-22.5	This study	Movie film
	50.0-60.0	Aleev 1976	Ship board
Pisces			
Clupea harengus (L = 1-2 cm)	5.0-30	Komarov 1976	
Sprattus sprattus (L = 5-7 cm)	10.0-25.0	Komarov 1976	
Stromateidae	1.2-3.8	Ponomareva & Suslyaev 1980	Movie film
Myctophidae	6.0-10.0	Roger 1977	Submersible
	20.0-27.0	Farmer & Grawford 1976	Acoustic
Diaphus sp.	2.5-30.0	This study	Ship board

[Pl] - Pleopod swimming by macroplankton crustaceans.

[Tail] - Caudal swimming by macroplankton crustaceans (escape-swimming).

L - Body length (biological).

Table 2. Comparative characteristics of swimming speeds of pelagic organisms.

Ecological groups	Type of movement	Body size (L, cm)	Average speeds of the ethological swimming types: Migrational swimming V, cm/s	V/L	Foraging swimming V, cm/s	V/L	Escape swimming V, cm/s	V/L
Macroplankton crustaceans	Rowing	1-3	0.5-3	0.2-2	2-10	1-5	20-50	10-27
Micronekton fishes	Undulation	1-5	1.5-10	2-5	2.5-30	2-15	20-50	10-22
Micronekton squids	Jet	1-3	1-3	0.5-2	30	15	20-70	10-30
Nekton fishes	Undulation	5-10	5-20	1-2	27-35	5-10	50-100	10-20
Nekton squids	Jet	5-10			50-60	10-20	50-100	10-25
Macronekton fishes	Undulation	>10			50-100	8-22	>100	>10
Macronekton squids	Jet	>10			30-120	8-20	>100	>10

Table 3. Comparative characteristics of swimming speeds and of the food composition of pelagic organisms.

Predator groups	Foraging-swimming speed (V, cm/s)	% of active swimming macroplankton prey in the diet	Author
Macroplankon crustaceans	2-10	2-3% (euphausiids)	Roger 1977, Ignatyev 1995
Micronekton fishes	2.5-30	6-12% (euphausiids, amphipods)	Greze 1983
Micronekton squids	30	3-15% (euphausiids, amphipods, fish larvae)	Chesalin 1994
Nekton fishes	27-35	30-57% (euphausiids, myctophids)	Zuev et al. 1996
Nekton squids	50-60	42-60% (euphausiids, decapods, cephalopods, myctophids)	Chesalin 1994
Macronekton fishes	50-100	>80% (myctophids, crustaceans, cephalopods)	Zuev et al. 1996
Macronekton squids	30-120	77-82% (myctophids, crustaceans, cephalopods)	Chesalin 1994

values are within the range of average swimming speeds, characteristic of small pelagic fishes.

Similar values of absolute and relative swimming speeds have been obtained for *Sagitta*, an active predator (Table 1) (Aleev 1976). The active swimming speeds of small squids (1-10 cm), which use water jets for swimming, are also within this range (Zuev et al. 1985). Pelagic squids have a wide range of swimming speeds, from 1 to 200 cm/s.

Summary

The analysis of these data shows that predators and their potential prey of similar body sizes have similar swimming speeds. Swimming speeds are not a characteristic of the taxonomic position of the animal or the type of swimming appendages, but are the result of general hydrodynamic principles only. Comparison of the relative swimming speeds of predators (pelagic fishes and squids) and their macroplanktonic prey (Table 3) indicates a clear relationship between consumption of the latter and its swimming ability. Increases in the absolute and relative swimming speeds with body size of pelagic predatory fishes are accompanied by corresponding increases in the percentage of actively swimming macroplanktonic organisms in their diets. The percentage increases from 6% in micronektonic myctophids to up to 82-90% in fast-swimming tuna and large squids.

References

Aleev, Yu. G. 1976. Nekton. Naukova Dumka, Kiev. 392 pp. (In Russian.)

Bainbridge, R. 1952. Underwater observations of the swimming of marine zooplankton. J. Mar. Biol. Assoc. U.K. 31(2):107-112.

Blaxter, I.H.S., and R.I. Currie. 1967. The effect of artificial lights on acoustic scattering layers in the ocean. Aspects of Marine Ecology. Symp. Zool. Soc. Lond. 19:1-14.

Chesalin, M.V. 1994. The feed of the nekton oceanic squids of the genus *Stenoteuthis* and their role in the trophic structure of communities of the pelagia. Ph.D. thesis, IBSS, Sevastopol. 24 pp. (In Russian.)

Farmer, D.H., and I.K. Grawford. 1976. Measurements of the acoustic correlation in the ocean with a frequency echo-counter. Nature 5902:697-700.

Gorelova, T.A. 1977. Some peculiarities of the feed of the larvae of nictoepipelagic and mesopelagic myctophids (Pisces, Myctophidae). Okeanologiya 17(2):342-346. (In Russian.)

Greze, E.V. 1983. Feeding of the epipelagic myctophids (Myctophidae, Pisces) of the tropical Atlantic. Ekol. Morya 14:18-23. (In Russian.)

Hammer, P.H.N. 1977. Chemosensory tracking of scent trails by the planktonic shrimp *Acetes sibogae australis*. Science 195(4281):886-888.

Harding, G.C.H. 1977. Surface area of the euphausiid *Thysanoessa raschii* and its relation to body length, weight, and respiration. J. Fish. Res. Board. Can. 34(2):225-231.

Hardy, A.C., and R. Bainbridge. 1954. Experimental observations on the vertical migrations of plankton animals. J. Mar. Biol. Assoc. U.K. 33(2):409-448.

Ignatyev, S.M. 1983. About speeds of movement of the nektobenthic of shrimps (Decapoda, Natantia). Ekol. Morya 15:51-61. (In Russian.)

Ignatyev, S.M. 1984. Functional morphology of the locomotion of the Eucarida (Crustacea, Euphausiacea, Decapoda). Ph.D. thesis, IBSS, Sevastopol. 26 pp. (In Russian.)

Ignatyev, S.M. 1988. Migrating sound scattering layers (SSL) and motion rates of scattering organisms. Communication 1. Rates of vertical SSL migrations in the tropical zone of the ocean (review). Ekol. Morya 30:13-18. (In Russian.)

Ignatyev, S.M. 1995. Tropic pelagic ecosystems. Problems on macroplankton levels. Workshop on the Concept of Ecosystems. Program and Abstracts. Wilhelmhaven, p. 17.

Kils, U. 1979. Swimming speed and escape capacity of Antarctic krill, *Euphausia superba*. Meeresforschung 27(4):264-266.

Klyashtorin, L.B., and A.I. Yarshombek. 1973. About power expenses on the active movement of planktonic organisms. Okeanologiya 15(5):891-897. (In Russian.)

Komarov, V.T. 1976. Speeds of movement of nekton animals. Naukova Dumka, Kiev. 97 pp. (In Russian.)

Konstantinov, A.S. 1979. General hydrobiology. Vishaya Shkola, Moscow. 600 pp. (In Russian.)

Lomakina, N.B. 1978. Euphausiids of the world ocean (Euphausiacea). Nauka, Moscow. 222 pp. (In Russian.)

Mauchline, J. 1980. The biology of mysids and euphausiids. Part 2. The biology of euphausiids. Adv. Mar. Biol. 18:373-623.

Myleikovsky, S.A. 1973. Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. Mar. Biol. (Berl.) 23(1):11-17.

Phillips, B.F., and L. Olsen. 1975. Swimming behavior of the puerulus larvae of the western rock lobster. Aust. J. Mar. Freshwater Res. 26(3):415-417.

Pogodin, A.G. 1980. Comparison of the sampling of euphausiids by two planktonic networks. Ekol. Morya 3:13-18. (In Russian.)

Ponomareva, L.A. 1963. Availability of fodder organisms for fishes. Tr. Inst. Okeanol. Akad. Nauk SSSR. 71:72-80. (In Russian.)

Ponomareva, L.A., and A.C. Suslyaev. 1980. About movement of some planktonic organisms. Okeanologiya 20(2):301-305. (In Russian.)

Roger, C. 1977. Use of a group of macroplanktonic organisms (euphausiids, crustaceans) in the study of warm water pelagic food webs. Proc. Symp. Warm Water Zooplankton, Goa, 1976. COA:309-316.

Saisho, J. 1966. Studies on phyllosoma larvae with reference to oceanographic conditions. Mem. Fac. Fish. Kagoshima Univ. 15:117-239.

Semenov, V.N. 1969. Aquarium supervision over behavior of the krill. Marine biological resources of Antarctica. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO) 66:235-239. (In Russian.)

Torres, J.J., and J. J. Childress. 1983. Relationship of oxygen consumption to swimming speed in *Euphausia pacifica*. I. Effects of temperature and pressure. Mar. Biol. (Berl.) 71(1):79-86.

Vinogradov, M.E. 1968. The vertical distribution of oceanic zooplankton. Nauka, Moscow. 320 pp. (In Russian.)

Zuev, G.V., Ch.M. Nigmatulin, and V.N. Nikolsky. 1985. Nekton oceanic squids. Agropromizdat, Moscow. 224 pp. (In Russian.)

Zuev, G.V., A.R. Boltachev, V.N. Nikolsky, S.A. Tsarin, and M.V. Chesalin. 1996. Ichthyo- and teuthofauna of the tropical regions of the ocean. Ekol. Morya 45:82-44. (In Russian.)

Predation by Sprat and Herring on Early Life Stages of Cod and Sprat in the Central Baltic

Friedrich W. Köster and Christian Möllmann
Institute of Marine Sciences, Kiel, Germany

Abstract

The reproductive success of cod in the central Baltic has decreased continuously since 1984. Although hydrographic conditions conducive for cod egg survival improved considerably during most recent years, recruitment is still far below the long-term average. The decreasing stock size of the predatory cod is related to increased stocks of herring and sprat, both species that have been identified as major predators on cod early life stages in the central Baltic. This predation may be an important process affecting the survival of cod eggs and larvae considerably and thus hampering stock recovery.

Concentrating on the major spawning area of cod in the central Baltic, i.e., the Bornholm Basin, the present report summarizes results from stomach content analysis for herring and sprat during cod spawning seasons in 1988-1994. Based on estimates of daily rations by individual predators and predator population sizes, daily consumption rates of cod eggs and larvae were calculated. To evaluate the impact of this predation the values were compared to corresponding egg production rates and standing stocks of larvae. As an additional aspect, predation on early life stages of sprat were incorporated into the analysis, as a possible self-regulatory mechanism inhibiting an even more pronounced clupeid outburst in the Baltic.

Despite the reservations and uncertainties in the estimation procedure, the findings suggest that predation on cod eggs and to a lesser extent also on sprat eggs is a substantial source of mortality. Especially in spring, sprat consumed a considerable part of the egg production. However, coinciding with major changes in the hydrographic environment in 1993, the importance of predation by sprat declined, whereas the consumption by herring increased. In contrast to the egg stage, cod and sprat larvae appear not to be substantially affected by predation.

Introduction

Since the middle of the 1980s the upper trophic levels of the central Baltic ecosystem were subject to significant changes. Due to a combination of reproduction failure and overfishing, the central Baltic cod stock decreased to historical low levels in 1992 (Bagge et al. 1994, Anon. 1996a). Recruitment failure is supposed to be caused by the specific hydrographic regime of the Baltic which is heavily dependent on inflows of oxygen-enriched water from the North Sea (e.g., MacKenzie et al. 1996a). Absence of inflow situations limits the volume of water where successful egg development is possible (e.g., Plikshs et al. 1993). This is especially the case for the more eastern spawning grounds, i.e., the Gotland Basin and Gdansk Deep (Figure 1), where hydrographic conditions did in general not allow successful egg development since 1986. Thus recruitment of the cod stock has been nearly entirely dependent on the survival of cod early life stages in the remaining major spawning area, the Bornholm Basin (Figure 1). The decreasing size of the predatory cod stock is related to increasing stocks of the major prey species herring and sprat since 1988 (Sparholt 1994, Anon. 1996a).

During the last decade predation has been discussed as a major factor controlling recruitment of marine fish species (e.g., Bailey and Houde 1989). However, field studies designed adequately for estimating predation mortalities of early life stages are scarce. A literature review identified herring and sprat as major potential predators on early life stages of marine fish species in the central Baltic (Köster 1994). In contrast to other cod stocks, there is a pronounced temporal overlap between the extended spawning season of Baltic cod (i.e., in general from March to August; e.g., Bagge et al. 1994), and the major feeding period of herring (i.e., after the return of spring spawners from their coastal spawning grounds in May; e.g., Aro 1989). Cod and sprat utilize the same spawning areas, with an in general slightly shorter spawning period of the latter (e.g., Elwertowski 1960). Contrary to other spawning areas of cod with salinities sufficient to keep eggs floating in the surface layer, in the central Baltic basins cod eggs occur exclusively in the lower part of the water column. They concentrate in a narrow depth range within or below the halocline (Müller and Pommeranz 1984, Wieland 1988). Sprat eggs have a slightly higher buoyancy, but their upper vertical distribution in spring months is limited by the relatively cold winter water (Müller and Pommeranz 1984, Wieland and Zuzarte 1991); i.e., the intermediate water layer between the thermo- and halocline. Therefore, eggs of both species are available as prey in relatively dense aggregations for the clupeids staying close to the bottom or above the oxygen-depleted bottom water while feeding during daytime (Köster and Schnack 1994).

A first attempt to quantify the consumption of cod eggs by herring and sprat in the Bornholm Basin revealed a significant predation pres-

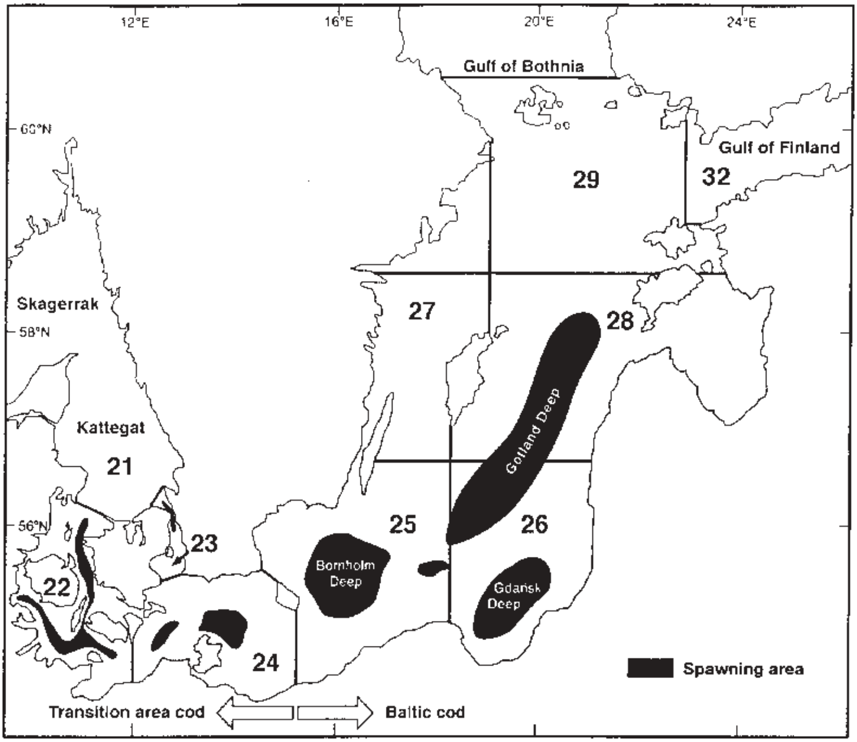


Figure 1. Principal cod spawning areas in the Baltic and ICES subdivision. Modified from Bagge and Thurow (1994).

sure during cod spawning seasons 1988-1991. Larvae of fish and especially cod larvae as well as 0-group cod were found to be preyed upon rather seldom (Köster and Schnack 1994).

The hydrographic conditions for cod egg development have improved considerably in the Bornholm Basin in 1993-1994, due to a major inflow in the beginning of 1993 (Matthäus and Lass 1995). However, reproductive success of cod appears still to be rather limited, which might be explained by high mortality rates of cod eggs caused by intense predation through clupeid fish stocks (Bagge 1996).

For the purpose of integrated fisheries management of Baltic fish stocks not only the interaction between the adult stock components, i.e., cod predation on herring and sprat as well as cannibalism (e.g., Sparholt 1994), but also significant interactions on the level of early life stages need to be considered. Thus in the present report the hypothesis that cod recruitment in the Baltic is controlled by clupeid fish through predation on eggs is tested by: (1) presenting new results from stomach content analysis conducted in 1993-1994, a period with a considerably changed hydrographic environment compared to preceding years; (2) checking assumptions made earlier with respect to stomach evacuation rate determination and predator abundance estimation; and (3) comparing the daily consumption rates by the predator populations to updated egg production values derived from ichthyoplankton surveys conducted concurrently to the stomach sampling.

Sprat eggs were regularly encountered in herring and especially sprat stomachs (Köster and Schnack 1994). Whether cannibalism on sprat eggs is a factor affecting sprat recruitment significantly, and thus inhibits an even more pronounced clupeid outburst in the Baltic, is a further topic addressed in the present report.

Results presented here should be seen as a further step to describe the species interaction in the central Baltic on the level of early life stages rather than a presentation of final conclusive results.

Materials and Methods

Stomach sampling scheme

Stomach sampling of herring and sprat in the Bornholm Basin was carried out on several cruises from March 1988 to August 1994. The fish were caught either by bottom trawl in water depths of 60-85 m or by pelagic trawl in different water layers over depths of 70-100 m. According to the daily vertical migration of herring and sprat, the bottom trawl was used during daytime only. Pelagic trawling was carried out close to the bottom or above the oxygen-depleted bottom water during the day and in the upper water column at depths of 5-30 m at night. At dawn intermediate depths of 20-60 m were chosen. On several surveys, especially in 1988, hauls were made at a fixed position at different times of the day to describe the diurnal feeding cycle of herring and sprat in relation to their vertical migration and to estimate stomach evacuation rates. On cruises conducted since 1990 a greater part of the cod spawning area was regularly covered in order to describe the spatial variability of predation (Table 1).

In view of an expected fast digestion of ichthyoplankton, especially if small larvae had been ingested (Hunter and Kimbrell 1980), the duration of trawling and the handling time on deck was reduced as far as possible, i.e., to 45-75 min from catching to conservation. Stomachs of both predators were collected according to a length-stratified sampling scheme. Conservation was done in an 8% formaldehyde/seawater solution buffered with borax.

Stomach content analysis

In total, 4,780 herring and 4,938 sprat stomachs sampled on 144 and 139 different stations, respectively, were analyzed to determine the

Table 1. Numbers of different stations covered and numbers of herring and sprat stomachs analyzed as well as average lengths (cm) for every sampling date considered.

	Herring			Sprat		
Month-year	No. of statons	No. of stomachs	Average lengths (cm)	No. of stations	No. of stomachs	Average lengths (cm)
3-88	12	598	20.8	11	528	13.5
4-91	7	283	19.6	9	355	13.8
4-93	10	138	21.4	10	412	13.3
4/5-94	16	410	21.8	16	517	13.0
5/6-90	12	562	23.4	12	506	13.7
5/6-91	12	474	21.8	14	526	13.9
5/6-93	10	281	19.5	9	293	13.7
5/6-94	13	311	19.8	14	398	12.8
6/7-88	8	233	23.6	2	87	13.7
7-91	15	473	21.8	14	535	13.8
7/8-88	4	165	22.7	3	86	14.1
8-91	11	461	21.3	11	326	14.1
8-94	14	391	20.6	9	169	14.0

food composition and especially the amount of ichthyoplankton in the stomachs. The amount of food in the stomachs was determined by weighing the stomachs before and after emptying. The numbers of eggs and larvae as well as small fish were in general determined from 6-10 stomachs per 2- and 1-cm length class for herring and sprat, respectively. The eggs, larvae, and fish were identified to species and developmental stage as far as possible. The remaining stomach content was differentiated into major taxonomic groups. These prey groups were quantified as wet weight by estimating the proportion they contributed to the total volume of the stomach content. Arithmetic mean numbers of eggs, larvae, and fish as well as weights of all major prey groups were derived for each cruise by computing total averages over all length classes, weighted by the proportion of each length class in the overall length distribution of herring and sprat during the cruise. The mean number of unidentified eggs was allocated to species according to the species composition of identified eggs. Only stomachs sampled between sunrise and sunset, i.e., the daily feeding period of herring and sprat in the Baltic basins (e.g., Köster and Schnack 1994, Fetter and Davidjuka 1996) were taken into consideration.

Individual daily rations

On the basis of repeated 24-hour fisheries, the diurnal feeding cycle was described and the main feeding period was determined (Köster and Schnack 1994). From the reduction in the average stomach contents during night and within special deck tank experiments (Köster et al. 1990), evacuation rates were estimated on the basis of the general model of gastric evacuation (e.g., Tyler 1970). This assumes that the instantaneous evacuation rate of stomach content in weight (dS/dt) is a power function of the instantaneous stomach content (S):

$$S / dt = -R \times S^B$$

Evacuation rates were estimated as the difference in median gut content between successive samples. Estimates of the constants B and R were obtained by linear regression of ln-transformed evacuation rates on the ln-transformed mean stomach contents of the corresponding intervals (Temming and Köster 1990). To avoid a bias introduced by an increasing number of zero observations (Olson and Mullen 1986), only medians greater than zero have been included in the estimation procedure. The data sets employed were derived from 3,210 herring and 3,802 sprat stomachs sampled during 4 and 5 different 24-hour fisheries as well as 6 and 5 tank experiments directed to each species, respectively (Köster and Schnack 1994). According to the low water temperatures of 3.5-7.0°C in the intermediate and bottom water, where herring and sprat feed during the day, tank experiments were performed in April and May only. Nevertheless, similar to the 24-hour fisheries, they refer to a wider temperature range of 4.4-14.0°C.

Based on an approach proposed by Pennington (1985) the daily rations (F_T) can be estimated as:

$$F_T = R \times \overline{S^B} \times T + S_t - S_0$$

where

S_t is the average stomach content at the end of the feeding period,
S_0 is the average stomach content at the beginning of the feeding period, and
T is the duration of the feeding period.

Average S^B were calculated by raising individual stomach contents from each sample to the power of B, and averaging these values over the feeding period. As the samples were more or less evenly distributed over time, no further weighting or subdividing into smaller time units was required. Values for S_t and S_o were estimated on the basis of 24-hour fisheries by calculating mean relative deviations from the average stomach content within the daily feeding period 2 hours before and after the food ingestion stopped and commenced, i.e., sunset and sunrise (Köster 1994). Based on daily rations of total food intake (F_T), daily rations of fish eggs were derived by assuming the same ratio between food intake and average stomach content for eggs in numbers as for total food in weight. As a final step, the daily ration of cod and sprat eggs ingested were calculated by dividing the daily rations of all fish eggs according to the proportion of eggs from both species within the total number of fish eggs.

For comparison, a new evacuation model based on an exponential version of the general model incorporating the actual environmental temperature (Temming 1996) has been applied for herring:

$$F_T = R' \times S \times e^{A \times C} \times T + S_t - S_0$$

where

R' is txhe food type constant,
S is the average stomach content,
A is the temperature coefficient, and
C is the ambient temperature (°C).

An exponential gastric evacuation model was used because the observed curvilinearity in the first approach is well in agreement with findings of Jobling (1986), who suggests exponential evacuation for fish feeding on small particles, e.g., zooplankton. Average ambient temperatures per quarter and year in the 60- to 80-m-depth layer, being the main water body where herring concentrate during daytime, were derived from the International Council for the Exploration of the Sea (ICES) hydrographic data base.

To estimate the daily rations of fish larvae consumed by individual herring and sprat an average digestion time of 2 hours was applied in a simple Bajkov (1935) approach. This average digestion time was estimated from two digestion experiments conducted with herring, which had ingested relatively high amounts of fish larvae (Köster 1994).

Predator population sizes

Population sizes of herring and sprat in Subdivision 25, i.e., the management area which encloses the Bornholm spawning ground (Figure 1), were determined by downscaling results of Multispecies Virtual Population Analysis (MSVPA) for the entire central Baltic (Anon. 1996a) by hydroacoustic data. Stock sizes calculated for Subdivisions 25-27 (herring) and 25, 26, and 28 (sprat) were allocated to individual subdivisions by using information on the relative horizontal distributions obtained from annual international hydroacoustic surveys in October (Köster 1994, Anon 1996b). Population sizes (ages 1+) referring to specific stomach sampling dates were derived by interpolating between different quarters, assuming an equal distribution of fishing and natural mortality within each quarter. Within Subdivision 25 hydroacoustic surveys were conducted in May-June 1979-1986 (five cruises by GDR, USSR, and Poland) and July-August 1981-1988 (four cruises by Poland and Sweden). The results were broken down to ICES statistical rectangles and used to estimate the proportions of the total populations aggregating in the entire and central Bornholm Basin (areas enclosed by the 60- and 75-m depth contours, respectively). Due to a lack of hydroacoustic data in March-April, i.e., the spawning time of spring spawning herring, the population sizes of herring were derived by using May-June values, corrected according to the difference in the average CPUE from pelagic trawl hauls in April compared to May-June 1990-1993. Sprat concentrate in the Bornholm Basin during their spawning season from March through July. Therefore, the mean percentage obtained for May-June was applied to March-April also.

To check the various assumptions made, a hydroacoustic survey was conducted in May 1995 to enable a comparison between calculated and directly observed population sizes. Hydroacoustic transects were covered during night, when herring and sprat disperse above the halocline, while cod remains in the lower water column, thus enabling a distinct differentiation between the clupeids and cod (Lehmann and Jensen 1996).

Prey abundance and production in relation to consumption

Information on the standing stock of cod eggs in the central Bornholm Basin to be compared to estimates of daily consumption by the predator populations were obtained by standard ichthyoplankton surveys conducted concurrently with the stomach sampling (Figure 2). As differentiation between dead and live eggs in the diets was impossible, dead eggs encountered in the plankton samples have been included in the abundance values.

Daily production values of different cod egg developmental stages were estimated on the basis of stage-specific abundance values and corresponding stage durations referring to environmental temperatures encountered in the depths with maximum cod egg densities (Wieland and Zuzarte 1991, Wieland et al. 1994, Wieland 1995, Wieland unpubl.). To estimate the actual daily production of the different egg stages, the obtained values were corrected for mortality within the stages by applying preliminary estimates of age-dependent egg mortalities (Wieland 1995) to the half stage duration times. To account for the different hydrographic situations (Hinrichsen and Wieland 1996), mortalities derived for 1987-1988 and 1991-1992 were applied to the periods 1988-1990 and 1991-1994, respectively. Afterward the stage-specific production rates were added and the abundance of dead eggs was included.

For sprat, corresponding egg abundance values are available for March, April, and August 1988 only. Thus preliminary seasonal egg productions were estimated for each sampling year on the basis of the average batch fecundity of female sprat in the Bornholm Basin (Müller et al.

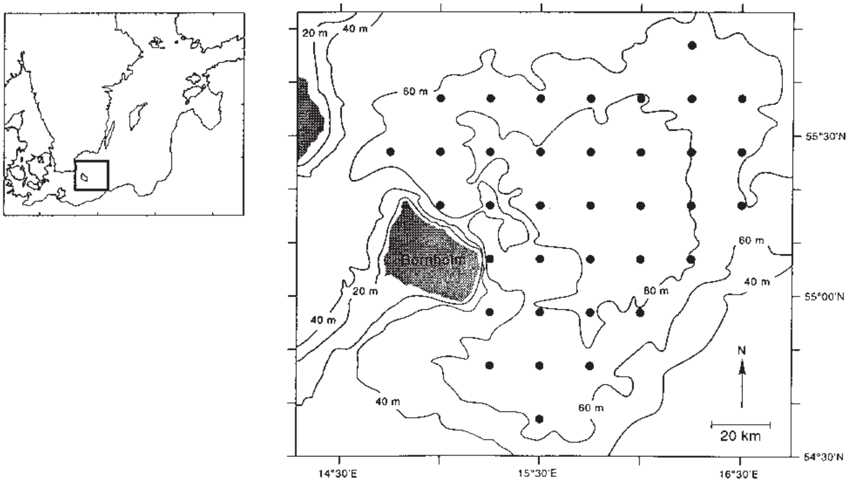


Figure 2. Study area: ichthyoplankton station grid in the Bornholm Basin, southern central Baltic.

1990) and the abundance of sprat (age groups 1+) in the entire Bornholm Basin in the second quarter. An average sex ratio of 0.50 determined on 33 stations covered in different years and months was utilized to calculate the female spawning stock, assuming all females to be mature. The number of batches spawned per individual female was assumed to average 10. This assumption is based on reported batch numbers of at least 10 in the western Baltic (Heidrich 1925) and the North Sea (Alheit 1988) as well as 8-10 in the southern central Baltic (Petrowa 1960). Rough daily egg production values for each sampling date were estimated by distributing the total annual egg production to different months in which sprat eggs were encountered in the ichthyoplankton (i.e., March to the middle of August). To account for increasing spawning intensity from March to May-June and decreasing intensity afterwards (Kändler 1949), relative average gonadosomatic indices determined in 1988 (Müller et al. 1990) were used as a weighting factor. Furthermore, the migration out of the spawning area was considered by introduction of a second scaling factor obtained from the comparison of proportions of sprat concentrating in the Bornholm Basin in relation to the entire stock in Subdivision 25 as obtained by hydroacoustic surveys.

For cod and sprat larvae production values are not available, thus the estimated daily consumption rates by herring and sprat populations are compared to the corresponding standing stocks in the Bornholm Basin (Grønkjær et al. 1995). Due to a drift out of the basin's center (Hinrichsen et al. In press), also for cod and sprat larvae the area enclosed by the 60-m depth contour was assumed to be the borderline of the distribution. Data on the standing stock of cod larvae are available for the entire period, but for sprat larvae only until 1991.

Results

General diet composition

The general diet composition of herring and especially sprat was dominated by mesozooplankton. Copepods were the most important prey taxa for herring in all months investigated. In total, the combined group of macrozooplankton and small fish added up to 10% of the average stomach content in weight. Significantly higher proportions of mysiids occurred only in March 1988 and August 1994. Cladocerans were ingested in increasing amounts in summer, whereas their share in spring was negligible. Fish eggs and larvae contributed up to 5% to the total stomach content in weight only. An exception was August 1994, when ichthyoplankton was the second most important prey group (16%). Copepods were also the main prey of sprat, with the exception of August, when feeding on cladocerans regularly took place. Fish eggs and larvae were in general the second important prey group in spring, contributing 7-25% to the diet in terms of weight. However, since May-June 1993 the proportion of ichthyoplankton in the diet has dropped considerably.

Ichthyoplankton and small fish in the diet

The amount of fish eggs in herring stomachs averaged 2-52 eggs per stomach with minimum values encountered in August 1988 and 1991. Highest values were found in April 1993, May 1991, and especially in August 1994 (Figure 3). With the exception of August 1988, a clear seasonal trend of increasing proportions of cod eggs from spring to summer is obvious. Due to the ceased spawning activity of sprat in August, sprat eggs were encountered in considerable quantities until July only. Other fish eggs were in general either flounder or rockling eggs. Maximum numbers of fish eggs in sprat stomachs were detected in general in April to June (28-55 eggs per stomach), whereas in summer and especially in August low amounts were found (Figure 4). Since May 1993, however, the amount of fish eggs encountered in the diet of sprat was relatively low independent from the sampling date (<12 eggs per stomach). When comparing the species composition of eggs consumed by both predator species at a given sampling date, a considerably lower proportion of cod eggs in the sprat diet is evident.

The amounts of fish larvae found in the diets of herring and sprat were rather low independent from month and year of sampling (Table 2). Maximum numbers were identified in herring and sprat stomachs in August 1991 and April 1993 (0.3 and 2.0 larvae per stomach, respectively). The relatively high standard errors calculated indicate occasionally

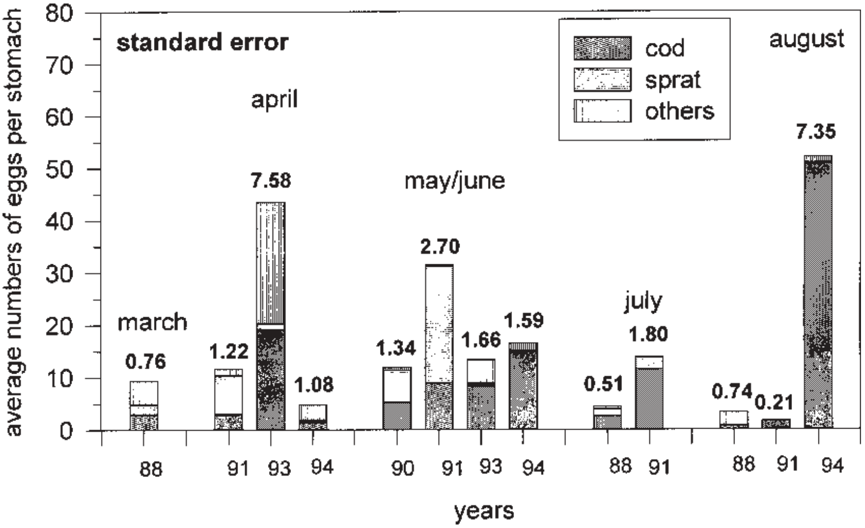


Figure 3. *Average numbers of cod, sprat, and other fish eggs per herring stomach at different sampling dates with corresponding standard error of the average number of total fish eggs per stomach.*

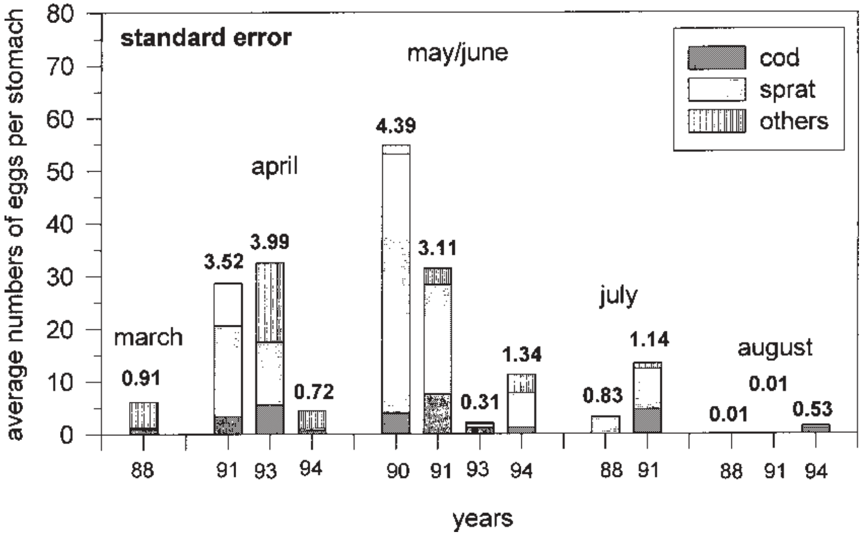


Figure 4. *Average numbers of cod, sprat, and other fish eggs per sprat stomach at different sampling dates with corresponding standard error of the average number of total fish eggs per stomach.*

Table 2. Average numbers of total fish, cod, and sprat larvae per herring and sprat stomach at different sampling dates.

Month-year	Fish larvae per herring stomach Total	SE	Cod	Sprat	Fish larvae per sprat stomach Total	SE	Cod	Sprat
3-88	0.010	0.005	0.004	0.006	0.061	0.017	0.000	0.000
4-91	0.002	0.002	<0.001	0.002	0.000	0.000	0.000	0.000
4-93	0.132	0.084	0.000	0.000	2.001	0.735	0.031	0.272
4/5-94	0.029	0.021	0.000	0.000	0.000	0.000	0.000	0.000
5/6-90	0.054	0.036	0.000	0.054	0.746	0.343	0.008	0.731
5/6-91	0.010	0.009	0.000	0.010	0.001	0.001	<0.001	0.001
5/6-93	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
5/6-94	0.002	0.002	0.000	0.000	0.013	0.009	0.000	0.000
6/7-88	0.001	0.001	<0.001	0.001	0.000	0.000	0.000	0.000
7-91	0.002	0.002	0.002	0.000	0.023	0.019	0.006	0.017
7/8-88	0.006	0.006	0.001	0.005	0.000	0.000	0.000	0.000
8-91	0.295	0.068	0.034	0.261	0.000	0.000	0.000	0.000
8-94	0.024	0.010	0.009	0.000	0.057	0.049	0.000	0.000

SE = standard error of the average number of total fish larvae per stomach.

high consumption of larvae by single predators. Most of the larvae identified to species (35 and 56% of larvae found in herring and sprat stomachs, respectively) were sprat larvae and those found in sprat stomachs were in general rather small (<10 mm in length). In contrast most of the larvae ingested by herring were larger (>10 mm).

Small fish were found in limited numbers in herring stomachs only (mean = 0.01 fish per stomach). They were mostly identified as gobiids and only two juvenile cod and six sprat were encountered.

Daily rations of individual predators

The daily rations of food consumed by individual herring and sprat in the Bornholm Basin estimated for the different sampling dates are presented in Table 3. The total daily food intake of herring and sprat amounted to 0.4-3.7% and 0.8-6.0% of body weight. A clear seasonal pattern with increasing daily rations from March to May, with in general the highest values in May-July followed by a reduction in August, is obvious for both predator species.

The individual rations of cod eggs ingested by herring were rather stable in May-June (24-69 eggs per day) but variable in the beginning and the end of the cod spawning season. The corresponding consumption of sprat eggs was in general considerably lower, i.e., maximum of

10 eggs per day, with the exception of spring dates in 1990-1991 (27-97 eggs per day). The daily rations of cod eggs consumed by individual sprat were in the same order of magnitude as estimated for herring in April 1993, May-June 1990 and 1991, as well as in July 1991 (27-49 eggs per day). For the remaining dates, only limited ingestion rates were calculated, with nearly no consumption in summer. The daily rations of sprat eggs consumed by sprat were in general higher than those estimated for herring, with maximum values in April-May (79-327 eggs per day). However, in May-June 1993 and April-May 1994 daily rations were considerably lower than in preceding years during spring.

Assuming an exponential stomach evacuation model, taking into account the actual ambient temperature resulted in 12-36% lower daily rations in comparison to the general model without temperature dependence. This refers to the food consumption rate in terms of total weight (Table 4) as well as to the number of cod eggs ingested per day. Especially in years with relatively low temperatures in the bottom water the differences were quite considerable, i.e., in 1994 about 34-36%.

The individual daily rations of cod larvae were in general rather low; i.e., no consumption in 6 and 9 out of the sampling dates and in maximum 0.25 cod larvae per day by herring and sprat in August 1991 and April 1993, respectively (Table 5). The corresponding ingestion rates for sprat larvae were somewhat higher, e.g., 2 larvae per day by herring and sprat in May-June 1990 and August 1991 respectively. However, a considerably higher amount of sprat larvae was ingested by sprat in May-June 1990 (6.2 larvae per day).

Predator population sizes

Stock sizes of herring and sprat (age 1+) in the central Baltic estimated by MSVPA for the period 1978-1995 are given in Figure 5. Stock sizes increased since 1987-1988 to highest values on record in 1992-1993. However, for the herring stock the increase is far less pronounced than for sprat. According to the annual international hydroacoustic surveys, 19-34% of the herring stock in the southern central Baltic were concentrating in Subdivision 25 considering the period covered by the analysis. After a decline of the western stock component at the beginning of the last decade, the proportion appears to be rather stable since 1989, apart from an outstanding high value in 1994. This value resulted in a considerably larger herring population determined for Subdivision 25 in 1993-1994 compared to preceding years (Figure 6). For sprat, a decline of the western stock component in the central Baltic is indicated by the hydroacoustic surveys for the second half of the 1980s to low levels in most recent years (6-18%). This resulted in relatively low population levels in Subdivision 25 in 1988-1990, a slight increase until 1992, and a decline afterward (Figure 6). However, the population of sprat in the area is still considerably larger than the herring population.

Table 3. Daily rations consumed by individual herring and sprat in terms of total food intake (g wet weight) and of cod, sprat, and other fish eggs (numbers), based on the general model of gastric evacuation.

		Daily ration consumed by individual herring				Daily ration consumed by individual sprat			
		Wet weight	Numbers of eggs			Wet weight	Numbers of eggs		
Month-year	Feeding period (hr.min)	(g)	Cod	Sprat	Others	(g)	Cod	Sprat	Others
3-88	7.14	0.33	9.0	6.3	14.2	0.13	4.4	1.2	22.0
4-91	8.91	0.79	11.1	28.2	4.8	0.24	18.6	95.0	44.4
4-93	8.91	0.65	65.9	4.0	80.4	0.30	37.1	79.0	99.0
4/5-94	9.33	0.96	8.0	2.4	12.2	0.64	4.2	3.0	22.4
5/6-90	10.26	2.20	24.0	27.2	2.3	0.54	26.5	327.1	11.2
5/6-91	10.14	1.58	39.3	96.6	1.2	0.58	49.2	135.4	20.0
5/6-93	10.01	1.45	34.4	2.2	18.0	0.66	8.7	4.6	1.6
5/6-94	10.26	1.93	68.6	1.5	6.5	0.74	9.1	46.3	24.8
6/7-88	10.32	2.00	11.9	5.8	2.3	0.34	0.0	20.4	0.0
7-91	10.16	2.42	50.3	10.2	0.6	1.02	33.0	53.4	7.3
7/8-88	9.45	0.74	3.1	<0.1	9.8	0.48	0.0	0.0	0.0
8-91	8.96	1.16	6.4	0.1	0.1	0.67	0.0	<0.1	0.3
8-94	9.26	0.92	219.8	1.2	5.0	0.59	6.4	3.2	0.0

Table 4. Daily rations consumed by individual herring (g wet weight) based on the exponential model of gastric evacuation, taking into consideration the actual ambient temperature and deviations compared to the estimates based on the general model.

Month-year	Ambient temperature (°C)	Daily ration consumed by individual herring (g)	Deviation to general model (%)
3-88	5.85	0.28	–11.6
4-91	4.89	0.62	–21.5
4-93	4.48	0.54	–17.8
4/5-94	3.82	0.62	–35.0
5/6-90	6.37	1.90	–14.2
5/6-91	4.89	1.19	–24.6
5/6-93	4.48	1.10	–24.1
5/6-94	3.82	1.24	–36.0
6/7-88	5.63	1.60	–19.7
7-91	5.63	1.90	–18.5
7/8-88	5.63	0.63	–13.8
8-91	5.63	0.97	–15.9
8-94	4.25	0.61	–34.1

Table 5. Daily rations of cod, sprat, and other fish larvae (in numbers) consumed by individual herring and sprat.

	Daily ration consumed by individual herring			Daily ration consumed by individual sprat		
	Numbers of larvae			Numbers of larvae		
Month-year	Cod	Sprat	Others	Cod	Sprat	Others
3-88	0.023	0.039	0.000	0.000	0.000	0.360
4-91	0.001	0.011	0.003	0.000	0.000	0.000
4-93	0.000	0.000	0.980	0.231	2.019	1.831
4/5-94	0.000	0.000	0.227	0.000	0.000	0.000
5/6-90	0.000	0.457	0.000	0.068	6.247	0.060
5/6-91	0.000	0.087	0.000	<0.001	0.005	<0.001
5/6-93	0.000	0.000	0.000	0.000	0.000	0.000
5/6-94	0.000	0.000	0.000	0.000	0.000	0.000
6/7-88	0.001	0.005	0.000	0.000	0.000	0.000
7-91	0.019	0.000	0.000	0.048	0.145	0.000
7/8-88	0.004	0.040	0.000	0.000	0.000	0.000
8-91	0.252	1.947	0.000	0.000	0.000	0.000
8-94	0.068	0.000	0.120	0.000	0.000	0.000

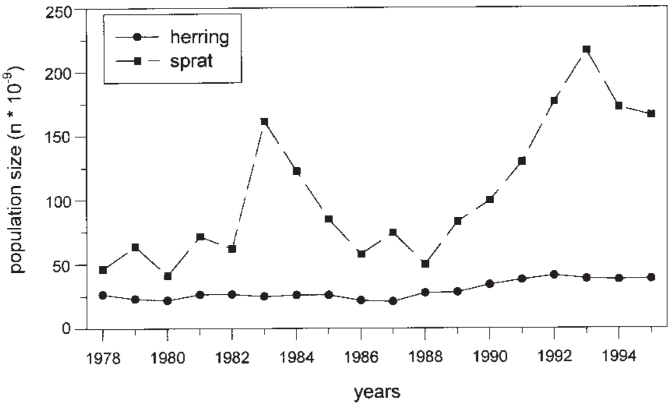


Figure 5. Herring and sprat stock size (age 1+, beginnning of the year) in the central Baltic (herring: Subdiv. 25-27, sprat: Subdiv. 25, 26, and 28) estimated by MSVPA (Anon. 1996a).

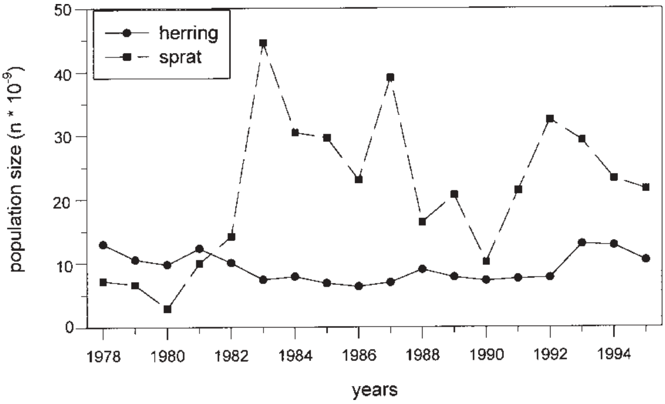


Figure 6. Herring and sprat population size (age 1+, beginning of the year) in Subdiv. 25 estimated by down-scaling MSVPA results for central Baltic stocks by horizontal distributions obtained by hydroacoustic surveys.

According to hydroacoustic surveys carried out in May-June and in August, on average 22 and 34% of the herring population in Subdivision 25 concentrate in the Bornholm Basin and 12 and 25% in the central basin, respectively. A 10-fold increase of the CPUE from March-April to May-June as determined from pelagic trawl surveys indicates that only about 1-2% of the herring population stays in the area during the spawning time of spring spawners. Unlike herring, prespawning sprat concentrate in the Bornholm Basin. This is reflected in the horizontal distributions derived from hydroacoustic surveys, indicating that approximately 58 and 36% of the sprat population aggregate in the Bornholm Basin (entire and central basin, respectively) in May-June. After the end of the spawning season sprat leave the area, resulting in a reduction of the corresponding proportion to about 21 and 8%. Applying these percentages to the population estimates derived for Subdivision 25 resulted in quarterly predator population sizes presented in Figures 7 and 8. For herring a pronounced seasonal fluctuation with lowest abundances in the first quarter and a drastic increase until the third quarter is apparent. For sprat the estimation procedure resulted in an opposite trend with lowest abundances in the third quarter, but considerably less seasonal fluctuation.

Comparing population sizes calculated for May 1995 with results from the hydroacoustic survey carried out in the same month revealed abundances in the same order of magnitude, while the hydroacoustic estimates are constantly lower (33 and 26% for herring and 27 and 40% for sprat in the entire and the central basin, respectively).

Daily consumption compared to the standing stock and daily production

The total daily consumption of cod eggs by herring and sprat populations in the central Bornholm Basin was calculated from individual daily rations determined by the temperature-independent model of evacuation and from the abundances of predators in the area enclosed by the 75-m depth contour (Table 6). Comparing these consumption rates with the standing stock of cod eggs in the area revealed an intermediate predation pressure by herring in spring months (15-23% of the standing stock), with the exception of April-May 1994, when only a rather limited ingestion rate was calculated. Highest consumption rates were estimated for July 1991 and August 1994 (29 and 40% of the standing stock), whereas for remaining dates rather low values were computed. For the predator sprat the ingestion rates determined for the spring period were considerably higher, i.e., ranging from 59% to well above the standing stock of cod eggs. The only sampling dates without high predation were March 1988 (with an overall low feeding intensity) and spring 1994. In summer, when sprat switched to cladocerans as the most important prey organisms, the daily consumption of cod eggs was well below the standing stock (<17%).

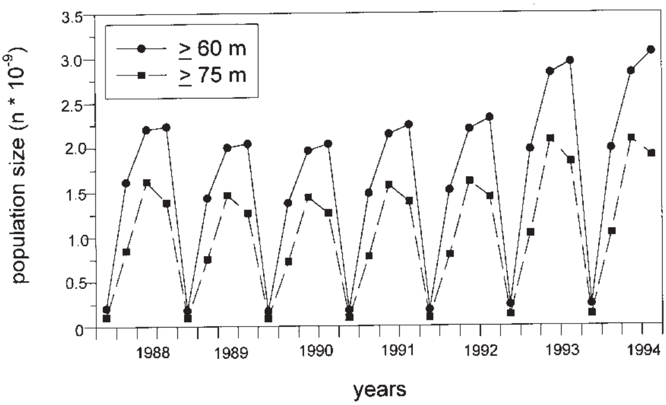


Figure 7. Herring population size (age 1+, midpoint of quarter) in the entire and central Bornholm Basin (areas enclosed by the 60- and 75-m depth contours, respectively).

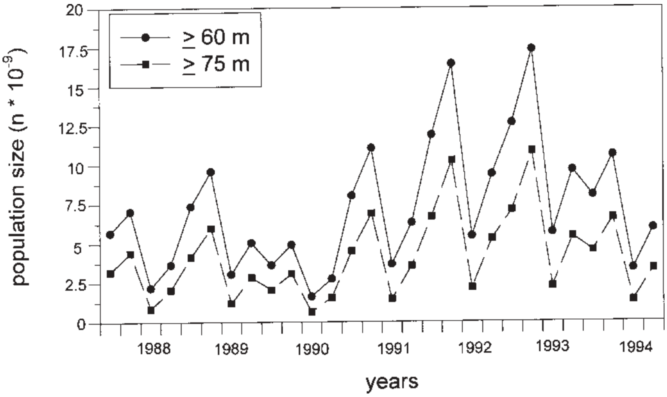


Figure 8. Sprat population size (age 1+, midpoint of quarter) in the entire and central Bornholm Basin (areas enclosed by the 60- and 75-m depth contours, respectively).

Table 6. **Herring and sprat population sizes (age 1+) in the central Bornholm Basin and daily consumption rates of cod eggs by these populations related to the standing stocks and daily production rates of cod eggs in the area.**

Month-year	Population size ($n \times 10^{-6}$)		Cod egg consumption ($n \times 10^{-9}$)		Cod eggs ($n \times 10^{-9}$)	
	Herring	Sprat	Herring	Sprat	Abundance	Production
3-88	103	5,014	0.9	22.2	82.1	47.4
4-91	89	6,896	1.0	127.9	96.6	56.7
4-93	87	11,124	5.7	412.1	144.6	91.7
4/5-94	313	6,751	2.5	28.6	119.5	72.9
5/6-90	720	3,069	17.3	81.3	78.5	52.6
5/6-91	767	6,587	30.2	324.0	134.4	75.5
5/6-93	667	10,570	22.9	92.2	156.0	106.6
5/6-94	1,022	6,435	70.0	58.3	459.4	284.4
6/7-88	1,724	905	20.6	0.0	125.13	79.2
7-91	1,611	1,432	81.0	47.2	282.2	193.0
7/8-88	1,655	875	5.2	<0.1	115.6	72.4
8-91	1,572	1,402	10.1	0.0	125.0	90.2
8-94	2,077	1,327	456.6	8.4	1,150.4	620.0

Table 7. **Herring and sprat population sizes (age 1+) in the Bornholm Basin and daily consumption rates of sprat eggs by these populations related to daily production rates of sprat eggs in the area.**

Month-year	Population size ($n \times 10^{-6}$)		Sprat egg consumption ($n \times 10^{-9}$)		Sprat egg ($n \times 10^{-9}$) Production
	Herring	Sprat	Herring	Sprat	
3-88	198	8,031	1.2	9.3	304.2
4-91	170	11,045	4.8	1,048.8	951.6
4-93	166	17,817	0.7	1,408.3	1,493.5
4/5-94	225	10,814	0.5	32.6	910.5
5/6-90	1,376	4,916	37.5	1,607.8	436.1
5/6-91	1,465	10,551	141.5	1,418.5	976.0
5/6-93	1,273	16,930	2.8	77.5	1,531.8
5/6-94	1,951	10,306	3.0	477.5	933.9
6/7-88	2,345	2,295	13.6	46.8	138.1
7-91	2,190	3,631	22.4	193.9	216.2
7/8-88	2,251	2,218	0.1	0.0	16.0

Comparing the total daily consumption by both predators with the daily production of cod eggs (Table 6), revealed for all April to June dates (with the exception of 1994) considerably higher consumption than production rates. Predation was well below production in March 1988 as well as in summer 1988 and 1991 (6-66%). In 1994 intensive consumption of cod eggs by herring in August and relatively low ingestion rates by sprat in spring led to an inverse seasonal trend of increasing predation pressure during the cod spawning season.

The daily consumption of sprat eggs by herring in the Bornholm Basin (area enclosed by the 60-m depth contour) was estimated to be far below the corresponding daily egg production (<15%). In contrast, cannibalism by sprat was considerably more important during the main spawning season (Table 7). With the exception of April-May 1994 and May-June 1993 at least 34% of the sprat egg production was consumed by sprat. Especially in 1990-1991 the rates of consumption either reached or exceeded the estimated production. In the beginning and the end of the sprat spawning season, the number of sprat eggs ingested per day was calculated to be well below the daily number of eggs produced.

Estimates of the daily consumption of cod and sprat larvae by herring and sprat populations in the Bornholm Basin are compared to the corresponding abundance values in Table 8. Highest ingestion rates of cod larvae by herring were obtained in summer months, reaching 0.4-1.7% of the abundance. The calculated consumption rates of cod larvae by sprat were in general also low, i.e., maximum of 7% of the corresponding abundance values. Exceptions were encountered in April 1993 and May-June 1990, when 89 and 26% of the abundance were estimated to be consumed by the sprat population.

The predation on sprat larvae by both clupeid populations was rather low, i.e., in general less than 1.5% of the standing stock. An exception was August 1981, when 12% of the standing stock was consumed per day by herring. Due to missing data on the abundance of sprat larvae in 1993-1994, it is presently impossible to evaluate the impact of the relatively high predation by sprat derived for April 1993.

Discussion

Comparing the estimated consumption by herring and sprat populations in the central Bornholm Basin with the standing stock of cod eggs revealed higher daily consumption rates than abundance values in 4 out of 13 sampling dates. Especially in spring, i.e., from April to June, high consumption rates were derived, with sprat being the most important predator. An exception was 1994, when especially sprat had ingested only limited amounts of fish and, in particular, cod eggs. In summer the numbers of cod eggs consumed were in general well below the corresponding standing stocks, especially because sprat migrated out of the area after spawning and remaining sprat switched from copepods and

Table 8. Herring and sprat population sizes (age 1+) in the Bornholm Basin and daily consumption rates of cod and sprat larvae by these populations related to the standing stock of larvae in the area.

Month-year	Population size (n × 10^{-6})		Cod larvae consumption (n × 10^{-6})		Sprat larvae consumption (n × 10^{-6})		Larvae abundance (n × 10^{-6})	
	Herring	Sprat	Herring	Sprat	Herring	Sprat	Cod	Sprat
3-88	198	8,031	5	0	8	0	1,067	4,177
4-91	170	11,045	0	0	2	0	2,133	*314,500
4-93	166	17,817	0	4,110	0	35,966	4,622	—
4/5-94	225	10,814	0	0	0	0	1,067	—
5/6-90	1,376	4,916	0	337	629	30,710	1,304	2,255,600
5/6-91	1,465	10,551	0	1	128	53	474	*136,280
5/6-93	1,273	16,930	0	0	0	0	1,304	—
5/6-94	1,951	10,306	0	0	0	0	1,541	—
6/7-88	2,345	2,295	1	0	13	0	3,318	97,052
7-91	2,190	3,631	42	176	0	527	2,726	*840,400
7/8-88	2,251	2,218	9	0	90	0	1,304	12,205
8-91	2,138	3,557	538	0	4,161	0	31,758	*35,669
8-94	2,825	3,367	193	0	0	0	45,267	—

*Preliminary data

fish eggs to cladocerans as preferred prey organisms (Köster and Schnack 1994).

A comparison of the calculated daily consumptions with daily production rates of cod eggs showed for all April and May-June dates up to 1993 higher consumption than production values. The deviations were quite considerable in single months, clearly demonstrating either an overestimation of the consumption or an underestimated production. Comparing daily rations based on the general model of evacuation in use and the exponential model taking into account actual ambient temperatures (Temming 1996), overestimated daily rations in the range of 12-36% are obvious for herring and may also be expected for sprat. The reason for this overestimation by the present procedure is slightly lower temperatures within and below the halocline, i.e., the water layer where herring and sprat feed during daytime, compared to temperatures during evacuation experiments. Adjustment to these lower temperatures resulted in decreasing stomach evacuation rates and hence consumption rates.

A further source of uncertainty is the estimation procedure of predator population sizes. As indicated by the hydroacoustic survey conducted in May-June 1995 (Lehmann and Jensen 1996), the predator population sizes might be overestimated on the order of 26-40%. Thus, for both predators updated VPA runs have to be conducted for Subdivision 25 to check the first step of the downscaling procedure adopted, i.e., from the central Baltic to Subdivision 25. Additional hydroacoustic survey results from August 1994 and June-July 1996 presently analyzed will be used to examine the second downscaling step to the area of the Bornholm Basin.

The relatively low predation on cod eggs by sprat in May-June 1993 and the two sampling dates in spring 1994 are presently difficult to explain. Although cod eggs were available in the plankton in high quantities, sprat preyed less intensively on them than in previous years. The substantial reduction in daily ingestion rates computed already for May-June 1993 is, however, partly compensated by a large sprat stock in the area, yielding still considerable consumption rates. Despite the differences in the amount of fish eggs in the stomachs in May-June 1990-1991 compared to May-June 1993-1994, the general diet compositions and also the total amounts of food ingested were rather similar in both periods. Data on the abundance and biomass of mesozooplankton available from vertically integrating plankton sampling on several stations in May-June 1991 and 1993 revealed a lower abundance of suitable food in the latter year (Schöler 1995). Assuming an inverse relationship of predation on eggs and the abundance of zooplankton suitable as food for sprat, as observed regularly during summer months (Köster and Schnack 1994), these data do not explain the reduction in predation on fish eggs by sprat in May-June 1993. Comparing the vertical distribution of cod eggs in May-June 1990-1991 (Wieland 1995) and May-June 1993-1994 (Wieland unpubl.) revealed a significant difference between both periods. Caused by the major Baltic inflow in January 1993 (Matthäus and Lass 1995), resulting in considerably increased salinities in and below the halocline, maximum cod egg concentrations were encountered in water depths of 50-70 m. Before the inflow, maximum cod egg densities were observed deeper in the water column (65-75 m). This indicates that vertically resolving data on the abundance and composition of mesozooplankton in relation to the corresponding data on fish eggs need to be analyzed to explain the different selection patterns encountered. The high consumption of cod eggs estimated for herring in May-June and August 1994 can be explained by the far-above-average egg abundances recorded during the ichthyoplankton surveys in these months.

A positive selection of older egg stages, due to better visibility of the more developed stages described by Wieland and Köster (1996), indicates the necessity to estimate daily consumption separately for individual egg stages. These values should be compared to the corresponding daily production of each egg stage.

Other potential predators show only limited horizontal, vertical, or temporal overlap with cod and sprat eggs as prey. If spatially overlapping, they are neither able to detect nor to capture the motionless relatively large eggs (Köster 1994). Scyphomedusae of *Cyanea capillata* appearing in considerable quantities in the plankton in later summer, i.e., in the final period of the cod spawning season, are an exception (Margonski and Horbowa 1996).

Despite the above reservations and uncertainties, the findings suggest that predation on cod eggs by herring and sprat may be a substantial source of egg mortality, especially during the early months of the spawning season, when the availability of mesozooplankton is rather restricted. In this respect the shift in peak spawning time from May to June-July as observed in recent years (Wieland and Horbowa 1996), may increase cod egg survival rates by reduced predation pressure. However, the importance of predation for the reproductive success of cod depends on other causes of mortality. Even a high predation mortality of cod eggs will have no effect on recruitment if the eggs are subject to death due to other reasons, i.e., lack of oxygen in and below the halocline (e.g., Plikshs et al. 1993). Thus the observed shift in peak spawning time to summer month may have a negative effect on egg survival caused by enhanced oxygen utilization in water masses (MacKenzie et al. 1996b) advected into the spawning area in the preceding winters (Matthäus and Franck 1992). In contrast to 1988, the hydrographic conditions in 1991 and especially after the 1993 inflow allowed a successful cod egg development in major parts of the bottom water throughout the spawning season (Bagge and Thurow 1993, Hinrichsen and Wieland 1996). Thus, predation probably created a considerable source of cod egg mortality in these years, especially caused by sprat in April to June 1991 and 1993, and by herring in May to August 1994. At least for 1991, this is in agreement with the observation that most surviving 0-group cod of this relatively abundant year class (Anon. 1996b) originated from cohorts which hatched late in the spawning season (Anon. 1993).

The comparison of sprat egg consumption and daily production revealed high predation pressures in April to July 1990-1991, whereas the ingestion rates computed for most recent sampling dates were considerably lower. This indicates a significant cannibalism in the first part of the investigation period. However, the egg production method applied and especially the assumptions made concerning the spawning intensity within the spawning season allowed for a rough estimation of the daily egg production only. Assuming the gonadosomatic index to be representative for the spawning intensity has probably produced rather high production estimates at the beginning and the end of the spawning season and too low values at peak spawning time. This is obvious when comparing abundance values derived from ichthyoplankton surveys in March, April, and the beginning of August 1988 with computed production values, i.e., the first being only 41, 59, and 6% of the latter and not vice versa as expected. Thus, the impact of egg cannibalism is probably underestimated in the first and last months of the sprat spawning season and overestimated for peak spawning time.

In other spawning areas of sprat in the central Baltic, i.e., the Gotland Basin and Gdansk Deep, sprat eggs generally float above the oxygen-depleted water layers and successful reproduction is regularly observed (Makarchouk 1995). In these spawning areas predation on fish eggs by clupeid fishes seems to be generally less pronounced than in the Bornholm Basin (Fetter and Davidjuka 1996, Patokina 1996). This might be due to a limited vertical overlap between predator and prey, a hypothesis to be tested by concurrent vertically resolving ichthyoplankton and stomach sampling. Thus the predation on sprat eggs quantified for the Bornholm Basin has considerable influence on the recruitment of the stock component in Subdivision 25 only. This may explain the decline of this component in the central Baltic within the second half of the 1980s to low levels in most recent years as indicated by hydroacoustic surveys.

Cod and sprat larvae are obviously not substantially affected by herring and sprat predation. This can be explained by a limited vertical overlap of prey and predator. Cod and sprat larvae show a bimodal distribution with highest concentrations of older larvae in intermediate and upper water layers (Wieland and Zuzarte 1991, Grønkjær 1994). Only newly hatched larvae concentrate within or below the halocline, where they are available as prey of herring and sprat aggregating in these water layers while feeding (Köster and Schnack 1994). Occasionally, substantial predation on cod larvae was observed for sprat, i.e., in April 1993 and May-June 1990. Comparison of the available prey in the food supply and the diet composition showed sprat to be obviously attracted by extraordinary high abundance of larvae from other fish species. While hunting these, they also consumed above-average numbers of cod larvae. Herring were not feeding on these larvae at the same time, which can be explained by the small size of the young larvae. Comparing the estimated cannibalism on sprat larvae with the restricted abundance data available may indicate a minor influence on the survival of sprat larvae only. The amount of fish larvae determined in herring and sprat stomachs may have been generally underestimated if digestion and evacuation continues during the time from catch to preservation. Although the duration of trawling and the handling time on deck was reduced as far as possible in the present study, the time lag was long compared to digestion times of less than 60 min reported for small larvae as prey of planktivorous fish (Hunter and Kimbrell 1980). However, this possible bias may be of minor importance for two reasons: (a) the digestion time of larvae is reported to be prolonged significantly if less quickly digestible prey organisms (e.g., copepods) are also ingested (Christensen 1983, Balfoort 1984); and (b) stomach evacuation seems to be retarded as a reaction to stress during the catching and handling process (Lockwood 1980, Köster et al. 1990). Despite this, the estimated consumption rates of cod and sprat larvae by clupeid fish in the Bornholm Basin are sensitive to the assumed average digestion time of a fish larva. Furthermore, data on larval abundance is biased by drift of older larvae out of the study area (Hinrichsen et al. In press). Thus, it is rather likely that the ichthyoplankton surveys as well as the stomach sampling programs have covered only a part of the distribution area. This refers especially to sprat larvae and to some extent also to sprat eggs, because sprat progressively enlarge their spawning area from spring to summer (e.g., Grimm and Herra 1984).

Conclusions

Daily consumption rates of cod and sprat eggs estimated for herring and sprat populations in the Bornholm Basin exceeded the daily egg production in several investigated periods in 1988-1994. Especially during the first months of the spawning seasons, when the abundance of suitable mesozooplankton food is low, the predation pressure by sprat is estimated to be rather high. During this time of the year herring concentrate in their coastal spawning areas as spring spawning herring form the major part of the stock in the central Baltic. Hence, they do not significantly contribute to the predation-induced egg mortality in the early cod and sprat spawning periods. Sprat spawn in the Bornholm Basin until July. Thereafter a part of the population leaves this area and remaining individuals switch from copepods and fish eggs to cladocerans as main prey organisms. Concurrent with the return of the herring from the coastal areas to their feeding grounds in the Bornholm Basin, predation on cod eggs by herring increases to considerably high levels. Coinciding with substantial changes in the hydrographic conditions caused by a major Baltic inflow in the beginning of 1993, having influence on the vertical distribution of prey and predator, consumption by sprat declined, whereas predation by herring increased, especially in late spring and summer.

The daily egg consumption rates presented for both predator populations have to be taken as overestimations. Considering the actual ambient temperature in the evacuation model resulted in a reduction of daily rations by 12-36% for herring, which may also be expected for sprat. Predator population sizes derived on the basis of MSVPA results downscaled by historical hydroacoustic survey data compared with results from a recent hydroacoustic survey indicate a possible overestimation of the predator populations by 25-40%. Thus the egg consumption rates by the herring and sprat populations may be overestimated on the order of 38-66%.

In contrast to the egg stage, cod and sprat larvae appear not to be substantially affected by predation, mainly due to a limited vertical overlap between prey and predator. As an exception, significant predation on cod larvae by sprat occurred when high abundances of other fish larvae were encountered in the plankton, triggering sprat to switch to fish larvae as prey. Herring did not feed on these larvae at the same time, probably due to the small average size of the newly hatched larvae.

Acknowledgments

We thank K. Wieland for supplying unpublished data on the abundance and stage duration of cod eggs, R. Voss for his support in estimating cod and sprat larvae abundance values, P.O. Larsson and M. St. John for coordinating the sampling on board R/V *Argos* and R/V *Dana* in August 1994, and K. Lehmann and J. Tomkiewicz for running the hydroacoustic survey in 1995. This work was performed as part of the Baltic CORE project funded by a research grant from the European Union (AIR2 94 1226).

References

Alheit, J. 1988. Reproductive biology of sprat, *Sprattus sprattus*: Factors determining annual egg production. J. Cons. Int. Explor. Mer 44:162-168.

Anonymous. 1993. Report of the Study Group on the Evaluation of Baltic Fish Data. ICES C.M. 1993/J:5.

Anonymous. 1996a. Report of the Working Group on Multispecies Assessments of Baltic Fish. ICES C.M. 1996/Assess:1.

Anonymous. 1996b. Report of the Baltic Fisheries Assessment Working Group. ICES C.M. 1996/Assess:13.

Aro, E. 1989. A review of fish migration patterns in the Baltic. Rapp. P.-v. Réun. Cons. int. Explor. Mer 190:72-96.

Bagge, O. 1996. Inflows to the Baltic, predation on cod eggs and year class strength in Subdivisions 25-28. ICES C.M. 1996/C+J:9.

Bagge, O., and F. Thurow. 1993. The Baltic cod stock, fluctuations and the possible causes. ICES Mar. Sci. Symp., 198:254-268.

Bagge, O., F. Thurow, E. Steffensen, and J. Bay. 1994. The Baltic cod. Dana 10:1-28.

Bailey, K.M., and E.D. Houde. 1989. Predation on early developmental stages of marine fishes and the recruitment problem. Adv. Mar. Biol. 25:1-83.

Bajkov, A.D. 1935. How to estimate the daily food consumption of fish under natural conditions. Trans. Am. Fish. Soc. 65:288-289.

Balfoort, H. 1984. Experiments on digestion rate of herring larvae in fish stomachs. ICES C.M. 1984/H:32.

Christensen, V. 1983. Predation by sandeel on herring larvae. ICES C.M. 1983/L:27.

Elwertowski, J. 1960. Biologische Grundlagen der Sprottenfischerei in der östlichen und mittleren Ostsee. Fisch. Forsch. 3(4):1-19.

Fetter, M., and A. Davidjuka. 1996. Herring daily feeding activity in the eastern Baltic Sea. ICES C.M. 1996/J:26.

Grimm, S.K., and T. Herra. 1984. Spawning cycles of southern Baltic fishes based on surveys of eggs and larvae. ICES C.M. 1984/J:30.

Grønkjær, P. 1994. Vertical distribution, nutritional condition and growth of cod larvae (*Gadus morhua* L.) in the Bornholm Basin. Progress Report, Institute of Biological Science, Aarhus University, 49 pp.

Grønkjær, P., C. Möllmann, and R. Voss. 1995. Abundance and distribution of larval cod (*Gadus morhua*) in the Bornholm Basin. ICES C.M. 1995/J:24.

Heidrich, H. 1925. Über die Fortpflanzung von *Clupea sprattus* in der Kieler Bucht. Wiss. Meeresunters., Neue Folge, Abt. Kiel 20:1-47.

Hinrichsen, H.-H., A. Lehmann, M. St. John, and B. Brügge. In press. Modelling the cod larvae drift in the Bornholm Basin in summer 1994.

Hinrichsen, H.-H., and K. Wieland. 1996. Reproduction volume of Baltic cod in the Bornholm Basin estimated from single point measurements. ICES C.M. 1996/C+J:7.

Hunter, J.R., and C.A. Kimbrell. 1980. Egg cannibalism in the northern anchovy, *Engraulis mordax*. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 78(3):811-816.

Jobling, M. 1986. Mythical models of gastric emptying and implications for food consumption studies. Environ. Biol. Fishes 16(1-3):35-50.

Kändler, R. 1949. Untersuchungen über den Ostseedorsch während der Forschungsfahrten mit dem R.F.D. “Poseidon” in den Jahren 1925-38. Ber. Wiss. Komm. Meeresforsch. 11:137-245.

Köster, F.W. 1994. Der Einfluß von Bruträubern auf die Sterblichkeit früher Jugendstadien des Dorsches (*Gadus morhua*) und der Sprotte (*Sprattus sprattus*) in der zentralen Ostsee. Ber. Inst. f. Meeresk., Kiel, 261, 286 pp.

Köster, F.W., and D. Schnack. 1994. The role of predation on early life stages of cod in the Baltic. Dana 10:179-201.

Köster, F.W., W. Schober, A. Korves, and R. Schneider. 1990. Tank experiments on board: A useful tool for the estimation of stomach evacuation rates? ICES C.M. 1990/G:34.

Lehmann, K., and T.F. Jensen. 1996. Abundance of sprat and herring in Bornholm Basin estimated during R/V DANA hydroacoustic trawl survey May 1995. Contribution to the AIR CORE Consolidated Progress Report 1995/96.

Lockwood, S.J. 1980. Density-dependent mortality in 0-group plaice (*Pleuronectes platessa* L.) populations. J. Cons. int. Explor. Mer 39:148-153.

MacKenzie, B.R., M.A. St. John, and K. Wieland. 1996a. Eastern Baltic cod: Perspectives from existing data on processes affecting growth and survival of eggs and larvae. Mar. Ecol. Prog. Ser. 134:265-281.

MacKenzie, B.R., M.A. St. John, M. Plikshs, H.-H. Hinrichsen, and K. Wieland. 1996b. Oceanographic processes influencing seasonal and interannual variability in cod spawning habitat in the eastern Baltic Sea. ICES C.M. 1996/C+ J:4.

Makarchouk, A. 1995. Abundance and composition of ichthyoplankton in early nineties. 14th BMB Symposium, Pärnu, 5-8 September 1995.

Margonski, P., and K. Horbowa. 1996. Vertical distribution of cod eggs and medusae in the Bornholm Basin. Polish-Swedish Symposium on Baltic cod. Medd. Havfiskelab. 327:7-17.

Matthäus, W., and H. Franck. 1992. Characteristics of major Baltic inflows: A statistical analysis. Continental Shelf Res. 12:1375-1400.

Matthäus, W., and H.U. Lass. 1995. The recent salt inflow into the Baltic sea. J. Phys. Oceanogr. 25:280-286.

Müller, A., and T. Pommeranz. 1984. Vertical distribution of fish eggs in the Bornholm Basin, Baltic. Int. Symp. on Early Life History of Fishes and 8th Annual Larval Fish Conf., Vancouver, 1984.

Müller, A., K. Muhsin, and F.W. Köster. 1990. Ovarian maturation and batch fecundity in Baltic sprat from the Bornholm Basin, 1988. ICES C.M. 1990/J:30.

Olson, R.J., and A.J. Mullen. 1986. Recent developments for making gastric evacuation and daily ration determinations. Environ. Biol. Fishes 16(1-3):183-191.

Patokina, F.A. 1996. Feeding peculiarities and interrelations of abundant fishes from the Baltic Sea. ICES C.M. 1996/J:5.

Pennington, M. 1985. Estimating the average food consumption by fish in the field from stomach contents data. Dana 5:81-86.

Petrowa, E.G. 1960. Fecundity and maturation of sprat in the Baltic. VNIRO 42:99-108 (in Russian).

Plikshs, M., M. Kalejs, and G. Grauman. 1993. The influence of environmental conditions and spawning stock size on the year-class strength of the eastern Baltic cod. ICES C.M. 1993/J:22.

Schöler, A. 1995. Der Einfluß von Einstromlagen auf die Zusammensetzung des Zooplanktons im Bornholm Becken, südliche Ostsee. Dipl. thesis, Universität Bonn, 92 pp.

Sparholt, H. 1994. Fish species interactions in the Baltic Sea. Dana 10:131-162.

Temming, A. 1996. Die quantitative Bestimmung der Konsumtion von Fischen: Experimentelle, methodische und theoretische Aspekte. Habilitation thesis, University of Hamburg, 235 pp.

Temming, A., and F.W. Köster. 1990. Stomach evacuation rates of cod and herring estimated from ship-board tank experiments and field data. ICES C.M. 1990/G:31.

Tyler, A. 1970. Rates of gastric emptying in young cod. J. Fish. Res. Board Can. 27(7):1177-1189.

Wieland, K. 1988. Distribution and mortality of cod eggs in the Bornholm Basin (Baltic Sea) in May and June 1986. Kiel. Meeresforsch. Sonderh. 6:331-340.

Wieland, K. 1995. Einfluß der Hydrographie auf die Vertikalverteilung und Sterblichkeit der Eier des Ostseedorsches (*Gadus morhua callarias*) im Bornholmbecken, südliche zentrale Ostsee. Ber. Inst. f. Meeresk., Kiel, 266, 114 pp.

Wieland, K., and K. Horbowa. 1996. Recent changes in peak spawning time and location of spawning of cod in the Bornholm Basin, Baltic Sea. ICES C.M. 1996/J:15.

Wieland, K., and F.W. Köster. 1996. Size and visibility of Baltic cod eggs with reference to size-selective and stage-dependent predation mortality. J. Appl. Ichthyol. 12:83-89.

Wieland, K., and F. Zuzarte. 1991. Vertical distribution of cod and sprat eggs and larvae in the Bornholm Basin (Baltic Sea) 1987-1990. ICES C.M. 1991/J:37.

Wieland, K., U. Waller, and D. Schnack. 1994. Development of Baltic cod eggs at different levels of temperature and oxygen content. Dana 10:163-177.

Bioenergetics Estimation of Juvenile Pollock Food Consumption in the Gulf of Alaska

Lorenzo Ciannelli and Richard Brodeur
National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle, Washington

Extended abstract

The juvenile stage of walleye pollock (*Theragra chalcogramma)* in the Gulf of Alaska is a key element in both the recruitment to the adult stage and the trophic web of the ecosystem (Brodeur and Wilson 1996a). The high biomass of age-0 pollock, coupled with the high feeding rate characteristic of juvenile fishes in general, suggests that a high proportion of the ecosystem energy flows through this stage (Brodeur and Wilson 1996b).

Although some investigations on food consumption of juvenile pollock have already been done, their energetic demand in relation to the availability of food in the environment is still uncertain. It is possible that juvenile pollock experience food limitation during high abundance years which could result in slower growth and a higher mortality rate. Indeed, recruitment models of pollock (Megrey et al. 1996) indicate that most of the interannual variability in mortality occurs during the passage from larvae to early juveniles.

We used empirical information on food habits, growth, fish density, and thermal history encountered by these juveniles, together with literature data on physiological rate to estimate total age-0 pollock food consumption for two high-density areas along the Alaska Peninsula in the Gulf of Alaska using bioenergetic modeling (Hewett and Johnson 1992). One objective of this study was to compare the total cohort consumption with zooplankton biomass and production estimates from the same areas and time of the year.

Over the month of bioenergetics simulation (20 August to 24 September), individual daily consumption ranged from 16.0% of body weight at the beginning to 6.0% of body weight at the end (Figure 1A).

Daily growth rate expressed as a percentage of body weight went from 9.3% at the end of the first day to 2.4% at the end of the last day (Figure 1B). Overall growth efficiency in terms of biomass was 47.9%, while daily growth efficiency decreased from 59.1% at the beginning of the simulation period to 40.7% at the end (Figure 1C). The model output corresponds rather well with field estimates of daily ration made by Merati and Brodeur (1996), based on gut fullness and evacuation time. For the same fish samples analyzed in this application, they estimated a daily ration between 7.4% and 8.4% of body weight depending on the model used. If we assume that this estimate applied to the median day of the field study (i.e., 15 September), model estimation of daily ration for the same day (25th day of the simulation period) was 7.0% of body weight.

Total age-0 cohort consumption at the end of the simulation period was 1,527 kg per km^2 and 491 kg per km^2 in the two areas. The difference was mainly due to the higher age-0 pollock density in the first area. In both areas, the consumption of euphausiids was more than 70% of the total consumption. When comparing instantaneous consumption of individuals and total cohort of age-0 pollock during the simulation period, we found the opposite pattern to hold: increasing in the former and decreasing in the latter, mainly because the effect of the population decline exceeded the effect of instantaneous individual consumption. It should be possible to use bioenergetics to study the whole generational consumption pattern, and identify the stage at which this consumption attains a maximum. This would be the cohort “trophic critical point,” at which the population is most sensitive to food limitation (especially when considering an ecosystem with few competing pelagic predators such as the one in the Gulf of Alaska). It has been shown that the biomass of a typical pollock cohort peaks during the age-0 stage (Brodeur and Wilson 1996a). Assuming that the maximum cohort biomass coincides with the highest cohort instantaneous consumption, it can be speculated that the passage from the late larval to the juvenile stage is the most demanding in terms of population food consumption. This theory is supported by evidence that this period is characterized by most of the variability in the stage-specific mortality rate (Megrey et al. 1996) and, in general, by a high mortality rate (Bailey et al. 1996).

From the observed zooplankton biomass we derived a zooplankton production rate using literature data of production to biomass (P/B) ratios. This analysis was restricted to copepods and euphausiids, which accounted for more than 85% in weight of the age-0 pollock diet. Comparison of total cohort consumption with zooplankton production and biomass indicated that there was a potential for food limitation, especially for euphausiids in Area 1 (Figure 2), although we recognize that euphausiids may not be adequately sampled by our plankton gear. It is unknown whether age-0 pollock have the ability to switch to other possibly less preferred prey at this time and what effect this switch may have on their growth potential. Nevertheless, this might be part of a nat-

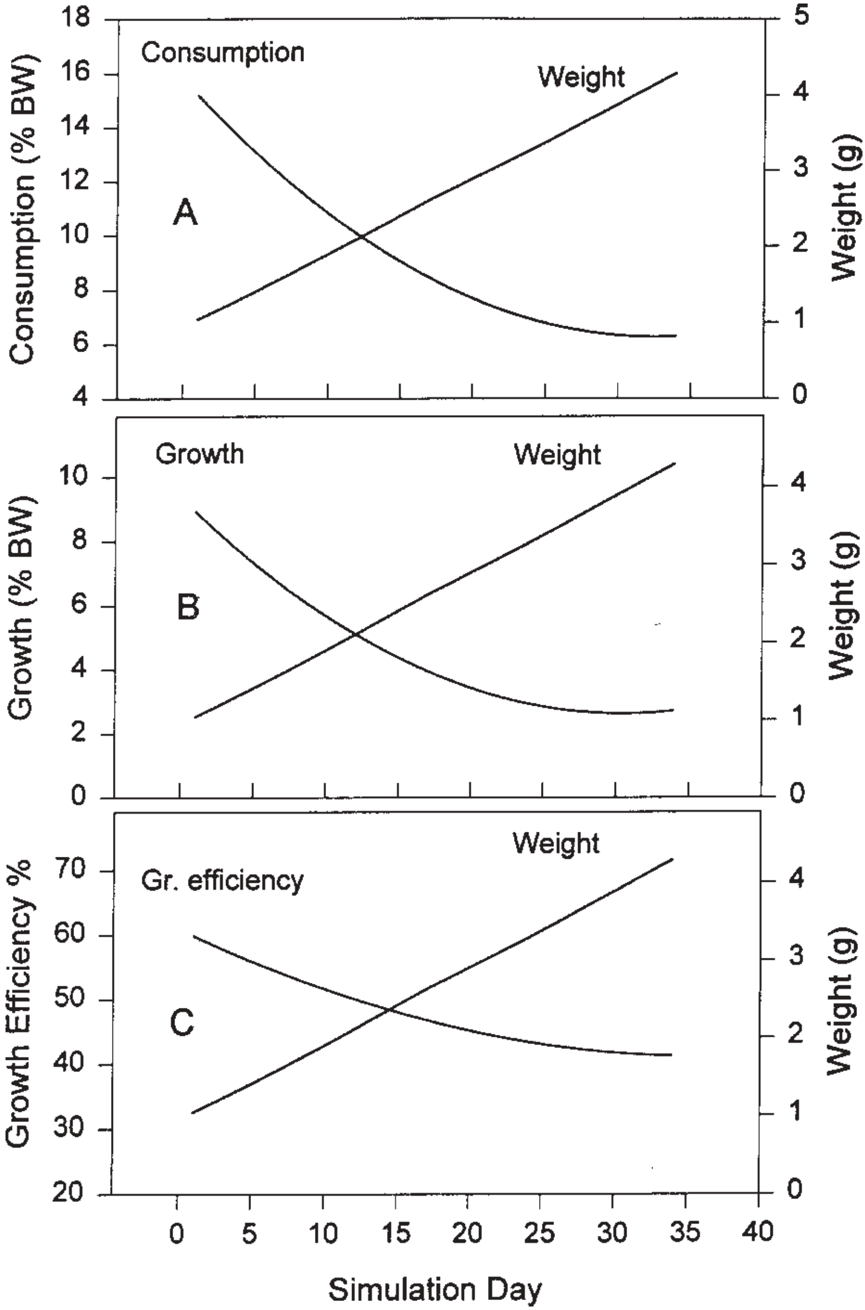


Figure 1. Model estimates of age-0 pollock daily individual consumption (A), growth (B), and growth efficiency (C).

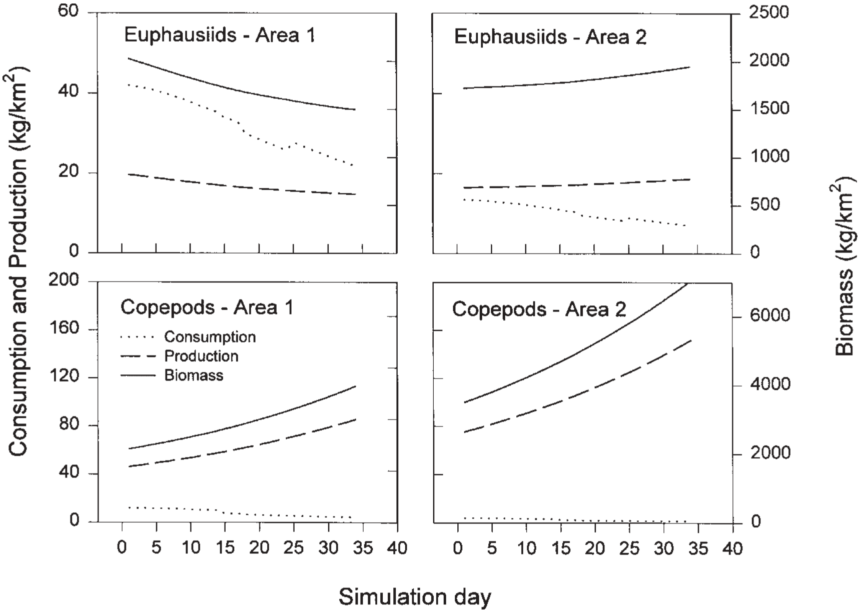


Figure 2. Estimates of age-0 cohort consumption of euphausiids and copepods in Areas 1 and 2 compared with euphausiid and copepod production and biomass in each area.

ural process which leads to the winter situation, when both age-0 pollock consumption and zooplankton biomass are very low. In order to gain more insight on food limitation analysis of age-0 pollock, we emphasize the importance of concurrent production and biomass estimates of the next lower trophic level (zooplankton).

References

Bailey, K.M., R.D. Brodeur, and A.B. Hollowed. 1996. Cohort survival patterns of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Alaska: A critical factor analysis. Fish. Oceanogr. 5(Suppl. 1):179-188.

Brodeur, R.D., and M.T. Wilson. 1996a. A review of the distribution, ecology and population dynamics of age-0 walleye pollock in the Gulf of Alaska. Fish. Oceanogr. 5(Suppl. 1):148-166.

Brodeur, R.D., and M.T. Wilson. 1996b. Mesoscale acoustic patterns of juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. Can. J. Fish. Aquat. Sci. 53:1951-1963.

Hewett, S.W., and B.L. Johnson. 1992. Fish bioenergetics model 2. An upgrade of a generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Tech. Rep. WIS-SG-92-250, 2nd edn., 79 pp.

Megrey, B.A., A.B. Hollowed, S.R. Hare, S.A. Macklin, and P.J. Stabeno. 1996. Contributions of FOCI research to forecast of year-class strength of walleye pollock in the Shelikof Strait, Alaska. Fish. Oceanogr. 5(Suppl. 1):189-203.

Merati, N., and R.D. Brodeur. 1996. Feeding habits and daily ration of juvenile walleye pollock in the western Gulf of Alaska. NOAA Tech. Rep. 126:65-80.

Proceedings • Forage Fishes in Marine Ecosystems
Alaska Sea Grant College Program • AK-SG-97-01, 1997

Top-Down Controls by Young-of-the-Year Herring (*Clupea harengus*) in the Northern Baltic Proper

Fredrik Arrhenius
Department of Systems Ecology, Stockholm University, Stockholm, Sweden

Abstract

I suggest several top-down controls acting on zooplankton in the northern Baltic proper. (1) The total estimated food consumption by zooplanktivores is high compared to the production of zooplankton. My calculations of consumption by young-of-the-year (YOY) herring indicate that they alone consume 30-60% of the zooplankton produced. (2) YOY clupeids selected certain zooplankton taxa over others. Selective predation on reproducing individuals will further stress the effects that fish may have in preventing zooplankton from achieving maximum possible population growth rate. (3) The calanoid copepods had stronger vertical migrations than less selected taxa. High feeding pressure forces copepods to lower temperatures, permitting longer reproductive cycles.

Introduction

Factors affecting fish stock recruitment often involve early life stages (i.e., between the egg and the end of the first year of life), before fish enter the fishery (Cushing 1975, Smith 1985). Mortality induced directly by starvation, or indirectly by retarded growth rate and subsequent increased vulnerability to predation, can strongly influence recruitment and population variability of major fish stocks (Crowder et al. 1987, Miller et al. 1988). Variability in the abundance of dominant fish populations may, in turn, influence lower trophic levels, producing "cascading trophic interactions" (Carpenter et al. 1985, Carpenter and Kitchell 1993). Therefore, information on the feeding ecology of young fish is important in understanding year-class variation and population growth

---

Author's corresponding address: Institute of Marine Resarch, Box 4, 453 21 Lysekil, Sweden.

rate, as well as ecosystem dynamics in general. These fish may selectively remove larger or preferable prey items, which are generally the most efficient grazers on zooplankton. Many investigations have showed that planktivorous fish can control zooplankton abundance and species composition (cf. Carpenter and Kitchell 1993). Almost all of this research has been done in fresh water, and mainly in relatively small lakes. Traditionally, marine areas have been viewed as structured from below. However, Nixon (1982, 1988) suggested a stronger coupling between fish and lower trophic levels in coastal marine areas than in lakes. One could also expect that trophic interactions should be more obvious in the semi-enclosed brackish Baltic Sea than in many other marine ecosystems, because of the relatively simple structure of the food web (Rudstam et al. 1994).

The goal of this paper was to consider the possibilities of top-down controls of young-of-the-year (YOY) herring, one of the most important zooplanktivorous species in the Baltic Sea, by using a bioenergetics model to simulate population consumption and reviewing the literature.

Material and Methods

To determine predation pressure on prey, food consumption estimates are needed. Direct measurements of food consumption by fish are, however, difficult to obtain and require considerable effort (Elliott and Persson 1978). Therefore, bioenergetics models based on physiological assumptions and field data on fish growth, habitat temperature, and diets have been developed (Kitchell et al. 1977, Rice and Cochran 1984, Ney 1990, Hewett and Johnson 1992). To estimate predator demands, I have used a bioenergetics model developed for metamorphosed YOY herring by Arrhenius (1995), partly based on Rudstam's (1988) model for adult herring, and a software package of Hewett and Johnson (1992). Using this model, the daily energy budget can be calculated for an individual fish. Rates of consumption and respiration are nonlinear functions of fish weight and water temperature. As input parameters to the model, I used information from earlier papers on prey and predator energy values and temperature from the area (Arrhenius 1995, Arrhenius and Hansson 1996). Abundance, growth, and mortality were calculated from International Council for Exploration of the Sea (ICES) rectangles 28-29 in the Baltic Sea (Table 1; Anon. 1991, map in Arrhenius and Hansson 1993).

From my own data and published information, I have tried to quantify the different components of the energy budget of metamorphosed YOY herring (Arrhenius 1995). Uncertainty about whether to model the larvae and larva-to-juvenile transition as a gradual or abrupt change stems from the general lack of observations on clupeids and on the physiology of fishes through the larval and the transition period, and

Table 1. Herring population biomass, mean weights, numbers, and mortalities for juveniles in the northern Baltic Sea (ICES areas 28-29).

Age-class	Date	Population numbers ($\times 10^6$)	Mean weight (g)	Population biomass ($\times 10^3$)	Daily mortality
Estimated eggs		1.03×10^8			
Eggs spawned	Apr 10	8.26×10^7	0.00054	32.69	
Eggs hatched	Apr 20	7.43×10^7	0.00044	53.52	0.01165
Start of exogenous feeding	May 1	6.69×10^7	0.0008	38.09	0.06874
Metamorphosed	Jul 20	2.93×10^5	0.13	141.20	0.02075
0	Oct 31	3.53×10^4	4.2	148.26	0.01485
1	Jan 1	14,483	5.3	76.76	0.00167

The values are based on average annual values for 1983-1990 estimated from a report of a working group on the assessment of pelagic stocks in the Baltic (Anon. 1991; Tables 2 and 4 in Arrhenius and Hansson 1993). The durations of larval and YOY periods are 80 and 157 days, respectively.

therefore the larval stage is excluded. Therefore, consumption by larval stage was estimated as in an earlier paper by Arrhenius and Hansson (1993), assuming a gross conversion efficiency of 30% (Checkley 1984, Kiørboe and Munk 1986, Houde 1989).

Results and Discussion

I estimated a population consumption of 4.5×10^6 metric tons for YOY herring in the northern Baltic proper (Figure 1). This is 30% lower than earlier estimations from the same area by Arrhenius and Hansson (1993). The difference is explained by modification of the physiological data since the original model for herring was constructed, and the consumption rate function, such that the length of the daily feeding period is included (Arrhenius 1995). This consumption is about 35% of the total population consumption of zooplankton, whereas 25% may be attributed to the larval fish (Figure 1). This is in accordance with a recent study by Rudstam et al. (1994), suggesting about 33% of the total adult consumption in the Baltic Sea is by the first year of life. In other areas, YOY clupeids are also likely to be important planktivores as they are abundant and have high specific consumption rates (Hewett and Stewart 1989, Rand et al. 1995).

There are few values for the average zooplankton production in the Baltic Sea. However, the total estimated food consumption by zooplank-

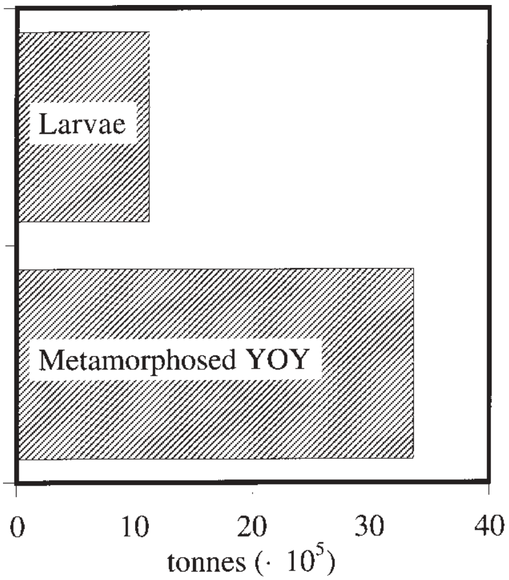


Figure 1. Total population food consumption of larvae and metamorphosed YOY herring in the northern Baltic proper (ICES areas 28-29). The durations of larval and YOY periods are 80 and 157 days, respectively.

tivores seems to be high compared to the production of zooplankton (6.3 $gCm^{-2}yr^{-1}$ in the Askö area [Johansson 1992], 10 $gCm^{-2}yr^{-1}$ in the open sea of the northern Baltic proper [Hernroth and Ackefors 1979], 12 $gCm^{-2}yr^{-1}$ in a eutrophicated coastal area [Johansson 1992]). Therefore, my calculation of consumption by YOY herring indicates that they alone consume 30-60% of the zooplankton produced (3.8 $gCm^{-2}yr^{-1}$, carbon content is 10% of the wet weight [von Bast and von Oertzen 1976]). These calculations show that YOY herring exert a strong predation pressure on zooplankton. However, other studies in the Baltic Sea have shown that consumption of zooplankton by YOY herring was never high enough to be a major source of annual zooplankton abundance (Mehner 1996, Thiel 1996).

In freshwater lakes there is often a decline of zooplankton populations in late spring. The reason for this is said to be primarily food limitation (DeMott 1989), but predation by fish may also be important (Gliwicz and Pijanowska 1989). However, the predation impact on the zooplankton community seems to be of little importance in the spring

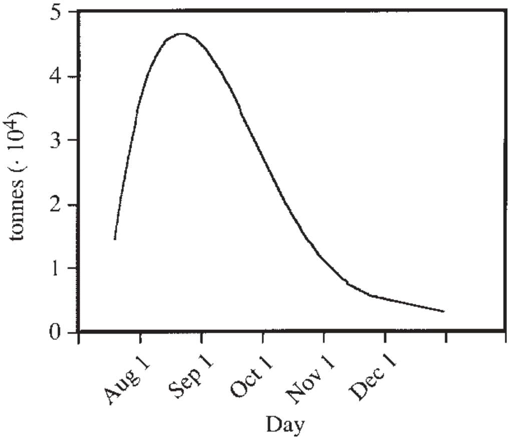


Figure 2. Daily population food consumption (metric tons x 10^4) by metamorphosed YOY herring (July 20-December 31) in the northern Baltic proper (ICES areas 28-29).

in the Baltic Sea (Mehner and Heerkloss 1994, Mehner 1996). This analysis predicts that the consumption of zooplankton by YOY herring varies with season and peaks during August (Figure 2). This peak is earlier than found by Hansson et al. (1990), Rudstam et al. (1992), and Arrhenius and Hansson (1993), but occurs during estimated second peak in zooplankton production (Johansson et al. 1993, Heerkloss and Schnese 1995). Consequently, predation by YOY herring on zooplankton may potentially impact zooplankton population dynamics.

From my research and discussion in a review by Rudstam et al. (1994), I suggest at least two other top-down controls acting on zooplankton in the coastal area. Young-of-the-year clupeids selected certain zooplankton taxa over others (Hansson et al. 1990, Flinkman et al. 1992, Rudstam et al. 1992, Arrhenius 1996, Mehner 1996, Thiel 1996). Selective predation on reproducing individuals will increase the effects that fish have on zooplankton, by preventing them from realizing their potential population growth rate (Vuorinen et al. 1983, Vuorinen 1987). The zooplankton community is dominated by calanoid copepods, but cladocerans and rotifers can be very abundant (Ackefors 1969, Wulff et al. 1986, Johansson 1992). The most preferred species were cladocerans (*Bosmina longispina maritimia*) in the summer and calanoid copepods (*Acartia* spp. and *Eurytemora affinis hirundoides*) in late summer and autumn (Arrhenius 1996). The visibility may explain the high selectivity for cladocerans (*Bosmina*) in summer (most were carrying eggs), and switch to *Eurytemora* later in the season when cladocerans are absent.

All of the preferred species in the coastal zone are relatively small. Generally, daphnids are the most predator-sensitive zooplankton species, but are absent from most of the Baltic Sea.

The calanoid copepods preferred by YOY herring have stronger vertical migrations than less-preferred taxa as discussed by Hansson et al. (1990). High feeding pressure may "force" copepods to occur at lower temperatures and a decreased amount of food is then available to them, resulting in longer generation times (Vuorinen 1982, 1987). There is support of diel vertical migration to reduce the risk of mortality from visual predators (Hays 1995) or at least migratory behavior (Neill 1990, Bollens and Frost 1991, Williamson et al. 1996). Zooplankton body size, body morphology, and pigmentation are all important for diel vertical migration (Hays et al. 1994).

Although these results and other publications (Hansson et al. 1990; Rudstam et al. 1992, 1994; Arrhenius and Hansson 1993) indicate strong predation by zooplanktivores, there are few clear and simple correlations between zooplankton abundance and zooplanktivory in the Baltic Sea. Planktivory is not equally distributed over seasons. In early summer, zooplankton increase in response to warmer temperature, adequate food resources, and relatively low predation rates (Mehner and Heerkloss 1994, Mehner 1996). Later in the season, zooplankton are restricted by cold temperature and low food supplies (Johansson 1992). In the central Baltic Sea and in the Gulf of Riga, there was a slight decrease of mainly the larger copepods, e.g., *Pseudocalanus minutes elongatus* and *Limnocalanus*, with increasing predation pressure during the 1980s (Kornilovs et al. 1992, Naglis and Sidrevics 1993). However, smaller copepods, e.g., *Acartia* sp. and *Temora longicornis*, have increased in abundance in these areas, and may have produced more favorable feeding conditions for larvae and YOY herring (Sidrevics et al. 1993). In the southern Baltic Sea, a high abundance of larvae has been shown to have little impact on zooplankton biomasses in the coastal waters (Schnack and Böttger 1981, Arndt 1989, Mehner and Heerkloss 1994, Mehner 1996). These results are, except Mehner (1996), however, based on only average densities, generated by different sampling methods and are hardly compatible. Further well-defined collections and analyses of zooplankton and zooplanktivores are necessary. However, such sampling programs must also include other parameters; as, e.g., salinity and temperature have been seen to correlate with, and probably influence, zooplankton production (Vourinen and Ranta 1987, Viitasalo et al. 1990).

My results imply that herring have a great impact on Baltic Sea zooplankton population dynamics. The precision or accuracy of the output from bioenergetics models must be weighted against other possible sources of errors. The weakest points in estimating predation by Baltic herring are still related to the abundance and mortality rates of YOY fish, as also discussed by several authors (Arrhenius and Hansson 1993, Brandt and Hartman 1993, Hansen et al. 1993). Abundance estimates and mortality rates for the youngest age groups are scarce and I had to extrapolate these data from abundance data for older fish.

Acknowledgments

This paper was completed while the author was a postdoctoral fellow of the Swedish Council for Forestry and Agricultural Research at Cornell University.

References

Ackefors, H. 1969. Seasonal and vertical distribution of the zooplankton in the Askö area (northern Baltic proper) in relation to hydrographical conditions. Oikos 20:480-492.

Anonymous. 1991. Report of the working group on assessment of the pelagic stocks in the Baltic. Comm. Meet. Int. Counc. Explor. Sea C.M.-ICES 1991/Assess. 20:1-163.

Arndt, H. 1989. Zooplankton production and its consumption by planktivores in a Baltic inlet. In: R.Z. Klekowski, E. Styczynska-Jurewicz, and L. Falkowski (eds.), 21st Eur. Mar. Biol. Symp., Gdansk, Poland, 1986. Institute of Oceanology, Polish Academy of Sciences, pp. 205-214.

Arrhenius, F. 1995. Bioenergetics of young-of-the-year herring (*Clupea harengus* L.) and a revision of a bioenergetics model. In: F. Arrhenius, Feeding ecology of Baltic Sea herring (*Clupea harengus* L.): Field and model studies of a dominant zooplanktivore. Ph.D. thesis, Department of Systems Ecology, Stockholm University, Sweden. 120 pp.

Arrhenius, F. 1996. Diet composition and food selectivity of 0-group herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* (L.) in the northern Baltic Sea. ICES J. Mar. Sci. 53:701-712.

Arrhenius, F., and S. Hansson. 1993. Food consumption of larval, young and adult herring and sprat in the Baltic Sea. Mar. Ecol. Prog. Ser. 96:125-137.

Arrhenius, F., and S. Hansson. 1996. Growth and seasonal changes in energy content of young Baltic Sea herring (*Clupea harengus* L.). ICES J. Mar. Sci. 53:792-801.

Bollens, S.M., and B.W. Frost. 1991. Diel vertical migration in zooplankton: Rapid individual response to predators. J. Plankton Res. 13:1359-1365.

Brandt, S.B., and K.J. Hartman. 1993. Innovative approaches with bioenergetics models: Future applications to fish ecology and management. Trans. Am. Fish. Soc. 122:731-735.

Carpenter, S.R., and J.F. Kitchell. 1993. The trophic cascade in lakes. Cambridge University Press. 385 pp.

Carpenter, S.R., J.F. Kitchell, and J.R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35:634-639.

Checkley, D.M., Jr. 1984. Relation of growth to ingestion for larvae of Atlantic herring *Clupea harengus* and other fish. Mar. Ecol. Prog. Ser. 18:215-224.

Crowder, L.B., M.E. McDonald, and J.A. Rice. 1987. Understanding recruitment of Lake Michigan fishes: The importance of size-based interactions between fish and zooplankton. Can. J. Fish. Aquat. Sci. 44:141-147.

Cushing, D.H. 1975. Marine ecology and fisheries. Cambridge University Press, London. 278 pp.

DeMott, W.R. 1989. The role of competition in zooplankton succession. In: U. Sommer (ed.), Plankton ecology: Succession in plankton communities. Springer, Berlin, pp. 195-252.

Elliott, J.M., and L. Persson. 1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47:977-991.

Gliwicz, Z.M., and J. Pijanowska. 1989. The role of predation in zooplankton succession. In: U. Sommer (ed.), Plankton ecology: Succession in plankton communities. Springer, Berlin, pp. 253-295.

Flinkman, J., I. Vourinen, and E. Aro. 1992. Planktivorous Baltic herring (*Clupea harengus*) prey selectively on reproducing copepods and cladocerans. Can. J. Fish. Aquat. Sci. 49:73-77.

Hansen, M.J., D. Boisclair, S.B. Brandt, S.W. Hewett, J.F. Kitchell, M.C. Lucas, and J.J. Ney. 1993. Applications of bioenergetics models to fish ecology and management: Where do we go from here? Trans. Am. Fish. Soc. 122:1019-1030.

Hansson, S., U. Larsson, and S. Johansson. 1990. Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. J. Plankton Res. 12:1099-1116.

Hays, G.C. 1995. Ontogenetic and seasonal variation in the diel vertical migration of the copepods *Metridia lucens* and *Metridia longa*. Limnol. Oceanogr. 40:1621-1465.

Hays, G.C., C.A. Proctor, A.W.G. John, and A.J. Warner. 1994. Interspecific differences in the diel vertical migration of marine copepods: The implications of size, color and morphology. Limnol. Oceanogr. 39:1621-1629.

Heerkloss, R., and W. Schnese. 1995. Long-term monitoring of zooplankton in the Bodden waters south of Darss-Zingst. In: J. Kohn and U. Schiewer (eds.), The future of the Baltic Sea: Ecology, economy, administration and teaching. Metropolis, Marburg, pp. 55-62.

Hernroth, L., and H. Ackefors. 1979. The zooplankton of the Baltic proper: a long term investigation of the fauna, its biology and ecology. Fish. Board Swed. Inst. Mar. Res. Rep. 2:1-59.

Hewett, S.W., and B.L. Johnson. 1992. Fish bioenergetics model 2. An upgrade of a generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Tech. Rep. WIS-SG-92-250, 2nd edn., 79 pp.

Hewett, S.W., and D.J. Stewart.1989. Zooplanktivory by alewives in Lake Michigan: Ontogenetic, seasonal and historical patterns. Trans. Am. Fish. Soc. 118:581-596.

Houde, E.D. 1989. Comparative growth, mortality and energetics of marine fish larvae: Temperature and implied latitudinal effects. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 87:471-495.

Johansson, S. 1992. Regulating factors for coastal zooplankton community structure in the northern Baltic proper. Ph.D. thesis, Department of Zoology, Stockholm University, Sweden. 127 pp.

Johansson, S., S. Hansson, and O. Araya-Nunez. 1993. Temporal and spatial variation of coastal zooplankton in the Baltic Sea. Ecography 16:167-173.

Kiørboe, T., and P. Munk. 1986. Feeding and growth of larval herring, *Clupea harengus*, in relation to density of copepod nauplii. Environ. Biol. Fishes 17:133-139.

Kitchell, J.F., D.J. Stewart, and D. Weininger. 1977. Applications of bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board. Can. 34:1922-1935.

Kornilovs, G., V. Berzinsh, and L. Sidrevics. 1992. The analysis of mean weight-at-age changes of Baltic herring in the Gulf of Riga. Comm. Meet. Int. Counc. Explor. Sea C.M. 1992/J:24, 12 pp.

Mehner, T. 1996. Predation impact of age-0 fish on a copepod population in a Baltic Sea inlet as estimated by two bioenergetics models. J. Plankton Res. 18:1323-1340.

Mehner, T., and R. Heerkloss. 1994. Direct estimation of food consumption of juvenile fish in a shallow inlet of the southern Baltic. Int. Rev. Gesamten Hydrobiol. 79:295-304.

Miller, T.L., L.B. Crowder, J.A. Rice, and E.A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: Toward a conceptual framework. Can. J. Fish. Aquat. Sci. 45:1657-1670.

Naglis, A., and L. Sidrevics. 1993. The analysis of mean weight-at-age changes of Baltic herring in the eastern Baltic proper, SD 28. Comm. Meet. Int. Counc. Explor. Sea C.M. 1993/J:24, 5 pp.

Neill, W.E. 1990. Induced vertical migration in copepods as a defence against invertebrate predation. Nature 345:542-546.

Ney, J.J. 1990. Trophic economics in fisheries: Assessment of demand-supply relationships between predators and prey. Rev. Aquat. Sci. 2:55-81.

Nixon, S.W. 1982. Nutrient dynamics, primary production and fisheries yield in lagoons. Oceanol. Acta 1982:357-371.

Nixon, S.W. 1988. Physical energy inputs and the comparative ecology of lake and marine ecosystems. Limnol. Oceanogr. 33:1005-1025.

Rand, P.S., D.J. Stewart, B.F. Lantry, L.G. Rudstam, O.E. Johannsson, A.P. Goyke, S.B. Brandt, R. O'Gorman, and G.W. Eck. 1995. Effect of lake-wide planktivory by the pelagic prey fish community in Lakes Michigan and Ontario. Can. J. Fish. Aquat. Sci. 52:1546-1563.

Rice, J.A., and P.A. Cochran. 1984. Independent evaluation of a bioenergetics model for largemouth bass. Ecology 65:732-739.

Rudstam, L.G. 1988. Exploring the dynamics of herring consumption in the Baltic: Applications of an energetic model of fish growth. Kiel. Meeresforsch. Sonderh. 6:312-322.

Rudstam, L.G., G. Aneer, and M. Hildén. 1994. Top-down control in the pelagic Baltic ecosystem. Dana 10:105-129.

Rudstam, L.G., S. Hansson, S. Johansson, and U. Larsson. 1992. Dynamics of planktivory in a coastal area of the northern Baltic Sea. Mar. Ecol. Prog. Ser. 80:159-173.

Schnack, D., and R. Böttger. 1981. Interrelation between invertebrate plankton and larval fish development in the Schlei fjord, western Baltic. Kiel. Meeresforsch. Sonderh. 5:202-210.

Sidrevics, L., R. Line, V. Berzinsh, and G. Kornilovs. 1993. Long-term changes of zooplankton abundance in the Gulf of Riga. Comm. Meet. Int. Counc. Explor. Sea C.M. 1993/L:15, 14 pp.

Smith, P.E. 1985. Year-class strength and survival of 0-group clupeoids. Can. J. Fish. Aquat. Sci. 42:69-82.

Thiel, R. 1996. The impact of fish predation on the zooplankton community in a southern Baltic bay. Limnologica 26:123-137.

Viitasalo, M., I. Vourinen, and E. Ranta. 1990. Changes in crustacean mesozooplankton and some environmental parameters in the Archipelago Sea (northern Baltic) in 1976-1984. Ophelia 31:207-217.

von Bast, H.-D., and J.-A. von Oertzen. 1976. Zusammenstellung von energieäquivalenten aquatischen Organismen unter besonderer Berücksichtigung der Ostsee. Wiss. Z. Univ. Rostock Math.-Naturwiss. Reihe 3:295-304.

Vuorinen, I. 1982. Vertical migration of *Eurytemora* (Crustacea, Copepoda): A compromise between risks of predation and decreased fecundity. J. Plankton Res. 9:1037-1046.

Vuorinen, I. 1987. The effects of temperature on the rates of development of *Eurytemora* (Nordquist) in laboratory culture. Ann. Zool. Fenn. 19:129-134.

Vuorinen, I., and E. Ranta. 1987. Dynamics of marine mesozooplankton at Seili, northern Baltic Sea, in 1967-1975. Ophelia 28:31-48.

Vuorinen, I., M. Rajasilta, and J. Salo. 1983. Selective predation and habitat shift in a copepod species: Support for the predation hypothesis. Oecologia (Berl.) 59:62-64.

Williamson, C.E., R.W. Sanders, R.E. Moeller, and P.L. Stutzman. 1996. Utilization of subsurface food resources for zooplankton reproduction: Implications for diel vertical migration theory. Limnol. Oceanogr. 41:224-233.

Wulff, F.G., G. Ærtebjerg, G. Nicolaus, A. Niemi, P. Ciszewski, S. Schulz, and W. Kaiser. 1986. The changing pelagic ecosystem of the Baltic Sea. Ophelia, Suppl. 4:299-319.

Biological Investigations on Pacific Sandfish *(Trichodon trichodon*) in the Northern Gulf of Alaska

Judy McDonald Paul and A.J. Paul
University of Alaska Fairbanks, Institute of Marine Science, Seward, Alaska

Tyson J. Vogeler and John P. Doyle
University of Alaska Fairbanks, Marine Advisory Program, Anchorage, Alaska

Abstract

This project was a preliminary examination of the size-weight relationships, length and age, stomach contents, and fecundity of Pacific sandfish, *Trichodon trichodon*. Most of the fish over 150 mm in fork length (FL) were females. Qualitatively, the most common prey items were sand lance (*Ammodytes* sp.), several types of shrimps, crab larvae, cumaceans, and polychaetes. Based on the break and burn method, fish with one annulus on the otolith averaged 71 mm FL and by age 2 they were 104 mm FL. The number of eggs increased linearly with fork length with a maximum of about 15,000 eggs in the largest female. There was a variation in egg diameter in the ovary, suggesting not all eggs are spawned at once. The time of spawning and the number of eggs spawned remain unknown.

Introduction

The Pacific sandfish is a little known species found throughout the Gulf of Alaska. However, it is not the target of commercial or sport fisheries, and its benthic habits make it difficult to sample. Sandfish are eaten by Pacific halibut, coho and chinook salmon, Pacific cod, and seals. Stomach content studies suggested that sandfish are a relatively common forage fish. This project provided one of the first opportunities to ex-

---

Current address for Tyson Vogeler is 7914 NW Fourth Avenue, Vancouver, WA 98665

plore the biology of this species. The goals of the endeavor were to study the following aspects of biology: size-weight-age profiles, size at maturity, and fecundity, all of which help to define the suitability of the species for harvest. We also examined the prey species which should aid in understanding habitat preference.

Methods

Sandfish were captured by various methods of opportunity at several sites in the Gulf of Alaska (Table 1). Because there are several collections that had only a few fish, all of the specimens were combined and the results considered to apply to the region in general rather than to specific sample sites. Most of the fish were collected during August over several years. Not enough fish were available for other months to look at seasonal biological parameters. Prey were identified with a dissection microscope. Whole ovaries were fixed in 20% formalin and blotted wet weights were obtained. A piece containing at least 100 eggs was removed and weighed after blotting. Eggs in the subsample were counted individually. The weight of one egg was estimated and multiplied against the whole ovary weight to obtain the total number of eggs in the gonad. Egg diameters were measured from 10 females. A piece of ovary was placed on a slide and the maximum diameter of the egg closest to the first line on the micrometer was measured. The eyes of the researcher were closed and the stage moved to provide randomness in the selection of the next egg. The egg closest to the first line on the micrometer was measured and the procedure repeated until 25 eggs from each female had been measured to the nearest micron. The fork lengths of fishes 1-10 from which egg diameters were taken were: 180, 172, 148, 188, 211, 141, 177, 168, 170, and 174 mm. Otoliths were aged by both the surface and break and burn techniques.

Limited behavioral observations were made from four sandfish captured in late September from lower Cook Inlet. These fish were held in aquaria with sand in the bottom to observe their habit of burying themselves up to the eyes.

Results and Discussion

Length-weight relationships

The smallest fish captured was 62 mm FL and the largest 303 mm FL (Figure. 1). The length-weight relationship for fish captured in August was described by a power function (Figure 1). However, when specimens >100 mm FL, which might be marketable, were considered separately, a linear relationship was more applicable for the two sexes (Figures 2 and 3). Most of the fish over 150 mm FL were females (Figure 2).

Table 1. Station locations and dates for Pacific sandfish (*Trichodon trichodon*) sampling in the northern Gulf of Alaska.

Number of fish	North latitude	West longitude	Depth (m)	Location	Date
28	55°13.61′	162°35.70′	55	Cold Bay	06/08/92
27	55°33.91′	161°31.20′	29	Pavlov Bay	12/08/92
26	55°06.60′	162°24.27′	49	Cold Bay	17/08/93
10	55°12.79′	162°32.77′	46	Cold Bay	17/08/93
9	55°33.90′	161°31.05′	29	Pavlov Bay	21/08/93
1	?	?	<10	Kamishak	24/04/94
2	60°00.84′	151°43.68′	<10	Ninilchik	08/07/94
1	56°33.05′	159°55.11′	<10	Port Moller	10/07/94
1	60°04.37′	151°38.88′	<10	Ninilchik	04/08/94
2	59°30.52′	151°29.96′	6	Kachemak	26/08/94

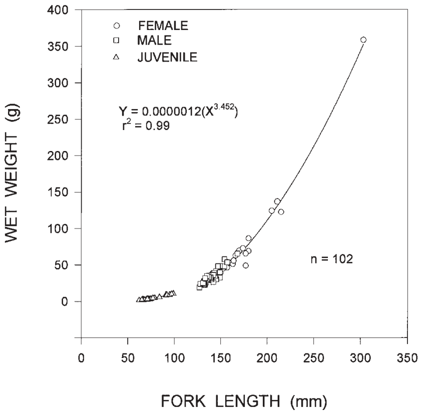


Figure 1. Wet weight of Pacific sandfish captured at several sites in the northern Gulf of Alaska.

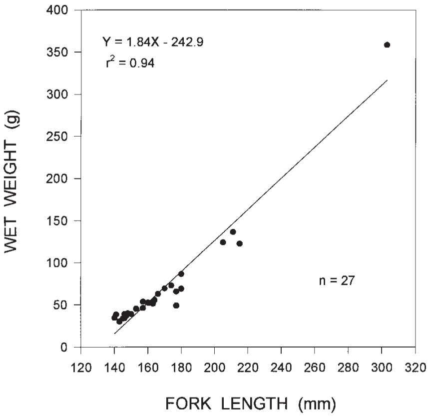


Figure 2. Wet weight of female Pacific sandfish captured at several sites in the northern Gulf of Alaska.

Age and growth

The mixed-sex samples of sandfish exhibited a linear growth pattern with both the surface and break and burn otolith aging methods (Figures 4 and 5). Based on the break and burn method fish with one annulus on the otolith averaged 71 mm FL, and by age 2 they were 104 mm FL. There were too few fish in the sample to statistically examine sex differences in age and growth, but sex-specific data are presented in Table 2. These age estimates are unverified so must be considered preliminary. However, the data do suggest that the species is relatively short-lived, and does not have the extended longevity typical of rockfishes.

Stomach analysis

Qualitatively, the most common prey items were sand lance, several types of shrimps, crab larvae, cumaceans, and polychaetes (Table 3). The frequency of occurrence method showed sandfish >100 mm FL ate primarily fish (90%). Most of the fish prey that could be identified was sand lance (64%). A lot of the fish tissue that could not be positively identified was probably sand lance, judging from size, shape, texture, and color. Sandfish <100 mm FL preyed more heavily on crustaceans, with shrimp (38%) and euphausiids (26%) the most common identifiable prey. In fish <100 mm FL the other prey category was mostly crustacean parts, some of which were amphipods. Both *Crangon*-like and pandalid-like shrimps were observed but they were too digested to identify. While the stomach contents were too digested to do a volumetric analysis of prey, it was obvious that sand lance was the major prey item we encountered in fish >100 mm FL. This suggests that the likely places to collect sandfish will be areas with large populations of sand lance. Sandfish are a forage species themselves and their strong preference for sand lance shows they are also dependent on one of Alaska's most common forage fish.

Fecundity

The number of unspawned eggs in the ovary increased linearly with fork length, with a maximum of about 15,000 eggs in the largest female (Figure 6). There was variation in diameter in the ovary, suggesting that not all eggs are spawned at once (Figure 7). One captive female (66 g live weight and 192 mm FL) extruded 269 eggs with diameters of 3.3-3.4 mm on 11 August. The female died after spawning so these values are unreliable predictors of how many eggs sandfish extrude, or when they spawn. More in situ observations and captive spawning will be needed to determine annual egg extrusion rates.

Burying habits

Captive fish often burrowed in the sand and came to rest with only their dorsal surface showing, sometimes with only the eyes, lip fringe, and

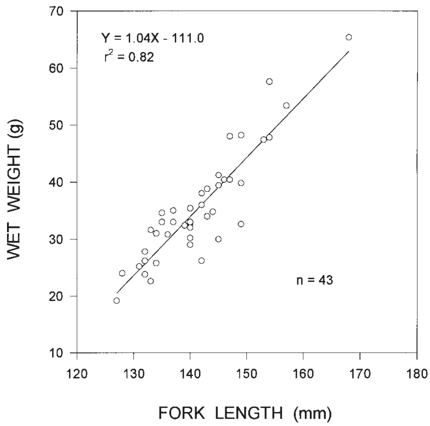


Figure 3. Wet weight of male Pacific sandfish captured at several sites in the northern Gulf of Alaska.

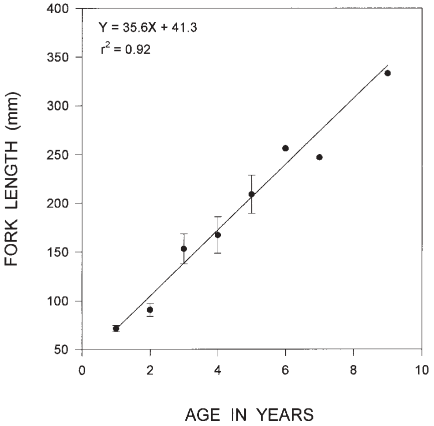


Figure 5. Age and fork length of Pacific sandfish captured at several sites in the northern Gulf of Alaska based on counting annuli of otoliths with the break and burn method.

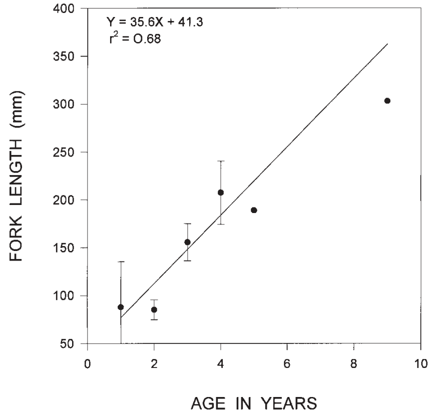


Figure 4. Age and fork length of Pacific sandfish captured at several sites in the northern Gulf of Alaska based on counting surface annuli of otoliths.

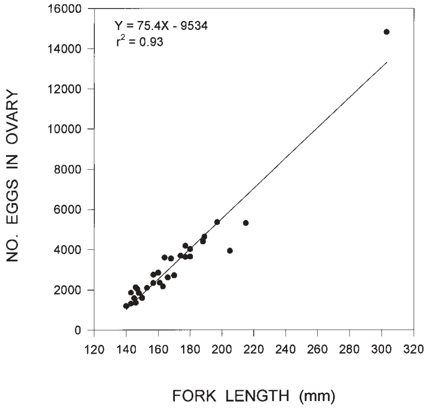


Figure 6. Number of unspawned ova in Pacific sandfish captured at several sites in the northern Gulf of Alaska. All fish were captured in August.

Table 2. Length and age data for Pacific sandfish based on surface and break and burn observations of annual rings on otoliths.

Fork length (mm)	Sex	Age (Surface)	Age (Break and burn)
67	m	1	1
68	m	1	1
70	m	2	1
71	f	1	1
72	f	2	1
72	f	1	1
73	m	2	1
74	?	2	1
77	?	2	2
79	m	1	1
84	?	2	2
91	?	2	2
91	f	2	2
91	m	2	2
92	m	2	2
95	f	2	2
97	f	2	2
99	m	2	2
133	m	3	3
135	m	3	3
137	m	3	3
141	f	3	4
147	m	3	3
147	m	3	3
148	f	3	4
149	m	3	3
150	m	3	4
154	m	4	3
154	m	3	3
157	m	3	3
168	f	3	3
170	f	3	4
174	f	3	4
177	f	3	3
177	f	3	4
180	f	4	3
180	f	4	5
188	f	5	4
189	f	5	4
197	f	4	5
205	f	3	5
211	f	4	5
227	f	4	5
234	f	4	5
247	f	4	7
256	f	4	6
333	f	9	9

Table 3. Frequency of occurrence of prey types in stomachs of Pacific sandfish in two size groups.

	115-303 mm FL (N = 72)		62-99 mm FL (N = 34)	
Prey	N	%	N	%
Sand lance	46	63.8	3	8.8
Herring	1	1.4	0	0
Other fish	18	25.0	2	5.8
Shrimp	7	9.7	13	38.2
Crab larvae	1	1.4	6	17.6
Cumaceans	0	0	2	5.8
Polychaetes	2	2.8	0	0
Euphausiids	0	0	9	26.4
Other	5	6.9	11	32.4

Data are number of fish with item in stomach and percentage of stomachs with that item.

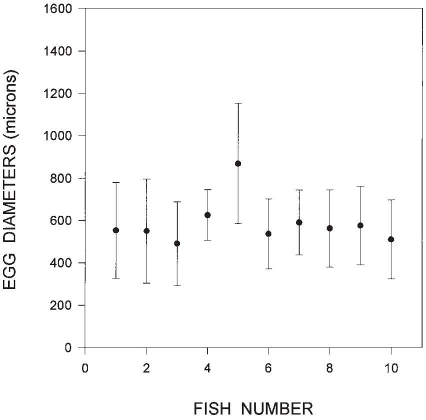


Figure 7. Egg diameters of unspawned ova (mean and standard deviation) for 10 Pacific sandfish captured in the northern Gulf of Alaska in August.

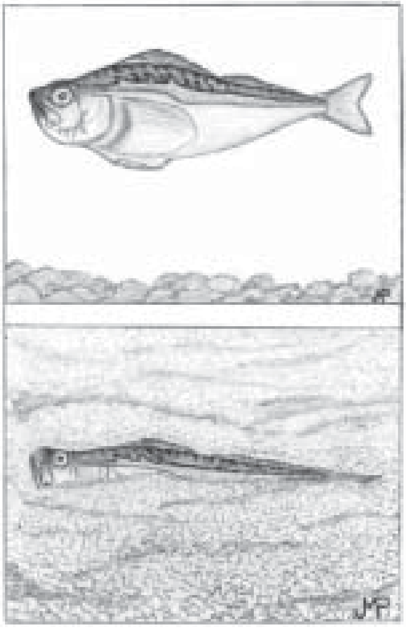


Figure 8. An illustration of Pacific sandfish by J.M. Paul with a standard length of 14 cm, swimming and partially buried in sand.

part of the tail exposed (Figure 8). Partly buried like this, they would not be susceptible to trawls and are difficult for diver or Remote Operated Vehicle monitoring.

Acknowledgments

This project was supported by funding from the City of Akita, Japan, with additional help from the Kenai Peninsula Borough and the Alaska Science and Technology Foundation. Several staff members of the Alaska Department of Fish and Game provided sandfish for this study, and W. Bechtol assisted with age estimations.

Winter Dormancy in the Pacific Sand Lance (*Ammodytes hexapterus*) in Relation to Gut Evacuation Time

Lorenzo Ciannelli
University of Washington, School of Fisheries, Seattle, Washington

Abstract

The life style of the Pacific sand lance (*Ammodytes hexapterus*), is very interesting and in some ways unique in that their habitat is divided on a diel basis. Sand lance spend part of the day feeding in the water column, where they are more exposed to predation. During the night they burrow in the sand; however, it is unclear how much of their entire life is spent in the sand on a seasonal basis. Low catches of Pacific sand lance during winter together with many morphological adaptations for a burrowing life style, suggest that they might enter a winter dormancy phase in the sand. *Ammodytes hexapterus* has a long digestion time (45-80 hr), and has the capability to retain food in the stomach for a long time (30 hr). This might be explained as an adaptation to optimize food uptake from the gut, to build up energy reserves in order to undertake a dormant winter stage.

Introduction

Sand lances are small thin fishes occurring throughout the higher latitudes of both the Pacific and the Atlantic oceans (Garrison and Miller 1982). All of them belong to the genus *Ammodytes*. The North Pacific species *Ammodytes hexapterus* has a very interesting and in some ways unique ecology. In Puget Sound and the Strait of Juan de Fuca they have been recognized as a very important link in neritic food webs; i.e., those of the surface waters and the water column, in the nearshore region (Simenstad et al. 1979). Since they are basically pelagic schooling feeders (secondary consumers), they often occur and feed together with juvenile

---

Author's current address is: NMFS/AFSC, 7600 Sand Point Way NE, Seattle, WA 98115

pelagic Pacific herring (*Clupea pallasi*). Most of their diet consists of calanoid and cyclopoid copepods with lower proportions of crustacean zoeae and nauplii, gammarid amphipods, and larvaceans (Simenstad et al. 1979, Field 1988).

Their spawning period occurs once a year, in late winter. They have external fertilization and their eggs are demersal and adhesive (Garrison and Miller 1982). The duration of the egg stage is very dependent on the water temperature, varying from 20 days to 40 days (Field 1988, McGurk and Warburton 1992). The larval stage usually lasts for 2 months, and it is possible to collect them in zooplankton samples in Puget Sound until late April (Garrison and Miller 1982). Maturation from juvenile to adult stage occurs after 2 or 3 years, when the fish reach a length of at least 128 mm (Field 1988). In spite of a great abundance in the northeast Pacific, Pacific sand lance is virtually unexploited as a food source for humans, which might explain the paucity of data on its stock size and distribution throughout the year.

One of the most interesting features of the ecology of *A. hexapterus* is its life style. The body morphology of sand lance suggests an adaptation for a burrowing life style: long, slender, mucus-covered bodies, absence of pelvic fins, and lack of a swim bladder. All these features help these fish to burrow in the sand. However, it is unclear how much time they actually spend living in the sand. It is believed that sand lance spend part of the day in the water column, feeding actively especially during flood tide, whereas during the night they burrow in the sand, to escape predation (Hobson 1986). However, little is known about their burrowing behavior throughout the year. Winslade (1974) found that a congener species of *A. hexapterus*, *A. marinus*, occurring on the northeast Atlantic coast, might undergo a dormant stage in the winter season, during which they remain buried in the sand. Many circumstances suggest this may also hold true for the Pacific species. These include: (1) their morphological adaptations for a burrowing life style (Hart 1973); (2) their capacity to accumulate fat bodies along the gut, with lowest and highest values at the beginning and at the end of the feeding season, respectively, between spring and summer (Winslade 1974, Field 1988); (3) abundant catches of sand lance in spring and summer, and low catches during the remainder of the year (Fresh 1979, Field 1988); and (4) their nonmigratory habit.

The object of this study was to investigate the gut evacuation time of the Pacific sand lance during the late summer in Puget Sound, Washington. Given the assumption that in the late summer they enter into a dormant stage, and that they need to accumulate food energy, I would expect to find: (1) long evacuation time, compared to other fishes, as a result of ecological adaptations for optimization of food uptake; and (2) long retention of food in gut compartments.

Material and Methods

The sampling area was the east side of Cape San Juan on San Juan Island, Washington. Sand lance used in the feeding experiments were collected on 23 July 1995 during flood tide at 1900 hours. The fish were collected by dipnetting. The schools were located by looking for flocks of rhinoceros auklets (*Cerorhinca monocerata*) which actively feed on sand lance. The animals used in the experiments ranged in size from 6.5 to 8 cm, so they can be considered as the first year-class of juveniles (0+) (Fresh 1979, Vermeer and Westrheim 1982).

Parallel feeding experiments between starved and fed animals were run in order to investigate differences in gut evacuation time. Once collected, the animals were kept alive in two round maintenance tanks (150 individuals each) measuring 1 m in diameter and 0.5 m in height, with a continuous flow of seawater, and sand on the bottom. The average temperature during the maintenance period was 15 °C. In the starved tank, the seawater was filtered in order to prevent introduction of natural food. The animals in the fed tank were supplied with zooplankton (mostly calanoid and cyclopoid copepods) once a day.

The actual feeding experiments were run using four individuals per experiment, in a round bucket 30 cm in diameter, filled with 4 liters of seawater with sand on the bottom. The sand lance were transferred from the maintenance tank to the bucket and allowed an acclimation time of at least 3 hr before running the feeding experiments. Two kinds of prey items had been offered to the animals: transparent copepods, mostly calanoid and cyclopoid, and distinct orange harpacticoid copepods (*Tigropus californicus*). The latter were very easy to recognize during digestion, allowing a better estimation of both the flow along the gut and the digestion state of the prey. The cyclopoids and calanoids were collected by towing a zooplankton net (220 µm). The harpacticoids were collected in high tide pools.

In each experiment, except those with harpacticoids, a prey concentration of 1 copepod per 1.5 ml was used. In the harpacticoid experiments the animals were fed in two consecutive events. First they were given harpacticoid copepods in concentrations of 1 copepod per 1.5 ml, and then after at least 2 hr, they were given the same concentration of calanoid and cyclopoid copepods.

For the analysis of the gut contents the whole gut was divided into five different morphological and functional parts: esophagus, stomach, anterior intestine, middle intestine, and posterior intestine. The estimation of the gut content was evaluated both quantitatively and qualitatively. For the esophagus and stomach two quantitative estimates were made: number of prey items and percentage of fullness. For the anterior, middle, and posterior intestines, only percentage of fullness was determined. For the whole gut, as a qualitative index, a subjective evaluation of the state of digestion was made, using a digestive index of

1 to 6 (Terry 1976). Index values correspond to the following description, referring to the prey item:

1 = intact, countable, full body
2 = fragmented, countable, full body
3 = fragmented, hard to count, full body
4 = fragmented, not countable, empty body
5 = very fragmented, not countable, empty body
6 = fecal pellets

Results

There was no significant difference (t-test; $P = 0.98$) between the stomach evacuation time of starved and fed sand lance, for both of them it was approximately 34 hr. The starved animals, though, fed more actively, reaching the highest numbers of prey items in the stomach (Figure 1).

The stomach evacuation time found in the sand lance can be considered very long when compared to that of other fish (herring, hake, and cod, feeding on copepods, euphausids, and shrimps, respectively). Only the largemouth bass had a digestion time similar to that of the sand lance (Figure 2).

The stomach showed a relatively long evacuation time, when compared to the evacuation time of the anterior, middle and posterior intestine. The last is also indicative of the evacuation time of the whole gut (45 hr) (Figure 3).

The sand lance that were fed first on harpacticoids (prey item concentration = 1 copepod per 1.5 ml) and then on calanoids and cyclopoids (same prey item concentration), had a gut evacuation time more than twice as long (80 hr) as that found in the experiments run with only calanoids and cyclopoids (26 hr) (Figure 4).

The average qualitative index of digestive state of copepods in the stomach never reached values higher than 2.6, suggesting little digestion in this compartment. In the three divisions of the intestine, it went from 2.6 to 6 (Table 1).

Discussion

The main assumption of this study was that Pacific sand lance do undergo a dormancy phase in winter and that they need to accumulate food energy (in the form of high caloric tissues) as sustenance for the non-feeding time. The findings were as follows: (1) no differences in gut evacuation times between starved and fed sand lance (Figure 1); (2) long gut evacuation time in Pacific sand lance when compared to other fishes (Figure 2) (Molnar and Istvan 1962; Tyler 1970; Tanasichuk et al. 1991; Arrhenius and Hansson 1994); and (3) long residence time of food and relatively low digestion in the stomach (Figure 3, Table 1).

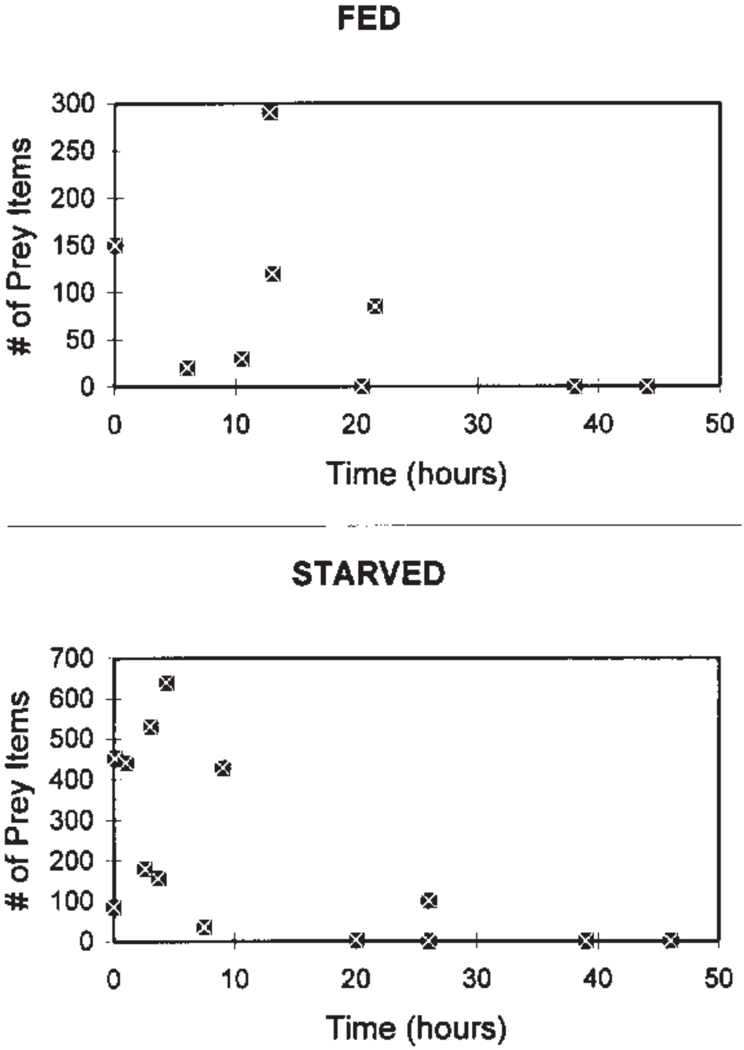


Figure 1. Stomach evacuation time: fed vs. starved.

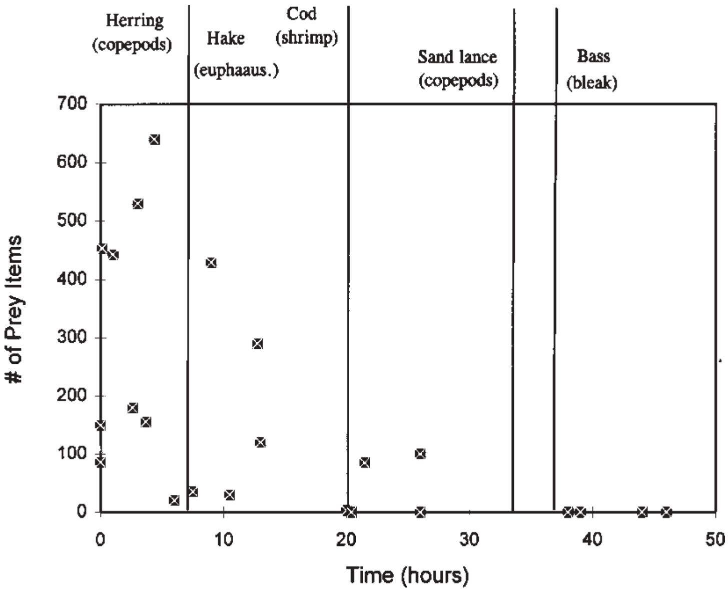


Figure 2. *Stomach evacuation time of sand lance vs. other fish species. Prey items indicated in parentheses.*

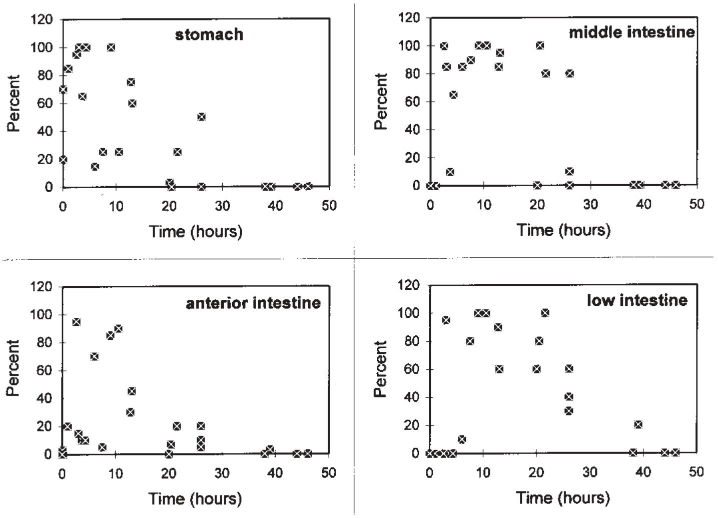


Figure 3. *Evacuation time in stomach, anterior intestine, middle intestine, and posterior intestine.*

Table 1. Qualitative index of digestive state of copepods per gut compartment of sand lance (*Amodytes hexapterus*).

Gut compartment	Digestive index
Esophagus	1.0
Stomach	2.6
Anterior intestine	4.5
Middle intestine	4.9
Posterior intestine	6.0

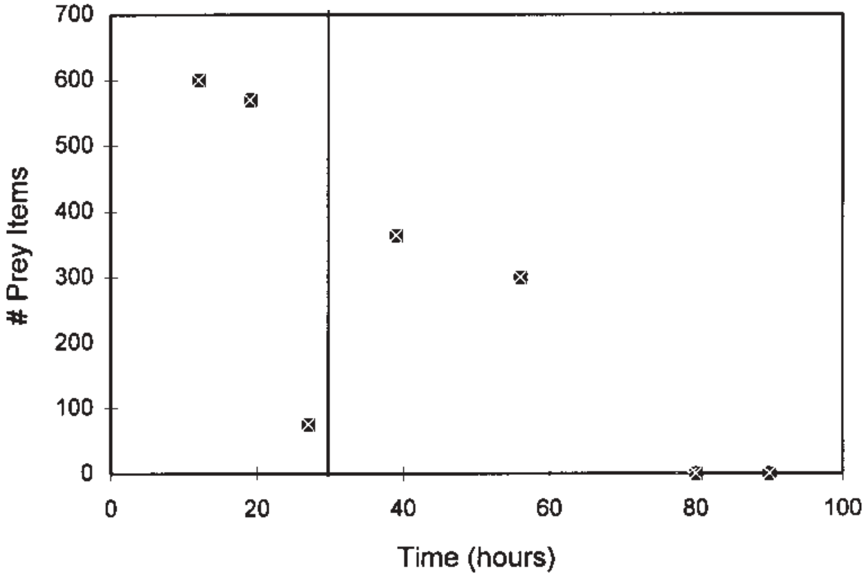


Figure. 4. Stomach evacuation time of sand lances fed on harpacticoid copepods, then calanoid and cyclopoid copepods (left of arrow), vs. sand lances fed only on calanoids and cyclopoids (right of arrow).

The lack of any difference in gut evacuation time between starved and fed sand lance might be explained given the assumption of winter dormancy. If late summer is the beginning of their dormant stage, they might enter a pre-adaptation phase in which they prepare themselves to fast for months. In that case, 3 weeks of starving should make no difference in gut evacuation time.

The long gut evacuation time of the Pacific sand lance might be an adaptation to two selective factors: (1) enhancement of food accumulation, and (2) predation. In the presence of abundant and easy-to-reach prey, there might be two opposing behaviors that lead to an accumulation of food energy: eating a lot of food and digesting it quickly versus eating a lot of food and digesting it slowly. The former strategy has lower growth efficiency, so it would be used by animals feeding continuously on an abundant resource and remaining for long periods in the feeding ground. The latter has higher growth efficiency so it would be used by animals that have limited access to an abundant food resource. Since the water column is both the feeding ground of the Pacific sand lance and the place in which they are most vulnerable to predation (Hobson 1986), it is likely that they have adapted to the second strategy.

The high values of evacuation time observed in the feeding experiments in which sand lance were fed twice (harpacticoids, then calanoids and cyclopoids), might also be in agreement with the above statement. Many species, in the presence of abundant resources, increase the digestion rate in order to ingest more food. Nevertheless, a species whose strategy is to decrease the rate of digestion, to optimize energy uptake, in the presence of abundant resources would have a longer digestion time. One has to remain cautious, however, since different prey items can have different digestion rates even within the same predator as can be seen in the case of the harpacticoid compared to the calanoid and cyclopoid copepods. In fact, in the parallel starved versus fed experiments, there was no significant difference in the gut evacuation time of starved and fed fish, in spite of a conspicuous difference in number of prey items ingested (Figure 1).

The long permanence of food in the stomach and the relatively low digestion occurring in it suggests that this is the part of the gut used as a storage compartment.

Given the above experimental and theoretical considerations, I suggest that a long gut evacuation time along with a stomach capable of long food retention favors the accumulation of food energy, and gives weight to the assumption that Pacific sand lance do undergo winter dormancy.

Acknowledgments

I thank the Friday Harbor Laboratories for facilities and financial support to conduct this study; Karel Liem, Bruce Miller, Donna Nemeth, and

Adam Summers for help and advice; Jen Zanon for collecting sand lance; Richard Brodeur for reviewing an early draft of this report; and Shonali Chandy for collecting and classifying copepods and reviewing an early draft.

References

Arrhenius, F., and S. Hansson. 1994. In situ food consumption by young-of-the-year Baltic Sea herring *Clupea harengus*: A test of predictions from a bioenergetics model. Mar. Ecol. Prog. Ser. 110:145-149.

Field, J.L. 1988. Pacific sand lance, *Ammodytes hexapterus*, with notes on related *Ammodytes* species. In: N.J. Wilimovsky, L.S. Incze, and S.J. Westrheim (eds.), Species synopses: Life histories of selected fish and shellfish of the northeast Pacific and Bering Sea. Washington Sea Grant Program and Fisheries Research Institute, University of Washington, Seattle. 111 pp.

Fresh, K.L. 1979. Distribution and abundance of fishes occurring in the nearshore surface waters of northern Puget Sound, Washington. M.S. thesis, University of Washington, Seattle. 120 pp.

Garrison, K.S., and B.S. Miller. 1982. Review of the early life history of Puget Sound fishes. Contract 80-ABA-3680, NMFS, NOAA, Seattle, Washington. School of Fisheries, University of Washington, Seattle.

Hart, J.L. 1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180, 740 pp.

Hobson, E.S. 1986. Predation on the Pacific sand lance, *Ammodytes hexapterus* (Pisces: Ammodytidae), during the transition between day and night in southeastern Alaska. Copeia 1986(1):223-226.

McGurk, M.D., and D.H. Warburton. 1992. Pacific sand lance of the Port Moller estuary, southeastern Bering Sea: Estuarine-dependent early life history. Fish. Oceanogr. 1:4, 306-320.

Molnar, G., and T. Istvan. 1962. Relation between water temperature and gastric digestion of largemouth bass (*Micropterus salmoides* Lacepede). J. Fish. Res. Board Can. 19:1005-1012.

Simenstad, A.C., M.S. Miller, C.F. Nyblade, K. Thornburgh, and L.J. Bledsoe. 1979. Food web relationship of northern Puget Sound and the Strait of Juan de Fuca. Office of Environmental Engineering and Technology, Office of Research and Development, U.S. Environmental Protection Agency, Washington, D.C. 335 pp.

Tanasichuk, R.W., D.M. Ware, W. Shaw, and G.A. McFarlone. 1990. Variation in diet, daily ration, and feeding periodicity of Pacific hake (*Merluccius productus*) and spiny dogfish (*Squalus acanthias*) off the lower west coast of Vancouver Island. Can. J. Fish. Aquat. Sci. 48:2018-2128.

Terry, C. 1976. Stomach analysis methodology: Still lots of questions. In: C.A. Simenstad and S.J. Lipovsky (eds.), Fish food habits studies. First Pacific Northwest Technical Workshop. Workshop Proceedings, Astria, Oregon. Washington Sea Grant Division of Marine Resources U.W. H.G. 30.

Tyler, A.V. 1970. Rates of gastric emptying in young cod. J. Fish. Res. Board Can. 27:1117-1189.

Vermeer, K., and S.J. Westrheim. 1982. Fish changes in diets of nestling rhinoceros auklets and their implications. Special publication compiled by Canadian Wildlife Service for Pacific Seabird Group Symposium. pps. 96-105.

Winslade, P. 1974. Behavioral studies on the lesser sand eel. III. The effect of temperature on activity and environmental control of the annual cycle of activity. J. Fish. Biol. 6:587-600.

Predator-Prey Interactions of Demersal Fish Species and Capelin (*Mallotus villosus*) in Icelandic Waters

Ólafur K. Pálsson
Marine Research Institute, Reykjavik, Iceland

Abstract

Extensive sampling of material on the food and feeding of demersal fish species in Icelandic waters was carried out in March, July, and November-December 1992. Based on this material the role of capelin (*Mallotus villosus*) as prey of nine demersal fish species is analyzed: Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), European whiting (*Merlangius merlangus*), Atlantic wolffish (*Anarhichas lupus*), spotted wolffish (*A. minor*), Greenland halibut (*Reinhardtius hippoglossoides*), American plaice (*Hippoglossoides platessoides*), and thorny skate (*Raja radiata*). The results indicate a large amount of seasonality in the consumption of capelin, with highest consumption by all predator species in March, which coincides with the spawning period of capelin. Only few predators, in particular the Atlantic cod and Greenland halibut, are found to prey significantly on capelin in other seasons. As a rule, predation on capelin rapidly increases with predator length and may decrease again among the largest predator length groups. Capelin of all size groups are preyed upon, although the largest, sexually mature fish are more frequently eaten. The calculated predation by all predators in March amounts to 270,000 metric tons, of which Atlantic cod consume 56%. Pollock consume similar amounts of capelin per individual fish, but markedly less on a stock basis due to lesser stock size, or 25%. Although consumption by other predators is rather insignificant in relation to that of Atlantic cod and pollock, it adds up to 50,000 tons over a period of 1 month. The calculated size of the spawning stock of capelin at spawning time in March 1992, based on acoustic measurements, was 475,000 tons. Thus, the calculated consumption by the nine predators amounts to 57% of the spawning stock. It is suggested that predatory impact of this order needs to be incorporated in stock projections and management considerations.

Introduction

The role of capelin as prey of a number of fish species in Icelandic waters has been described in several publications during this century; e.g., for Atlantic cod (Meschkat 1936, Rae 1968, Pálsson 1983), haddock and Atlantic wolffish (Pálsson 1983), pollock (Pálsson 1983, Jónsson 1996), Greenland halibut (Sólmundsson 1994), Atlantic wolffish, and American plaice (Pálsson 1983). The contribution of capelin as prey for these fish species differs in time and space. Such differences may arise exclusively from species-specific life-history differences, e.g., in distribution or behavior. Furthermore, sampling of the material for the feeding studies was carried out in different years, seasons, and areas, which may, in part, account for some of the differences in results. The purpose of the present paper is to analyze the trophic role of capelin as prey of nine demersal fish species, based on material sampled at the same time for all, or most, predator species covered. The obvious advantage of such material is to exclude, or at least reduce markedly, differences which may arise from the timing of the sampling alone. Thus, the differences encountered between predator species are expected to result from life-history differences, such as spatial overlap with the prey or the ability of the predator to prey on this particular prey type. To some extent, however, sampling may differ in space since the distribution areas of some predators are different in this respect.

Materials and Methods

The largest part of the material was sampled during three research cruises in 1992, i.e., in March, July, and November-December, covering the continental shelf area around Iceland as well as the western part of the Iceland-Faeroes ridge in March. A limited part of the material was sampled in 1991. The total number of stomachs sampled of each predator species was: Atlantic cod 8,414; haddock 7,408; pollock 1,358; European whiting 1,006; Atlantic wolffish 3,485; spotted wolffish 1,209; Greenland halibut 1,742; American plaice 9,255; and thorny skate 3,100. The composition of the material by species, season, and predator length group is given in Table 1.

In the sampling process the stomachs of each predator length group and station (which constitutes “a sample”) were emptied and their contents bulked in a container for later analysis in the laboratory. The aim was to sample five stomachs for each length group and station. Since this objective was not always achieved the resulting range in the number of stomachs in a sample is 1-5. Stomach contents were analyzed using standard methods, with identification of fish and other commercially important species to species level. Other items were identified to species level or higher taxa according to the general importance of the prey for the respective predator.

Table 1. Number of stomachs collected in 1991 and 1992 by predator species and length group.

Predator	5-6	7-9	10-14	15-19	20-24	25-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-119	120-129	Total
								March								
Atlantic cod	—	4	88	134	357	467	520	503	562	593	509	378	195	87	13	4,410
Haddock	—	—	209	275	390	567	612	598	452	378	237	26	1	—	—	3,745
Pollock	—	—	—	7	12	47	133	166	185	209	158	63	26	3	—	1,009
European whiting	—	—	15	33	63	105	159	116	17	2	—	—	—	—	—	510
Atlantic wolffish	—	32	194	247	307	327	413	404	363	260	144	63	13	3	—	2,770
Spotted wolffish	—	2	2	39	54	47	97	96	102	142	119	79	36	16	—	833
Greenland halibut	—	—	1	0	2	1	19	65	114	80	47	12	1	—	—	342
American plaice	1	69	484	615	704	711	741	317	3	—	—	—	—	—	—	3,645
Thorny skate	1	2	142	184	269	304	401	452	501	63	—	—	—	—	—	2319
								July								
Atlantic cod	—	—	5	19	63	156	310	363	316	256	181	129	55	22	10	1,885
Haddock	—	—	21	171	233	278	355	298	202	136	66	15	—	—	—	1,775
Pollock	—	—	—	—	—	—	5	29	80	85	74	40	26	10	—	349
European whiting	—	—	—	10	21	31	66	28	5	—	—	—	—	—	—	161
Atlantic wolffish	1	0	24	51	41	74	83	69	63	26	17	8	2	—	—	459
Spotted wolffish	—	—	3	8	8	6	29	35	52	61	43	26	10	1	—	282
Greenland halibut	—	1	4	11	25	47	205	305	252	139	77	36	25	8	—	1,135
American plaice	1	59	454	572	617	639	646	223	—	—	—	—	—	—	—	3,211
Thorny skate	—	—	52	81	101	102	115	148	161	21	—	—	—	—	—	781
								November-December								
Atlantic cod	—	42	80	32	83	114	348	398	368	277	200	105	48	21	1	2,117
Haddock	—	15	174	128	129	220	389	376	277	126	48	6	—	—	—	1,888
European whiting	—	2	22	41	11	45	127	82	5	—	—	—	—	—	—	335
Atlantic wolffish	—	2	21	23	29	31	40	65	26	15	2	3	—	—	—	256
Spotted wolffish	—	—	4	1	2	0	5	7	18	28	15	10	4	94		
Greenland halibut	—	—	—	—	—	2	15	71	114	41	10	8	—	—	—	265
American plaice	1	24	365	427	469	498	495	129	—	—	—	—	—	—	—	2,399

Pollock samples were collected in March and in June-July 1991 and 1992. Greenland halibut samples were collected in February and March 1992, in May, July, and August 1991-1992, and in October-December 1991-1992. All others were collected in March, July, and November-December of 1992.

Length in centimeters.

For all predators capelin was identified to species, the number of identifiable capelin in a sample were counted, and the total weight of the capelin in the sample was found by electronic weighing. Furthermore, the total length of capelin was measured for all specimens which allowed this due to degree of digestion.

The spatial distributions of capelin contents were described by first calculating the average proportion of capelin of the total content per stomach and then taking the average of the proportions over all length groups on a station. This gives the average capelin proportion (*ACP*) on a station as,

$$ACP_{station} = \frac{1}{S}\sum_{l}\frac{w_l^{cap}/n_l}{w_l^{tot}/n_l}$$

where w^{cap} is the stomach content weight of capelin, w^{tot} is total stomach content weight, n is number of stomachs in the sample, l is length group, s is sample, and S is number of samples.

The length distribution of capelin, identified in the stomach contents, is shown as number of fish per length interval (1 cm), with respect to season and predator length group when the material was extensive enough to permit such disaggregation. This was only possible for Atlantic cod. The percentage of capelin contents (CP) by predator length group was found by first calculating the weight of capelin and total contents per stomach in a sample. Then the weights within each predator length group were averaged and, finally, the capelin contents were calculated as a proportion of the total contents:

$$CP_l = \frac{\frac{1}{S}\sum_{s}(w^{cap}/n)_s}{\frac{1}{S}\sum_{s}(w^{tot}/n)_s}$$

The calculation of capelin partial fullness index (PFI^{cap}) and total fullness index (*TFI*) for the relationship between these indices was based on expressions of the indices as described in, e.g., Fahrig et al. (1993):

$$PFI^{cap} = \frac{1}{S}\sum_{s}\left(w^{cap}/L^3\times 10^4\right)_s$$

and

$$TFI = \frac{1}{S}\sum_{s}\left(w^{tot}/L^3\times 10^4\right)_s$$

The consumption of capelin by the predators was calculated using the formula derived by Magnússon and Pálsson (1989) where the average daily consumption (R) of a fish in a length group i, at a temperature T, is estimated as:

$$R_i^{cap} = 2.6\left(L_i \big/ 40\right)^{1.15} 1.09^{T-6}\sqrt{AvStom_i^{cap}} \text{ g/day}$$

where $AvStom_i^{cap}$ is the average stomach content of capelin in predator length group i, and L_i is the median of the length group.

Consumption by length groups was transformed into consumption by age, applying age-length keys based on otoliths collected during the same period. Using results from *VPA* of January 1, 1992 (Anon. 1996) daily consumption for cohorts and four stocks were calculated as shown in Table 2. Age groups not available as *VPA* estimates were backcalculated using assumed *M* values. These values should be regarded as fairly crude but conservative estimates. Near-bottom temperatures are available as recorded by Scanmar instruments. Average temperature values were calculated for each predator and month (Table 2) based on the approximate distributions of the stomach data.

Results

Spatial distributions of capelin

In March high proportions of capelin were found in Atlantic cod virtually all over the continental shelf (Figure 1). In limited areas, such as on the Iceland-Faeroes ridge and off the southwest coast, capelin was absent in the food or found in lower proportions. In July and November-December capelin proportions in Atlantic cod stomachs were generally lower, much more limited in space, and mainly confined to the continental shelf edge off the north and east coasts.

Capelin was identified as a high proportion of the stomach contents of Greenland halibut in all seasons, especially in material sampled in May-August 1991 and 1992, when sampling was most intense (Figure 2). However, it should be noted that this sampling effort did not cover the stock as a whole in any of the seasons.

In March, capelin was found in American plaice stomachs all around Iceland and often in high proportions of the total contents (Figure 3). In July, capelin was occasionally recorded but in relatively low proportions. Capelin was also occasionally found as prey in November-December and as a rule in fairly high proportions of the total contents.

For other predators, distributions are only shown for the month of March since capelin was virtually absent in their stomach contents in other seasons (Figure 4). In haddock, capelin was recorded mainly off the west and the south coast in considerable proportions. In other areas, i.e., off the north and east coasts, capelin was rarely recorded and mainly in a limited area off the northeast coast. In March, capelin was found in pollock stomachs in all areas and in high proportions, except off the southeast coast. Capelin was recorded in March in high proportions in European whiting stomachs in the main distribution area of this preda-

Table 2. **Stock size (N) and consumption of capelin by demersal predators in March, July, and November-December. Bottom-temperature (T) by predator species and month used in consumption calculations.**

Atlantic cod														
Age (years)	1	2	3	4	5	6	7	8	9	10	11	12	13	14
F 1992	0	0	0.078	0.373	0.648	0.928	1.076	1.016	0.612	0.468	0.373	0.678	0.344	0.495
M	0.5	0.3	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
N Jan 1	133,532	242,975	180,138	76,475	60,702	20,508	16,567	14,129	4,787	752	162	71	45	22
N Mar 15	120,323	228,253	170,001	67,870	50,872	16,213	12,700	10,967	4,042	654	144	59	40	19
g/fish/day	0.4	1.9	6.4	11.8	20	27.2	35.3	43.7	55.6	70.4	99.6	78.1	63.1	0
tons/day	48	434	1088	801	1017	441	448	479	225	46	14	5	3	0
T March	3.2	—	—	—	—	—	—	—	—	—	—	—	—	—
Age (years)	1	2	3	4	5	6	7	8	9	—	—	—	—	—
N July 15	101,851.0	206,532	154,956	56,069	38,346	11,132	8,300	7,312	3,084	—	—	—	—	—
g/fish/day	0.8	1.5	2.8	5.2	8.6	9.5	10.9	7.2	4.4	—	—	—	—	—
tons/day	81	310	434	292	330	106	90	53	14	—	—	—	—	—
T July	1.7	—	—	—	—	—	—	—	—	—	—	—	—	—
Age (years)	1	2	3	4	5	6	7	8	9	10	11	—	—	—
N Nov 15	86,215	18,6878	141,242	46,321	28,904	7,643	5,424	4,876	2,352	419	98	—	—	—
g/fish/day	0.6	2.5	5	7.7	12.8	17.9	18	15.6	14.8	18.9	0	—	—	—
tons/day	52	467	706	357	370	137	98	76	35	8	0	—	—	—
T Nov—Dec	3.2	—	—	—	—	—	—	—	—	—	—	—	—	—
Haddock														
Age (years)	1	2	3	4	5	6	7	8	9	—	—	—	—	—
F 1992	0	0.019	0.137	0.414	0.709	0.829	0.819	0.967	0.872	—	—	—	—	—
M	0.5	0.3	0.2	0.2	0.2	0.2	0.2	0.2	0.2	—	—	—	—	—
N Jan 1	54,408	160,915	63,045	13,513	8,929	7,706	11,558	2,302	247	—	—	—	—	—
N Mar 15	49,026	150,568	58,771	11,890	7,389	6,219	9,347	1,805	198	—	—	—	—	—
g/fish/day	0.3	0.9	3.0	5.8	9.8	13.8	16.0	16.9	21.8	—	—	—	—	—
tons/day	15	136	176	69	72	86	150	31	4	—	—	—	—	—
T March	5.2	—	—	—	—	—	—	—	—	—	—	—	—	—
July		Virtually no capelin consumption (<0.1 g/per age group)												
November		No capelin consumption												

Table 2. cont'd.

							Pollock							
Age (years)	1	2	3	4	5	6	7	8	9	10	11	12	—	—
F 1992	0	0	0.014	0.132	0.344	0.458	0.434	0.338	0.458	0.414	0.296	0.178	—	—
M	0.5	0.3	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	—	—
N Jan 1	89,022	44,545	18,824	25,990	14,495	12,981	12,074	15,488	3,845	1,132	840	378	—	—
N Mar 15	80,215	41,846	18,003	24,253	12,942	11,318	10,580	13,846	3,352	996	758	349	—	—
g/fish/day	0	3.8	7.4	12.1	17	24.7	32.1	36.5	50.1	57.4	73.4	78.2	—	—
tons/day	0	159	133	293	220	280	340	505	168	57	56	27	—	—
T March	5.2	—	—	—	—	—	—	—	—	—	—	—	—	—
Age (years)	1	2	3	4	5	6	7	8	9	10	11	12	—	—
N July 15	67,901	37,864	16,764	21,712	10,796	9,089	8,565	11,573	2,692	812	—	—	—	—
g/fish/day	0	0	0.4	0.6	0.4	0.2	0.2	0.1	0	0	—	—	—	—
tons/day	0	0	7	13	4	2	2	1	0	0	—	—	—	—
T July	3.6	—	—	—	—	—	—	—	—	—	—	—	—	—
November	Insufficient data													
							Greenland halibut							
Age (years)	1	2	3	4	5	6	7	8	9	10	11	12	13	14
F 1992	—	—	—	—	0.001	0.024	0.108	0.225	0.271	0.488	0.445	0.525	0.404	0.169
M	0.3	0.25	0.2	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15
N Jan 1	63,950	47,375	36,896	30,208	22,137	19,187	21,298	17,414	11,967	8,368	5,851	3,346	1,640	996
N Mar 15	60,075	44,971	35,390	29,278	21,451	18,504	20,183	16,105	10,962	7,327	5,169	2,907	1,461	932
g/fish/day	—	—	—	—	0.3	2.5	2.8	3.3	4.3	5.4	6.2	6.9	7.7	8.2
tons/day	—	—	—	—	6	46	57	53	47	40	32	20	11	8
T March	3.5	—	—	—	—	—	—	—	—	—	—	—	—	—
Age (years)	1	2	3	4	5	6	7	8	9	10	11	12	13	14
N July 15	54,358	41,375	33,108	27,850	20,398	17,461	18,520	14,213	9,527	5,923	4,239	2,321	1,215	838
g/fish/day	0.2	1.1	1.9	2.3	3.4	3.8	4.1	4.3	4.6	5	5.4	5.7	4.9	4.3
tons/day	11	46	63	64	69	66	76	61	44	30	23	13	6	4
T July	2	—	—	—	—	—	—	—	—	—	—	—	—	—
Age (years)	1	2	3	4	5	6	7	8	9	10	11	12	13	14
N Nov 15	49,804	38,466	31,232	26,658	19,520	16,597	17,178	12,740	8,426	4,917	3,564	1,906	1,034	764
g/fish/day	0	2.5	3.1	3.6	5.7	6.8	8	9.3	11.4	13.1	13.4	12.2	10.1	9.2
tons/day	0	96	97	96	111	113	137	118	96	64	48	23	10	7
T Nov—Dec	3.3	—	—	—	—	—	—	—	—	—	—	—	—	—

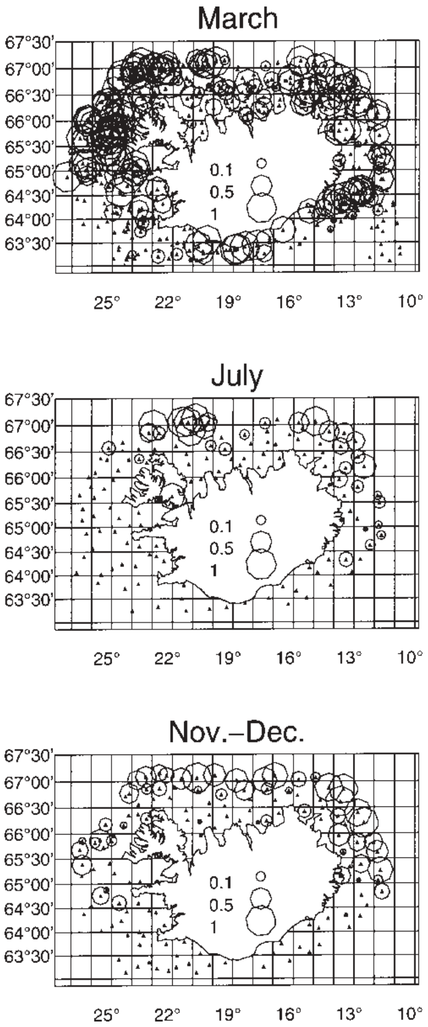


Figure 1. Spatial distribution of capelin contents (proportion of capelin in total stomach content) in Atlantic cod stomachs in 1992.

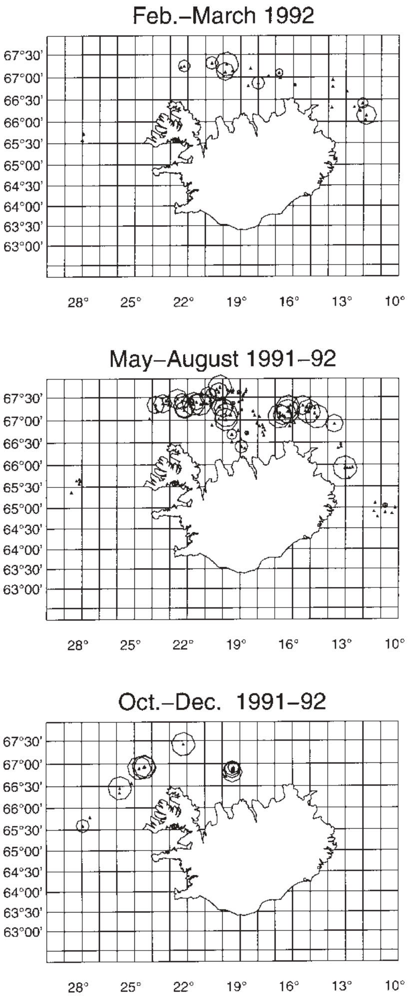
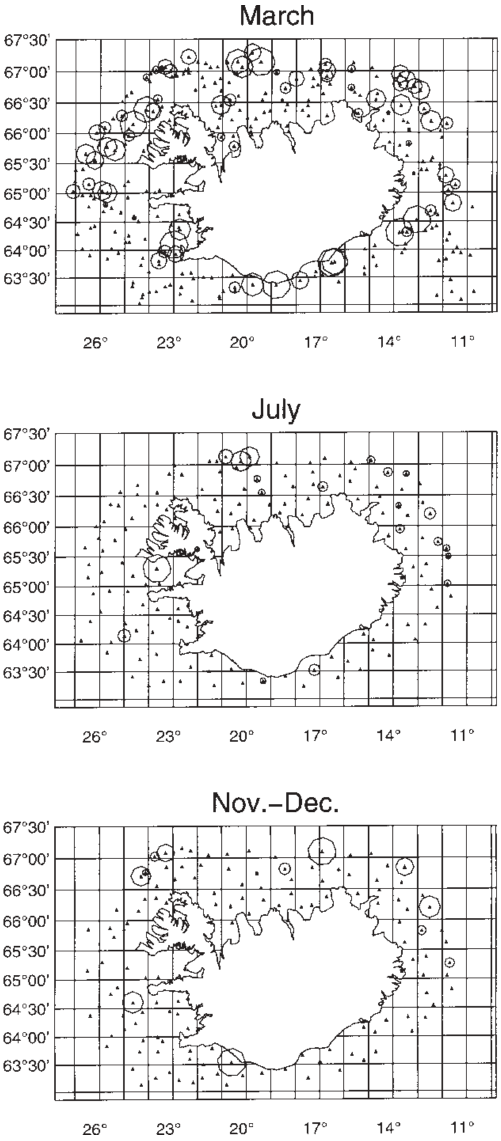


Figure 2. Spatial distribution of capelin contents (proportion of capelin in total stomach content) in Greenland halibut stomachs in 1992.


March

July

Nov.–Dec.

Figure 3. Spatial distribution of capelin contents (proportion of capelin in total stomach content) in American plaice stomachs in 1992.

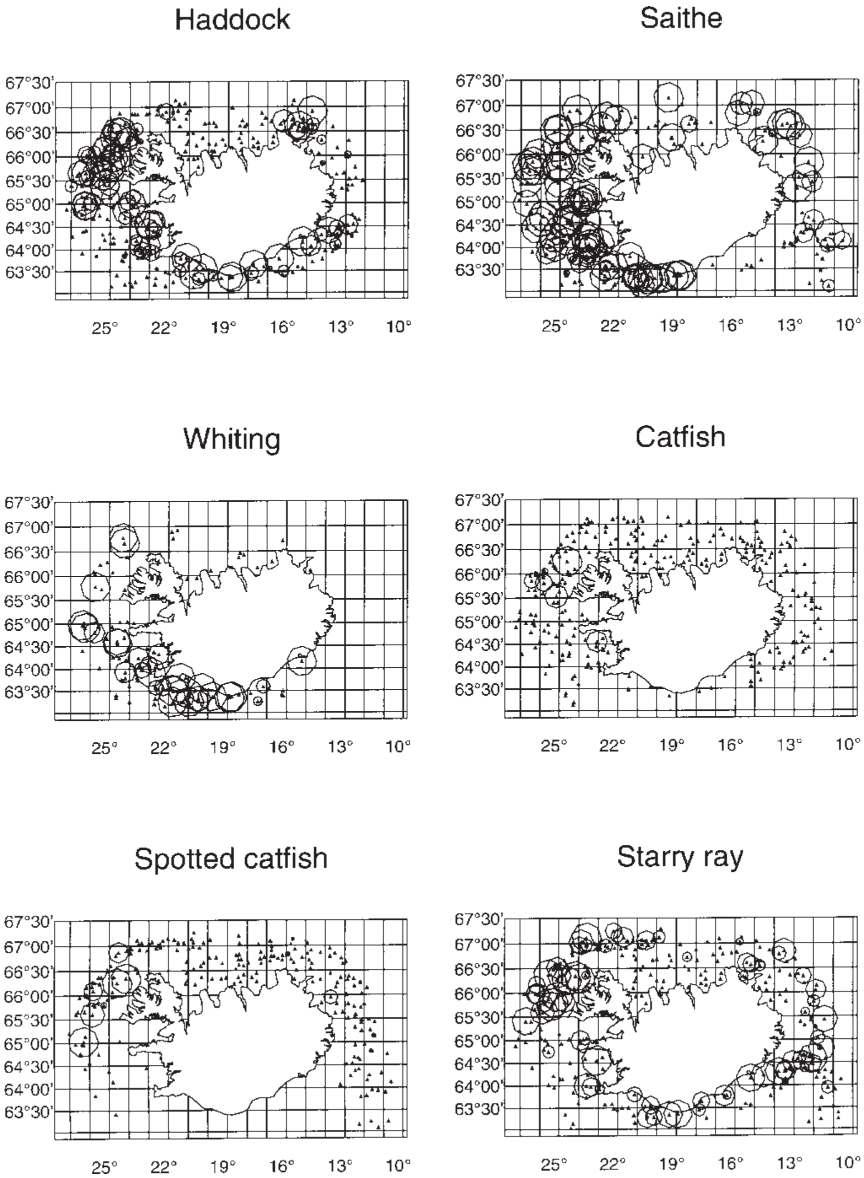


Figure 4. Spatial distribution of capelin contents (proportion of capelin in total stomach content) in stomachs of other predators in March 1992.

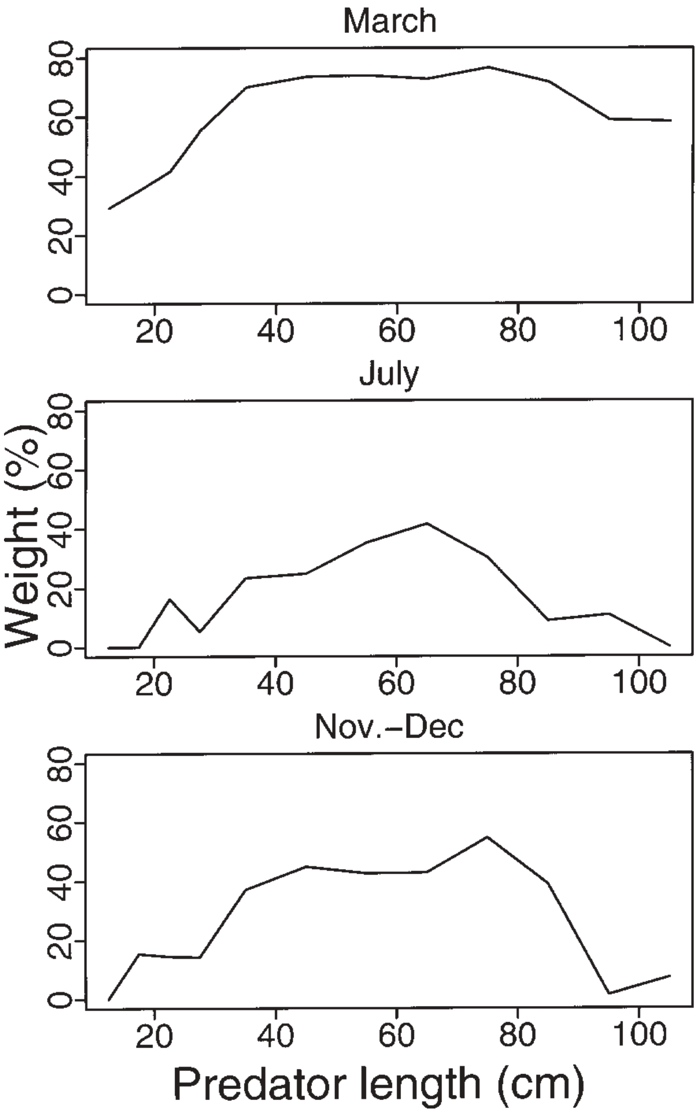


Figure 5. Relative capelin contents (% weight of total stomach content) in Atlantic cod in 1992 by predator length and season.

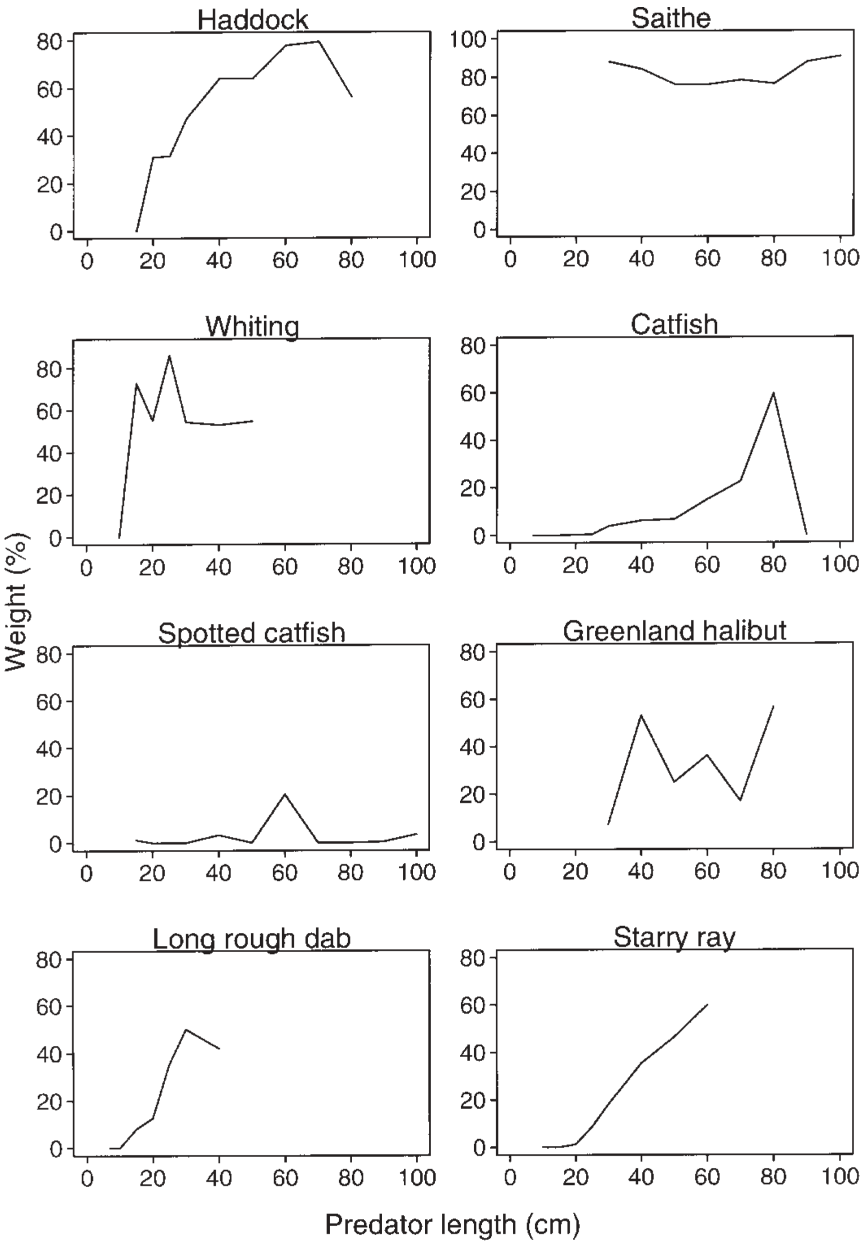


Figure 6. Relative capelin contents (% weight of total stomach content) in other predators in March 1992.

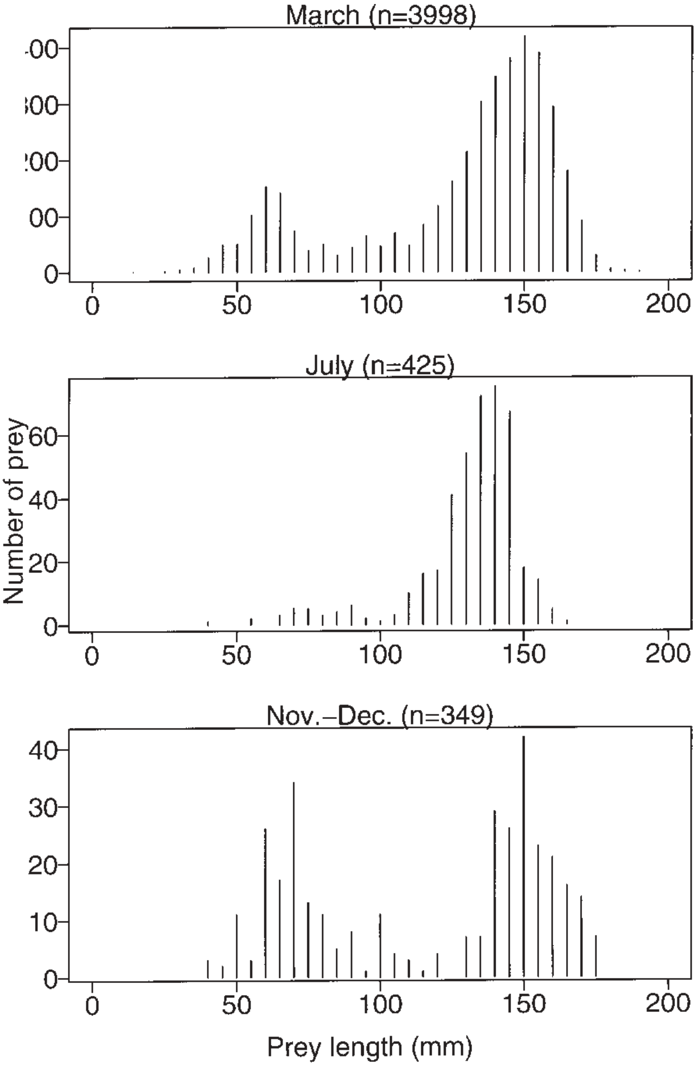


Figure 7. Length distribution of capelin (number of fish by length) in Atlantic cod stomachs in 1992.

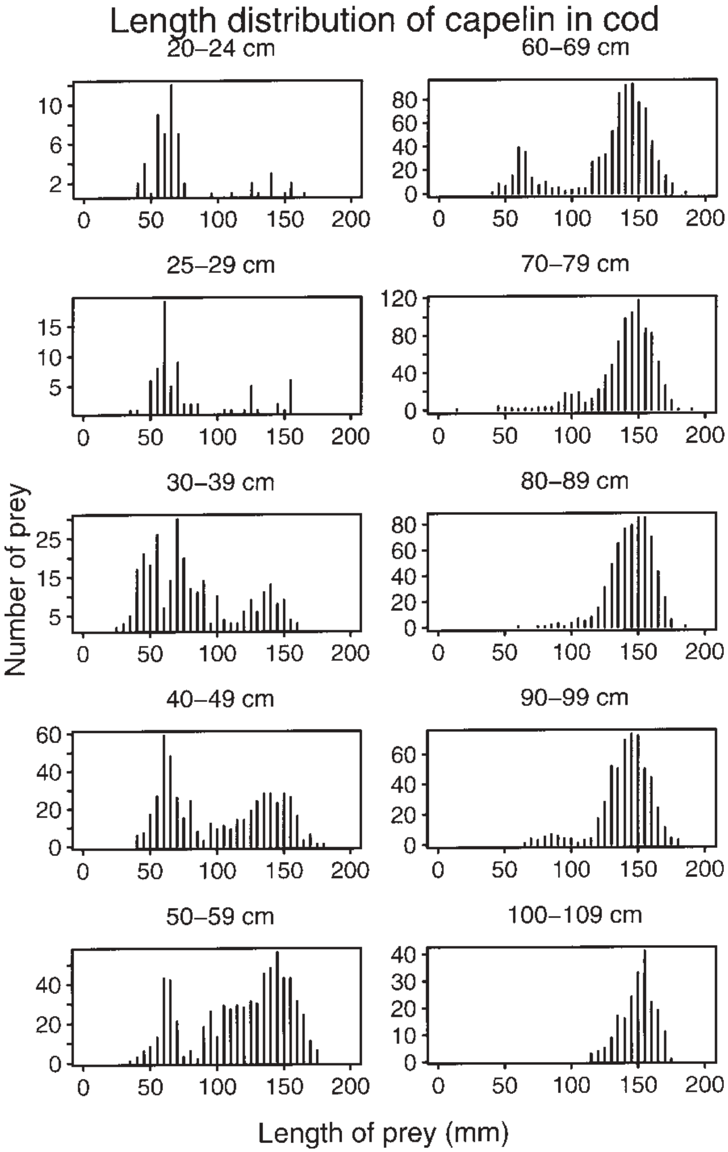


Figure 8. Length distribution of capelin (number of fish by length) in Atlantic cod stomachs by predator length groups in March 1992.

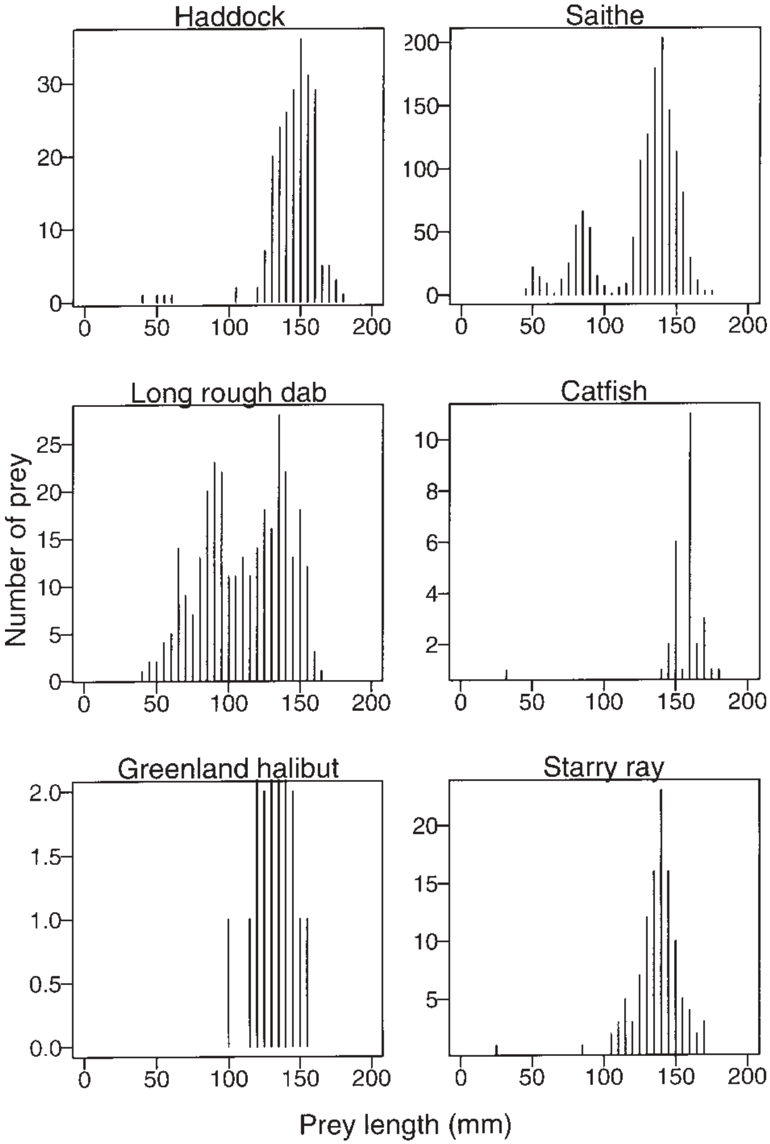


Figure 9. Length distribution of capelin (number of fish by length) in other predators in March 1992.

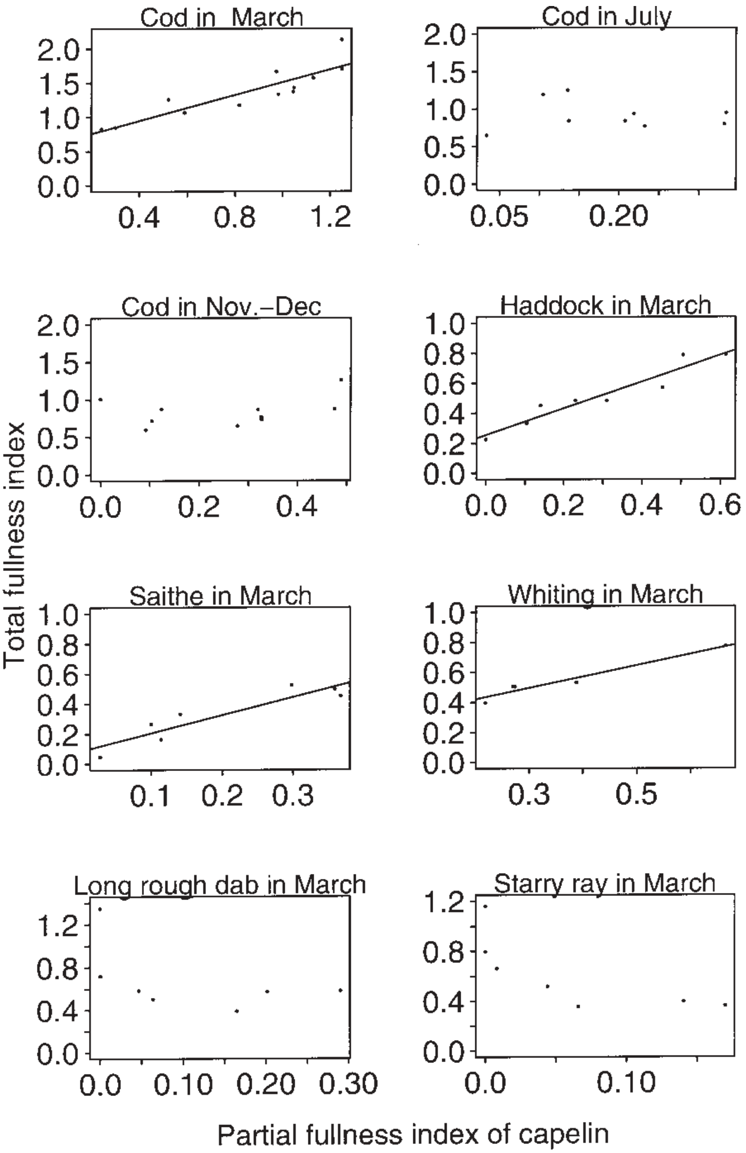


Figure 10. Relationships between capelin partial fullness index (PFI) and total fullness index (TFI) for different predators.

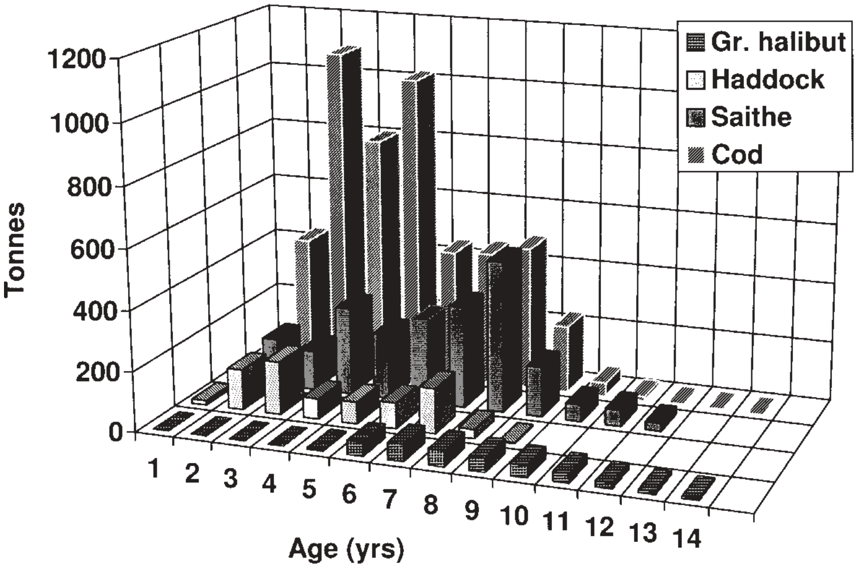


Figure 11. Calculated daily consumption (tons) in March 1992 by predator age for Atlantic cod, haddock, pollock, and Greenland halibut.

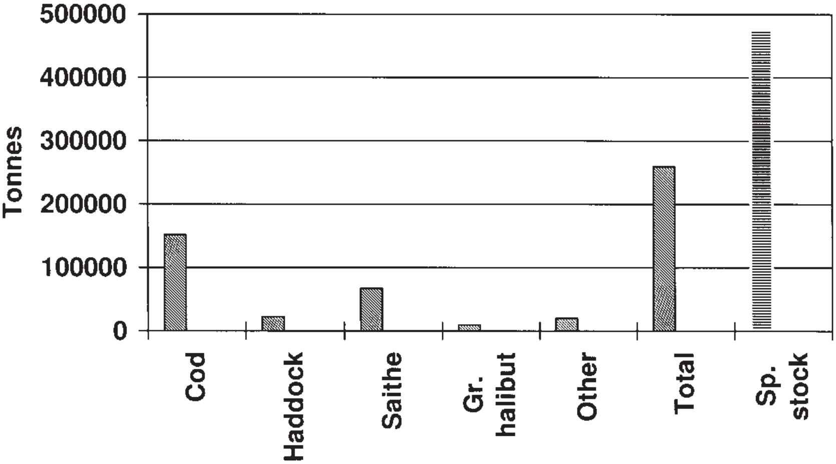


Figure 12. Calculated monthly consumption (tons) in March for Atlantic cod, haddock, pollock, Greenland halibut and other predators, and the size of capelin spawning stock at spawning time.

tor off the west and south coasts. On the other hand, it was not found in European whiting stomachs off the north coast. Capelin was found in stomachs of Atlantic wolffish and spotted wolffish stomachs only on a few stations off the northwest and west coasts in March. Capelin was identified in stomachs of thorny skate in March in various areas on the continental shelf and in particularly high proportions off the northwest coast. Off the north and east coasts, capelin was mainly recorded along the edge of the continental shelf, whereas off the south and west coasts it occurred more frequently in shallower waters.

Capelin contents by predator length

Predation by fish on capelin, in terms of proportion of capelin of total stomach content, is highly dependent on predator length. For Atlantic cod, relatively high levels of capelin contents were reached at a predator length of 30 cm (Figure 5). As a rule, a high level was maintained, or even increased, over the length range 30-60 cm, even up to 80 cm, depending on season. On a seasonal basis, capelin contents are most pronounced in March, both in terms of proportion, and predator length range. Even the largest Atlantic cod, around 100 cm in length, had capelin contents close to 50%. In July, the level of capelin contents was much reduced, whereas in November an intermediate situation was observed.

For haddock, capelin contents increased rapidly with predator length in March and high proportions (60-80%) of capelin were seen in the predator length range 40-79 cm (Figure 6). Very high capelin proportions (75-90%) were recorded for pollock in March over the predator length range 30-99 cm. The material was insufficient for pollock smaller than 30 cm. For European whiting, high capelin contents (53-85%) were observed over most of the predator length range. For Atlantic wolffish in March, on the other hand, a gradual increase in capelin proportions to 23% was observed in the predator length range 25-79 cm followed by a rapid increase to 60% in predator length group 80-89 cm and a subsequent drop in the next length group above.

For Greenland halibut, a rather irregular pattern was observed which may be explained by a less consistent sampling scheme in February and March. The proportion of capelin was 16-56% in the predator length range 40-79 cm. In other seasons capelin proportions of American plaice in March gradually reached 50% at a predator length of 30 cm. For thorny skate, a similar level was reached in March at a predator length of 60 cm. In July, capelin proportions of thorny skate stomach contents were much lower and more irregular.

Capelin length distributions

The material on length distributions of capelin in Atlantic cod stomachs is relatively extensive by seasons and even by predator length group in March. In March three distinct peaks are seen in the length distribution, around 60 mm, 100 mm, and 150 mm, representing ages 1, 2, and 3 years and older capelin, respectively (Figure 7). Clearly, the contribution of age 3+ capelin is the highest and that of 2-year-old capelin lowest.

In July, two modes are observed in the length distribution, that of age 2+ capelin around 140 mm and age 1 year around 80 mm, of which the former is the main component. In November-December, age-0 capelin are seen as a mode around 60 mm in addition to age 1 and 2+ fish around 100 mm and 150 mm, respectively. In this season, the age-0 fish are somewhat less numerous in the length distribution than age 2+ capelin.

The length distributions of capelin in Atlantic cod stomachs in March by predator length group indicate a clear shift in prey size selection with predator length (Figure 8). Among the smallest Atlantic cod (<30 cm) the small (around 60 mm) 1-year-old capelin are mainly found in the stomachs. In the predator length range 30-79 cm, a shift occurs from the smallest capelin to the medium-sized age 2 prey (around 100 mm) and to the largest age 3+ capelin (around 150 mm). In the larger predator length groups (>80 cm) the smaller capelin are virtually absent from the food.

Capelin length distributions from haddock stomachs, including all material sampled in 1992, mainly in March with respect to capelin, show that it is mostly the largest capelin which is eaten (Figure 9). For pollock, a more mixed capelin length distribution is observed, with 1- and 2-year-old capelin eaten to some extent although the largest prey is clearly preferred. On the other hand, capelin distributions in stomachs of Atlantic wolffish as well as Greenland halibut, are entirely limited to the largest prey. It should be noted, however, that the material for these predators is limited.

For American plaice, an opposite situation is observed with rather even capelin length distribution over the whole prey length range. In thorny skate, however, the capelin distribution is again mainly limited to the largest prey.

Capelin contents versus total contents

The relationships between capelin partial fullness index (PFI^{cap}) and total fullness index (TFI) are shown in Figure 10 for each predator where material allowed. For Atlantic cod in March, a significant linear relationship is found between the indices, showing that total stomach content is highly dependent on the capelin content. In the absence of capelin, the total stomach content is reduced by approximately 50%. In July and November-December, on the other hand, no such relationship is found. In these seasons the level of TFI is comparable to the level in March in the absence of capelin, i.e., at the intercept of the regression line with the y-axis.

For pollock in March, the total fullness index is significantly dependent on the capelin content. This appears reasonable in view of the high proportion of capelin in the food of pollock in this month (Figure 10).

The total stomach content of haddock and European whiting in March is also significantly dependent on capelin contents. In the absence of capelin, the TFI of haddock and pollock is reduced to 25% of the maximum. For American plaice and thorny skate in March, total fullness index does not increase with increasing capelin index. Even the opposite trend is indicated for thorny skate where higher total index is observed at lower capelin index values.

Consumption

Input and output values of consumption calculations are shown in Table 2. Since most of the predators mainly prey on capelin in March, and only a few in other seasons, consumption is clearly most pronounced in March and negligible in other seasons except for Atlantic cod. The total consumption of capelin in July is 70,000 tons and in November-December is 100,000 tons, of which about 70% is eaten by Atlantic cod and the remainder by Greenland halibut.

The age-disaggregated daily consumption by four predators on capelin in March is shown in Figure 11. The role of Atlantic cod is evident, especially that of some of the younger age groups due to their abundance. The pollock consume very much the same amount as Atlantic cod per individual fish (Table 2). Their consumption per most age groups, however, is considerably less because of lesser abundance than Atlantic cod. Other predators consume much less, due both to their lower abundance and their smaller stomach contents.

In order to evaluate the impact of predation on the spawning stock of capelin, the daily consumption in March was calculated for a period of 1 month. The proportion of capelin in Atlantic cod stomachs, although fluctuating heavily on a day-to-day basis, remained on the whole stable during the sampling period 4-18 March 1992. Thus, it seems justified to extend this period over 1 month. This results in a total estimate of 270,000 tons of capelin consumed in March (Figure 12), of which Atlantic cod consume 56% or 151,000 tons. Pollock is also a noteworthy consumer of capelin with 67,000 tons per month. Each of the other predators consumes rather limited amounts, which add up to approximately 50,000 tons for all of these predators. Of this, 20,000 tons have, somewhat arbitrarily, been allocated to other predators than shown in Figure 12, i.e., European whiting, Atlantic wolffish, spotted wolffish, American plaice, and thorny skate.

Discussion

The role of capelin as prey of other fish species has hitherto mainly been dealt with in detail for Atlantic cod as predator. The present data confirm the overwhelming role of cod in this context since cod prey on capelin to a larger extent in all seasons considered than any other predator species. However, two other species, Greenland halibut and American plaice, also prey on capelin in all seasons. Greenland halibut is probably the most relevant predator following the cod, since its distribution is likely to overlap to a large extent with that of capelin during most of the year. Other predators are found to prey only on capelin in March and some, i.e., Atlantic wolffish and spotted wolffish, are found to have limited effect in this respect.

Consumption by pollock in March is 67,000 tons, which is significantly less than calculated by Jónsson (1996), where the monthly consumption by pollock was found to be 100,000 tons. Although Jónsson applied a different consumption model and somewhat different data treatment than the present author, the difference in results is mainly due to changes is stock size input data. That is, the current stock size estimate of pollock for 1992 is markedly lower than that presented in 1995 and applied by Jónsson.

The large amount of capelin in fish stomachs in March, and hence the relatively large amount consumed in this month, merits some explanation. In fact, the obvious explanation relates to the spawning migration of capelin onto and along the continental shelf during this time of year. This leads to maximum spatial overlap between the prey and its potential predators. In addition, the capelin are loaded with spawning products of up to 25% of their body weight, which is bound to increase its suitability as prey. Furthermore, some of the capelin may have completed spawning and died and need only be picked up from the bottom. According to an analysis of maturity stages of capelin as prey in March 1993 some 10% of the mature fish may have been in this category.

The calculated predation by the nine demersal predators in March of 230,000 tons appears high in relation to the size of the capelin spawning stock at spawning time, which was estimated to have been 475,000 tons at spawning time in 1992 on the basis of acoustic measurements (Vilhjálmsson 1994). Obviously, the consumption estimates are subject to some sources of errors due to sampling and assumptions regarding evacuation rates. Furthermore, there are no apparent negative effects on capelin stock and recruitment due to this predation. Nevertheless, it seems appropriate to incorporate such a substantial source of mortality into stock projections and management considerations.

Acknowledgments

The author acknowledges the contributions of Höskuldur Björnsson, Marine Research Institute, for his advice on data treatment and of Hjálmar Vilhjálmsson, MRI, for his reading and improvement of the manuscript.

References

Anon. 1996. State of marine stocks in Icelandic waters 1995/96. Prospects for the quota year 1996/97. Fjölrit Hafrannsóknastofnunarinnar, pp. 175. (English summary.)

Fahrig, L., G.R. Lilly, and D.S. Miller. 1993. Predator stomachs as sampling tools for prey distribution: Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 50:1541-1547.

Jónsson, S.Th. 1996. Pollock on a shelf: Two studies of *Pollachius virens* in Icelandic shelf waters. I. Food and feeding of pollock (*Pollachius virens*) at Iceland. Cand. scient. thesis, University of Bergen, Bergen, Norway, pp. 1-97.

Magnússon, K.G., and Ó.K. Pálsson. 1989. Trophic ecological relationships of Icelandic cod. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 188:206-224.

Meschkat, A. 1936. Untersuchungun uber den Aufbau der Kabeljaunahrung im Bereich der Vestmannainseln. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 99:3-19.

Pálsson, Ó.K. 1983. The feeding habits of demersal fish species in Icelandic waters. Rit Fiskideildar 7(1):1-60.

Rae, B.B. 1968. The food of cod in Icelandic waters. Mar. Res. 6:3-19.

Sólmundsson, J. 1994. Food of Greenland halibut at Iceland Natturufraedingurinn 64:67-76. (English summary.)

Vilhjálmsson, H. 1994. The Icelandic capelin stock: Capelin, *Mallotus villosus* (Mueller) in the Iceland-Greenland-Jan Mayen area. Rit Fiskideildar 13(1):1-281.

Blue Whiting (*Micromesistius poutassou*) as a Forage Fish in Portuguese Waters

A. Silva and M. Azevedo
Instituto Português de Investigação Marítima, Lisboa, Portugal

H. Cabral
Faculdade de Ciências da Universidade de Lisboa, Lisboa, Portugal

P. Machado
Instituto Português de Investigação Marítima, Lisboa, Portugal

A. Murta
Faculdade de Ciências da Universidade de Lisboa, Lisboa, Portugal

M.A. Silva
Instituto da Conservação da Natureza, Lisboa, Portugal

Abstract

Studies on the feeding ecology of several marine organisms conducted in Portuguese waters emphasized the importance of blue whiting as a forage species. Information from these studies was assembled, reanalyzed, and complemented with data from the literature to describe trophic interactions and to identify the most important trophic links involving blue whiting as prey.

Hake (*Merluccius merluccius*), john dory (*Zeus faber*), monkfish (*Lophius* spp.), mackerel (*Scomber scombrus*), small spotted catshark (*Scyliorhinus canicula*), horse mackerel (*Trachurus trachurus*), and common dolphin (*Delphinus delphis*) are confirmed blue whiting predators in Portuguese waters. Potential predators inferred from studies in other areas include other fishes, marine mammals, and scavenging seabirds.

Blue whiting are shown to be important prey within three distinct food webs: deep demersal, shallow demersal, and pelagic. The role of blue whiting is probably more critical within the deep demersal food web which includes the adults of demersal species inhabiting the shelf edge and upper slope (e.g., hake and monkfish). The trophic interaction

between hake and blue whiting is noteworthy, due to the similarity in the species distributions and to the importance of the trophic link in both juvenile and adult stages, suggesting that changes in blue whiting abundance may have a more serious impact on hake than on any other predator population.

Introduction

Sustainable exploitation of marine communities depends on the understanding of the way their constituent species interact with each other and with the environment (Beddington and May 1982). This principle has been incorporated in models of fish stock assessment for a long time (e.g., Andersen and Ursin 1977), and although most routine assessments continue to rely on single-species models, scientific advisors are concerned with multispecies interactions.

Forage species, considered to be those with a broad geographic distribution, high abundance, and relatively modest body size, are expected to have a central role in community dynamics. This is the case of blue whiting in the northeast Atlantic which has been repeatedly recognized as an important item in the diet of fishes, cephalopods, and marine mammals in different areas of its distribution range (Du Buit 1994, Rocha et al. 1994, Santos et al. 1996). Several studies conducted in Portuguese waters corroborate the importance of blue whiting as a prey for other marine animals. This fact has motivated the assemblage of data from these studies (most of which are not yet published) and their reanalysis in the "perspective of the prey" as a first step to understand the role of blue whiting in food webs. As a complement, potential predators are inferred from the literature considering their feeding habits in other areas. This information is used to describe trophic interactions and to identify the most important trophic links involving blue whiting as a prey in the Portuguese waters.

Brief Account of Blue Whiting Biology and Exploitation

Blue whiting is a small schooling gadoid quite abundant along North Atlantic continental slopes. It is distributed in the western side of the Atlantic from 40°N to western Greenland and in the eastern side from Spitsbergen (82°N) to the Canary Islands (26°N) (Zilanov 1980). It occurs also off Iceland and in the Mediterranean Sea as far as 27°E.

The vertical distribution of blue whiting extends from mid-shelf (50-100 m) to depths exceeding 1,000 m but the highest densities are usually found on the upper part of the slope (200-500 m) (Bailey 1982). On the shelf edge and slope, the species has a typical pelagic behavior with diel vertical migrations apparently of trophic nature while on the shelf it remains close to the bottom in a typical demersal behavior (Polonskiy 1966, Bailey 1982, Degnbol and Munch-Petersen 1985). The average size of blue whiting has been observed to increase with depth (Guichet 1968, Bailey 1982).

Large-scale seasonal migrations are well documented for this species in the northeast Atlantic (see Bailey 1982 for references). Blue whiting spawns in the spring and summer and its main spawning grounds are located in the area to the west of the British Isles. After spawning, most of the adults undertake a feeding migration toward the Norwegian Sea and in the autumn they return to the spawning grounds.

Blue whiting has a long life span (15 years) and can reach a total length of 40-45 cm and an individual weight of 300-500 g. Growth is sexually differentiated, the females presenting higher growth rates and larger maximum lengths than males (Monstad 1990). Maximum ages of 8-10 years and total lengths of 30-35 cm for males and 35-40 cm for females have been commonly observed.

Length at first maturity is 18-20 cm (fish 1-2 years old) and tends to become smaller as one moves south along the distribution range of the species (Ehrich and Robles 1982, Cunha 1992, Mazhirina 1994).

Blue whiting diet is dominated by crustaceans: juvenile individuals feed mainly on copepods and Euphausiacea (with emphasis on *Meganicthyphanes norvegica* and *Nicthyphanes couchi*). With growth, decapods and fish (mainly myctophids) gradually increase in relative importance (Cabral 1992).

The exploitation of blue whiting increased considerably in the late 1970s (Monstad 1990). In recent years, landings from the whole northeast Atlantic are around half a million tons a year, 90% of which are from the areas to the north of the Celtic Sea (Anon. 1996a). Blue whiting is used partly in the fishmeal industry and partly in the production of higher-valued products such as surimi (Dagbjartsson 1975).

Two kinds of fisheries, carried out by midwater trawlers, take place in the northern areas (Bailey 1982): one in the spawning grounds conducted mainly by Norway and another in the Norwegian Sea carried out mainly by Russia. In the southern areas, most of the catches are taken by Spanish vessels, part in a directed fishery by paired bottom trawlers in the Celtic Sea, and part as a bycatch in single bottom trawlers fishing a mixture of groundfish species (hake, monkfish, megrims). Off the Portuguese coast blue whiting is a bycatch in bottom trawl fisheries catching groundfish (hake, horse mackerel, monkfish, megrim) and crustaceans (Norway lobster, rose shrimp). Annual landings have fluctuated around 3,000 tons in recent years. The commercial value of larger individuals has increased considerably in recent years.

The amount of discards in the southern area is thought to be high. First estimates of blue whiting discarded by single and paired trawlers in 1994 were, respectively, 62% and 22% in weight (Anon. 1996a).

Table 1. Brief information on the exploitation, state of stock, distribution and behavior of confirmed blue whiting predators in Portuguese waters.

Species	Fisheries	% total fish yield		State of stock	Bathymetric distribution	Behavior	References
		weight	value				
Hake	Bottomtrawl Gillnet, longline	2	8	Outside safe biological limits	30-1,000 m Highest abundance: 100-200 m	Demersal, schooling Mean length increases with depth	Anon. 1996a,b Cardador 1995
John dory	Bottomtrawl Gillnet	0.3	1.2	Unknown	Up to 500 m depth Highest abundance: 100-200 m	Demersal Isolated or small groups	Bauchot & Pras 1980 Silva 1992
Monkfish	Gillnet Bottomtrawl	1	4		100-800 m Scarce beyond 400 m	Benthic Partially burrowed	Quéro 1984 Azevedo 1996
Mackerel	Bottomtrawl	1	0.2		Up to 350 m	Pelagic	Lockwood & Johnson 1976
	Purse seine				Highest abundance: 20-100 m	Diel vertical migrations	Martins & Cardador 1996
S.s. catshark	Bottomtrawl	0.3	0.01	Unknown	100-400 m	Benthic	Figueiredo et al. 1995 Moura 1995
Horse mackerel	Purse seine	11	11		Up to 500 m, highest abundance: juveniles	Pelagic	Lockwood & Johnson 1977
	Bottomtrawl				within 100 m; large adults in 200-400 m	Diel vertical migrations	Murta & Borges 1994
Common dolphin	Protected by Portuguese legislation	Most common cetacean in the Portuguese waters			Continental shelf and shelf edge	Pelagic, found in the upper 50 m	Evans 1994 Sequeira et al. 1992 Sequeira & Teixeira 1988

Predators of Blue Whiting

Confirmed predators

Six fish species (hake, john dory, monkfish, mackerel, small spotted catshark, and horse mackerel) and one marine mammal (common dolphin) have been shown to feed on blue whiting in Portuguese waters. Table 1 summarizes information regarding exploitation (conservation status for common dolphin), state of stock, distribution, and behavior of these species.

Other predators and potential predators

Megrims (*Lepidorhombus whiffiagonis* and *L. boscii*) are deepwater flatfishes occurring off the Portuguese coast beyond 200 m (Silva and Azevedo 1995). They are a bycatch of bottom trawl fisheries directed to crustaceans representing about 0.3% of total fish yield. There is no information on the diet of megrims in Portuguese waters but studies in the Celtic Sea and off north and west Scotland demonstrated that blue whiting represents an important part of the diet of megrim (*L. whiffiagonis*) (Du Buit 1984, 1992). Sharks have also been referred to as blue whiting predators in the works of Probatov and Mikheev (1965) and Zilanov (1968). We could not find references to the diet of deepwater selachians off the Portuguese coast but it is plausible that blue whiting represents a significant prey for some species.

Blue whiting occurs in the diet of European squid (*Loligo vulgaris*) and of veined squid (*Loligo forbesi*), two species commonly found off the Portuguese coast. Pierce et al. (1994) found negligible amounts of blue whiting in samples collected between the south of Portugal and the Faeroe Islands. Contrasting results are reported by Rocha et al. (1994) who observed that blue whiting was the second most important prey for these squids in Galician (northwest Spain) waters. Ommastrephid squids, *Todarodes sagitattus*, *Todaropsis eblanae*, and *Ilex coindetti*, are also common in Portuguese waters and have more pronounced pelagic habits than loliginid squids. The former of these has been shown to eat mainly blue whiting off Norway, Shetland, and Faeroe Islands (Wiborg 1987). Blue whiting was also the dominant species in the diet of *T. eblanae* and *I. coindetti* in Galician waters, composing nearly 50% of the diet of the former (Rasero et al. 1996).

Marine mammals other than the common dolphin that inhabit Portuguese waters are also potential blue whiting predators. Such is the case of the striped dolphin (*Stenella coeruleoalba*), for whom blue whiting represents the main prey in the area between the French coast and the Faeroe Islands (Desportes 1985) and in the Ligurian Sea (Mediterranean, Italy) (Wurtz and Marrale 1993). Recent data for the Galician shelf (Santos et al. 1996) do not agree with these findings but the small sample size may be responsible for the apparent contradiction. The bottlenose dolphin (*Tursiops truncatus*), another species commonly found along the

Portuguese coast, feeds mainly on blue whiting off Galicia (Santos et al. 1996), along the shelf from the French coast to the Faeroe Islands (Desportes 1985) and in the Ligurian Sea (Rellini et al. 1994).

The large amount of blue whiting that is undoubtedly discarded off the Portuguese coast raises questions about its possible use by seabirds. The consumption of fish offal and discards by scavenging seabirds has been largely reported (e.g., Furness et al. 1988, Thompson and Riddy 1995). Blue whiting discards may represent an important food source for gannets (*Sula bassana*) and gulls (*Larus fuscus* and *L. cachinnans*) wintering along the Portuguese coast (Pers. comm., J.P. Granadeiro, Instituto da Conservação da Natureza, Lisbon, October 1996).

Origin of Data

Methods used in the studies of the diet of blue whiting predators are briefly described in Table 2. Since these studies were planned independently and had distinct objectives, sampling design and intensity and time periods and areas covered are different among them, except occasional coincidences.

Standardization and Synthesis of Data

To achieve a more detailed description of trophic relationships, data were standardized and synthesized as follows.

The populations of predators and blue whiting were subdivided into juveniles and adults.

This procedure was not followed for common dolphin because it would decrease the sample size considerably. Horse mackerel was also excluded from this analysis due to the small number of stomachs sampled from large individuals. The relative importance of blue whiting in the diet of each component was computed using numerical (%n), gravimetric (%w), and/or occurrence (%f) indices. In addition, the percentage of juvenile and adult blue whiting in the diet of each predator (juvenile and adult) was computed whenever data on prey size was available (this was the case for hake, john dory, and common dolphin). The juvenile-adult division was based on published L_{50} values (length at which at least 50% of the individuals matured for the first time). When different L_{50} exist for each sex, an average value was adopted. For john dory and small spotted catshark, the division was based on the length corresponding to the main ontogenetic diet shift, which appears also to be close to the onset of sexual maturity (Silva 1995, Machado 1996).

Confirmed and potential blue whiting predators off the Portuguese coast were classified, according to their main distribution and behavior patterns, into three groups: deep demersal, shallow demersal, and pelagic. This classification reflects the biogeography of the Portuguese coast (Gomes and Serrão In press). It is assumed that the shelf edge es-

Table 2. Materials and methods used in studies of food habits of blue whiting predators.

Species (length range)	Objectives of study	Source of samples	Sampling periods/date	Number of stomachs (with food)	Type of data collected for each prey	References
Hake (17-67 cm)	Food habits, diet growth shifts, time/space variation	Groundfish surveys entire coast, 20-750 m	Jun/Jul 1990-1991 Oct/Nov 1990-1991 Feb/Mar 92	1,950	Taxa, frequency, number, weight, length	Cabral 1992
John dory (8-56 cm)	Food habits, diet growth shifts, temporal variation	Groundfish surveys entire coast, 20-750 m	Oct/Nov 1990-1992 Feb/Mar 1992 Jun/Jul 1992	326	Taxa, frequency, number, weight, length	Silva 1995
Monkfish (20-121 cm)	Qualitative description of food	Groundfish surveys SW/s coast, 100-700 m	1988-1994	213	Frequency	Azevedo 1966
Mackerel (21-36 cm)	Food habits, diet growth shifts, time/space variation	Groundfish surveys entire coast, 20-750 m	Jun/Jul 1990-1991 Oct/Nov 1990-1991 Feb/Mar 1992	274	Taxa, frequency, number, weight, length	Murta 1992
S.s. catshark (14-64 cm)	Food habits, diet growth shifts, spatial variation	Groundfish surveys west coast, 80-800 m	Aug/Sep 1995	534	Taxa, frequency, number, weight, length	Machado 1966
Horse mackerel (9-40 cm)	Food habits, diet growth shifts, time/space variation	Groundfish surveys entire coast, 20-750 m	Jun/Jul 1990-1991 Oct/Nov 1990-1991 Feb/Mar 1992	1,328	Taxa, frequency, number, weight, length	Murta 1992
Common dolphin (86-227 cm)	Food habits	Strandings entire coast	Jan 1987 - Mar 1996	26	Taxa, frequency, number, weight, length	Silva 1996

tablishes the approximate boundary between shallow and deep demersal groups.

The diet composition of the predators is presented in numbers (%n), weight (%w), and/or frequency of occurrence (%f). The choice of the prey species included in each table is intended to provide a general picture of the diet and to give some insight into possible alternative prey to blue whiting. When blue whiting is the main prey just for one component of the predator population (juveniles or adults) only the diet of that component is presented. Data for different seasons and/or years are presented when available (hake and john dory).

Finally, a diagrammatic representation of food webs for each of the three groups of species was built integrating all the information regarding trophic links between juvenile and adult components of predators and prey populations, predator behavior and distribution patterns, and alternative prey species for blue whiting predators.

Results

Table 3 shows the percentages, in numbers and weight, of blue whiting in the diet of juveniles and adults of its predators. Blue whiting is in general more important in the diet of adult fishes, a result that is not unexpected since most piscivorous species feed mainly on invertebrates (frequently zooplankton) as juveniles (Gibson and Ezzi 1987). Blue whiting has, nevertheless, a considerable importance in the diet of juvenile hake (gravimetric index = 20%).

The percentage of blue whiting juveniles and adults in the diet of hake, john dory, and common dolphin is presented in Table 4. Hake adults prey on juvenile and adult blue whiting in similar proportions but the other predators almost exclusively consume juvenile individuals. This is also a predictable result since both john dory and common dolphin occur mainly on the shelf where juvenile blue whiting is expected to be more abundant. In the case of john dory, the mouth gape may be another limiting factor.

The classification of blue whiting predators (confirmed and potential) as deep demersal, shallow demersal, or pelagic is shown in Table 5. Within the deep demersal group are included strictly deepwater species (possibly deepwater sharks) and adults of demersal species which occur from mid-shelf to the slope, showing an increase in length with depth.

For example, the adults of hake inhabit the shelf edge and upper slope while juveniles occur mainly on the shelf and are therefore included in the shallow demersal group. Also in this group are species typical of the shelf, either demersal (e.g., john dory) or pelagic that migrate vertically spending the day close to the bottom (e.g., mackerel). The pelagic group includes typical pelagic species that feed close to the bottom and/or meet blue whiting in its vertical migrations to more superficial waters (e.g., adult mackerel and common dolphin). This group also includes species that occur more offshore (ommastrephid squids, striped dolphin).

Main prey species in the diet of blue whiting predators

Hake

Crustaceans and fish dominate the diet of hake (Table 6). Juveniles feed mainly on mysids and decapods (mainly processids). Blue whiting is the most important fish prey and due to the small size of crustaceans, the dominant prey in terms of weight. As hake grows, fish becomes increasingly more important, especially blue whiting, sardine (*Sardina pilchardus*), and snipefish (*Macroramphosus scolopax*) (Cabral 1992). Blue whiting 7-28 cm in total length were observed in the stomachs of hake measuring 17-67 cm.

John dory

John dory juveniles feed mainly on dragonets (*Callionymus* spp.) and silvery pout (*Gadiculus argenteus*) (Silva 1995) (Table 7). When data from all surveys are pooled, the diet of john dory adults is dominated by blue whiting, sardine, and snipefish (Table 7). Argentine (*Argentina sphyraena*), horse mackerel, and flatfishes were relevant in some surveys.

Monkfish

Blue whiting occurred in stomachs of monkfish greater than 32 cm, and was the most frequent prey in the diet of adult individuals where it often made up the only food type (Table 8). Flatfishes like spotted flounder (*Citharus macrolepidotus*) and flounder (*Arnoglossus* spp.) followed by rose shrimp (*Parapenaeus longirostris*) and boarfish (*Capros aper*), are the most frequent prey in the diet of juveniles (Azevedo 1996).

Mackerel

Table 9 presents the composition of the diet of adult mackerel. Due to the mixture of prey with quite different sizes (e.g., zooplankton and fish), fish prey are relevant only in terms of weight. Blue whiting and argentine are the most important fish in the diet. However, copepods and decapod larvae are numerically dominant. Juvenile mackerel feed almost exclusively on the euphausiid *Nyctiphanes couchi* (Murta 1992).

Small spotted catshark

Small spotted catshark feed mainly on polichaetes, teleostean fishes, and crustaceans. Cluster analysis revealed a clear increase in fish consumption from juveniles to adults and a reduction of small crustaceans in the same direction (Machado 1996). Blue whiting is the most important fish species (Table 10).

Horse mackerel

The analysis of horse mackerel ontogenetic diet shifts (Murta 1992) revealed three main size groups of fish: 9-18 cm (juveniles), feeding mainly on the euphausiacean *Nicthyphanes couchi* and on copepods; 19-35 cm, basing their diet on euphausiaceans (in addition to *Nicthyphanes couchi*, *Meganicthyphanes norvegica* dominates) but with increased importance of small squids and fishes (mainly blue whiting); and greater than 36 cm, feeding mainly on blue whiting but with euphausiaceans still important in the diet.

Common dolphin

The diet was mainly composed of fish (%n = 85 and %f = 96) but cephalopods (mainly squids and cuttlefish) were also present. Sardine and blue whiting are the main prey species of common dolphin (Table 11). The estimated total lengths of blue whiting consumed were 7.5-22.5 cm (Silva 1996).

Blue whiting remains were observed in stomachs belonging to mature and immature dolphins of both sexes.

Food webs in Portuguese waters

Collating the information presented above, three diagrams of simplified food webs were constructed (Figure 1A-C). These food webs describe blue whiting trophic interactions within the three different groups of species previously defined: deep demersal, shallow demersal, and pelagic. The thickness of the lines represents roughly the relative abundance of the species in the environment (boxes) and the strength of the trophic interaction between the species (arrows). Potential predators are enclosed in dashed boxes.

Discussion

Blue whiting plays an important role in the trophic relationships within three groups of species associated with distinct habitats. This role is primarily a consequence of its high abundance off the Portuguese coast. Survey abundance indices for blue whiting are 10-15 times higher than those for hake and 5-10 times higher than those for horse mackerel (Cardador et al. 1994). Furthermore, blue whiting has a wide bathymetric distribution that extends from mid-shelf to the slope, making it available both for typical shelf predators and for deepwater predators. Due to the vertical migrations performed by most pelagic species and to its diel migratory behavior on the shelf edge and oceanic area, blue whiting becomes also accessible to pelagic species.

The diagrams illustrating trophic relationships show that other species apart from blue whiting appear to play central roles in the trophic webs in the shallow demersal group (sardine, argentine, snipefish) and

Table 3. Relative importance of blue whiting in the diet of juveniles and adults of predators (size classes defined in last column).

Predator	Group	%n	%f	%w	Predator length
Hake	juvenile	~0		20	<35 cm
	adult	51		62	≥35 cm
Monkfish	juvenile		2		<40 cm
	adult		34		≥40 cm
John dory	juvenile	0		0	<25 cm
	adult	37		44	≥25 cm
Mackerel	juvenile	0		0	<25 cm
	adult	≈0		52	≥25 cm
Catshark	juvenile	2		8	<31 cm
	adult	12		27	≥31 cm

Symbols are: %n, numerical index; %w, gravimetric index; and %f, frequency of occurrence.

Table 4. Percentage of blue whiting juveniles and adults in the diet of hake (juveniles and adults), john dory (adults), and common dolphin (juveniles and adults) from a sample of N blue whiting individuals measured.

		Blue whiting		
		Juveniles	Adults	N
Hake	Juvenile	96	4	326
	Adult	49	51	119
John dory	Adult	100	0	52
Common dolphin	Juv. + Adult	91	9	136

Table 5. Classification of blue whiting predators according to their distribution/behavior pattern. Potential predators are shown in parentheses.

Deep demersal	Shallow demersal	Pelagic
Adult hake	Juvenile hake	Common dolphin
Adult monkfish	Juvenile monkfish	(Striped dolphin)
Adult catshark	Juvenile catshark	(Bottlenose dolphin)
	Adult john dory	(Seabirds)
	Adult mackerel	Adult mackerel
	Adult horse mackerel	Juvenile horse mackerel
(Adult megrims)	(Juvenile megrims)	(Ommastrephid squids)
(Deepwater selachians)	(Loliginid squids)	(Loliginid squids)

Table 6. Composition of the diet of hake juveniles (<35 cm) and adults (≥35 cm) sampled in groundfish surveys in summer (S) 1990-1991, autumn (A) 1990-1991, and winter (W) 1992.

	S 1990		A 1990		S 1991		A 1991		W 1992	
Prey	%n	%w	%n	%w	%n	%w	%n	%w	%n	%w
Hake juveniles <35 cm										
Mysidacea	12	0	27	0	15	0	11	0	6	0
Euphausiacea	1	0	7	0	8	0	8	0	17	0
Decapods	36	3	6	0	32	2	24	3	12	1
Argentine anchovy	2	2	3	3	0	0	1	3	10	11
Sardine	5	16	4	11	7	22	3	17	4	7
Blue whiting	21	61	27	68	8	34	15	55	23	67
Snipefish	0	0	1	0	1	1	20	11	5	2
Hake adults ≥cm										
Argentine	1	1	0	0	0	0	4	3	0	0
Sardine	12	15	7	8	2	3	22	33	10	16
Blue whiting	52	63	39	58	40	64	30	36	56	78
Snipefish	6	1	18	12	37	4	32	2	10	1
Horse mackerel	2	8	5	4	2	7	0	0	0	0
Mackerel/Spanish mackerel	0	0	4	8	2	4	0	0	0	0
Bogue	0	0	2	7	4	8	2	7	0	0
Hake	2	4	5	12	0	0	3	3	0	0
Scabbardfish	1	2	0	0	2	8	3	18	0	0

Table 7. Composition of the diet of john dory adults (≥25 cm) sampled in groundfish surveys in summer (S) 1992, autumn (A) 1990-1992, and winter (W) 1992.

	A 1990		A 1991		W 1992		S 1992		A 1992	
Prey	%n	%w	%n	%w	%n	%w	%n	%w	%n	%w
Flatfishes	0	0	0	0	15	6	5	8	3	1
Argentine	11	8	4	5	7	6	13	12	3	2
Sardine	0	0	12	33	5	15	23	62	6	28
Blue whiting	57	58	52	54	37	55	0	0	0	0
Snipefish	20	4	20	6	17	6	27	7	63	36
Horse mackerel	11	31	0	0	1	8	18	7	9	11

Table 8. Composition of the diet of monkfish adults (≥40 cm) sampled off the Portuguese coast in the period 1988-1994.

Prey	%f
Blue whiting	34
Boarfish	14
Spotted flounder	1
European conger	5
Flounder	2
Octopus	7
Rose shrimp	5

Table 9. Composition of the diet of mackerel adults (≥25 cm) based on pooled data from groundfish surveys in summer and autumn 1990 and 1991 and winter 1992.

Prey	%n	%w
Copepods	34	0
Decapod larvae	61	0
Other crustaceans	0	5
Squids	0	6
North Atlantic anchovy	0	5
Blue whiting	0	52
Argentine	0	31

Table 10. Composition of the diet of adult small spotted catshark (≥31 cm) sampled in a research survey in August-September 1995.

Prey	%n	%f	%w
Polychaetes	26	45	10
Crustaceans	7	16	3
Blue whiting	18	36	28

Table 11. Composition of the diet of common dolphin sampled from stranded animals in the period 1987-1996. Estimates of %w were based on the total weight of the more important prey (horse/jack mackerel, sardine, blue whiting, and snipefish).

Prey	%n	%f	%w
Sand smelt	2	12	—
Horse/jack mackerel	4	39	6
Sardine	27	85	66
Blue whiting	31	35	23
Pouting	2	15	—
Snipefish	12	23	5
Hake	2	15	—
Mackerel	2	15	—

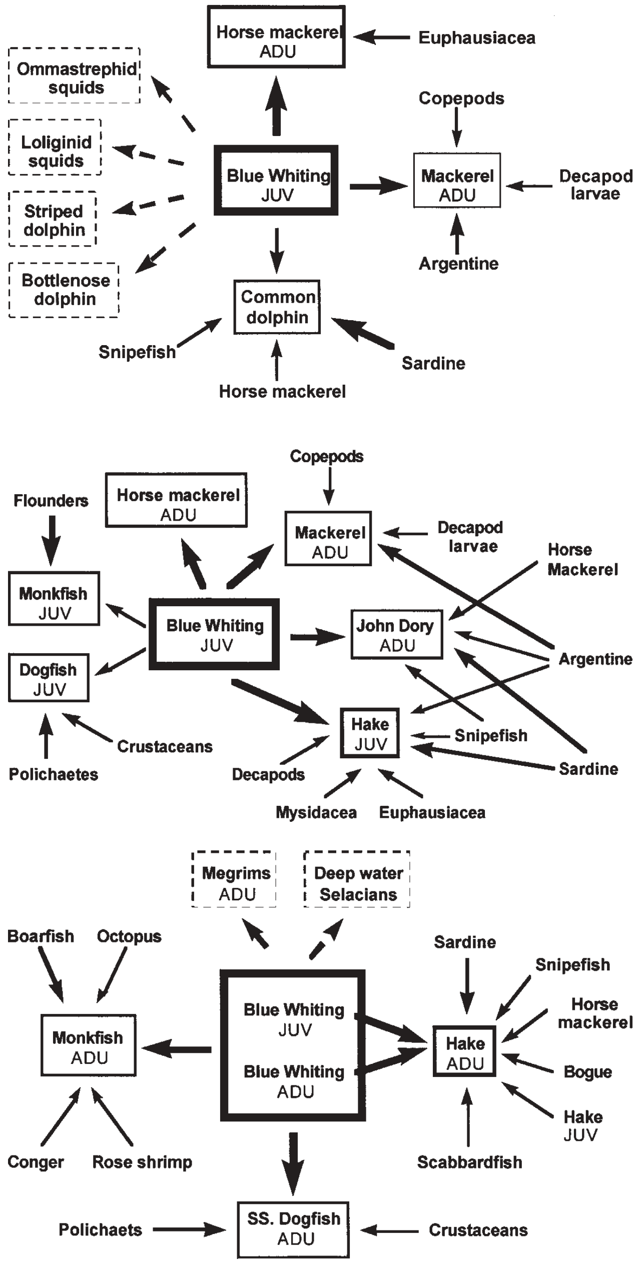


Figure 1. Diagrams of trophic webs involving blue whiting as prey in Portuguese waters: top, deep demersal; middle, shallow demersal; and bottom, pelagic.

in the pelagic group (mainly zooplankton). Species like sardine and snipefish occur in great abundance over the Portuguese shelf (Cardador et al. 1994), making them alternative forage species in that area. On the contrary, blue whiting seems to be the only forage species in the deep demersal group. This is in agreement with the biogeography of the Portuguese coast (Gomes and Serrão In press) that identifies blue whiting as the dominant species of the groundfish assemblages that occupy the shelf edge and upper slope (depth greater than 150-180 m).

The trophic association between hake and blue whiting in different areas of its distribution has been frequently emphasized (Hickling 1927, Guichet and Mériel-Bussy 1970, Gonzalez et al. 1985, Olaso et al. 1994, Guichet 1995). In this study, the relationship between hake and blue whiting is also noteworthy because the two species establish important trophic links in both the juvenile and the adult phase and present an extensive overlap of their distributions (both horizontal and vertical). These facts suggest that changes in blue whiting abundance or population structure are more liable to influence hake than any other predator. Since hake is one of the most important Portuguese fisheries resources and its stock is overexploited, possible negative impacts may have more critical effects.

Acknowledgments

The authors are indebted to Ana Moreno for guidance on cephalopod literature and to Manuel do Carmo Gomes and Carlos Afonso Dias for revision of the first draft.

References

Andersen, K.P., and E. Ursin. 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts to phosphorus circulation and primary production. Medd. Dan. Fisk. Havunders. NS 7:319-435.

Anon. 1996a. Report of the Northern Pelagic and Blue Whiting Fisheries Working Group. ICES C.M. 1996/Assess:14, 158 pp.

Anon. 1996b. Report of the ICES Advisory Committee on Fishery Management 1995. ICES Coop. Res. Rep. 214, Part 2, 355 pp.

Azevedo, M. 1996. Studying the feeding habits of anglerfish (*Lophius* spp.) in Portuguese waters: A qualitative approach. ICES C.M. 1996/G:19, 9 pp.

Bailey, R.S. 1982. The population biology of blue whiting in the North Atlantic. Adv. Mar. Biol. 19:257-335.

Bauchot, M.-L., and A. Pras. 1980. Guide des poissons marins dÉurope. Delachaux and Niestlé, Eds., Paris, 427 pp. (In French.)

Beddington, J.R., and R.M. May. 1982. The harvesting of interacting species in a natural ecosystem. Sci. Am. 247(5):42-49.

Cabral, H. 1992. Ecologia alimentar da Pescada, *Merluccius merluccius*, (L. 1758), e do Verdinho, *Micromesistius poutassou*, (Risso, 1826), na costa Portuguesa. Relatório final do Estágio Profissionalizante para conclusão da Licenciatura em Recursos Faunísticos e Ambiente. Faculdade de Ciências de Lisboa, Instituto Nacional de Investigação das Pescas, 246 pp. (In Portuguese.)

Cardador, F., A. Silva, G. Pestana, M.F. Borges, M. Azevedo, M.M. Martins, and A. Caramelo. 1994. Distribuição e abundância de peixes na costa Portuguesa. Poster apresentado no 1 Simpósio sobre a Margem Continental Ibérica Atlântica, Lisboa, 28-30 Novembro 1994. (In Portuguese.)

Cardador, F. 1995. Factors influencing the distribution and abundance of hake (*Merluccius merluccius*) in Portuguese waters (ICES Div. Ixa) based on groundfish survey data. ICES C.M. 1995/G:20, 14 pp.

Cunha, M.M. 1992. On the reproductive biology of blue whiting (*Micromesistius poutassou*, Risso 1826) from the Portuguese coast (ICES- Division Ixa). Bol. Inst. Nac. Invest. Pescas. 17:5-17.

Dagbjartsson, B. 1975. Utilization of blue whiting, *Micromesistius poutassou*, for human consumption. J. Fish. Res. Board Can. 32:747-751.

Degnbol and Munch-Petersen. 1985. On the relation between diurnal migration and feeding of blue whiting in the Skagerrak. ICES C.M. 1985/H:46, 9 pp.

Desportes, G. 1985. La nutrition des Odontocetes en Atlantique Nord-Est (côtes Françaises-Iles Faeroe). Thésis Université de Poitiers, France. 190 pp. (In French.)

Du Buit, M.H. 1984. Prédation de la cardine (*Lepidorhombus whiffiagonis* W.) au nord et à l´óuest de l´Ecosse. J. Cons. Int. Explor. Mer 41:194-198. (In French.)

Du Buit, M.H. 1992. Alimentation de la Cardine, *Lepidorhombus whiffiagonis* en Mer Celtique. Cah. Biol. Mar. 33:501-514.

Du Buit, M.H. 1994. Blue whiting in food webs in the Celtic Sea. J. Fish Biol. 45, Supplement A:245 (abstract).

Ehrich, S., and R. Robles. 1982. Investigations on maturity of blue whiting (*Micromesistius poutassou*) populations between 42°N (Vigo, Spain) and 61°N during February and March 1982. ICES C.M. 1982/H:42, 6 pp.

Evans, W.E. 1994. Common dolphin, white-bellied porpoise *Delphinus delphis* Linnaeus, 1758. In: S.H. Ridgway and R.J. Harrison (eds.), Handbook of marine mammals, vol. 5. Academic Press, London.

Figueiredo, I., M.J. Figueiredo, and O. Moura. 1995. Distribution, abundance and size composition of blackmouth catshark (*Galeus melastomus*) and small spotted catshark (*Scyliorhinus canicula*) on the slope of the Portuguese south and southern west coasts. ICES C.M. 1995/G:9.

Furness, R.W., A.V. Hudson, and E. Kenneth. 1988. Interactions between scavenging seabirds and commercial fisheries around the British Isles. In: J. Burger (ed.), Seabirds and other marine vertebrates. Competition, predation and other interactions. Columbia University Press, New York. 339 pp.

Gibson, R.R., and I.A. Ezzi. 1987. Feeding relationships of a demersal fish assemblage on the west coast of Scotland. J. Fish Biol. 31:55-69.

Gomes, M.C., and E. Serrão. In press. Spatial patterns of groundfish assemblages on the continental shelf of Portugal.

Gonzalez, R., I. Olaso, and P. Pereda. 1985. Contribución al conocimiento de la alimentacion de la merluza *Merluccius merluccius* en la plataforma continental de Galicia y del Cantábrico. Bol. Inst. Esp. Oceanogr. 2(3):49-60. (In Spanish.)

Guichet, R. 1968. Le merlan-bleu (*Micromesistius poutassou*) dans le Golfe de Gascogne. ICES C.M. 1968/G:9, 5 pp. (In French.)

Guichet, R. 1995. The diet of European hake (*Merluccius merluccius*) in the northern part of the Bay of Biscay. ICES J. Mar. Sci. 52:21-31.

Guichet, R., and M. Mériel-Bussy. 1970. Association du merlu *Merluccius merluccius* (L.) et du mérlan-bleu *Micromesistius poutassou* (Risso) dans le Golfe de Gascogne. Rev. Trav. Inst. Pêches Marit. 34:69-72. (In French.)

Hickling, C.F. 1927. The natural history of the hake, parts I and II. Fish. Inv. Ser. II Mar. Fish. G.B. 10(2), 100 pp.

Lockwood, S.J., and P.O. Johnson. 1976. Mackerel research in the Southwest. Lab Leaflet MAFF Direct. Fish. Res. 32, 26 pp.

Lockwood, S.J., and P.O. Johnson. 1977. Horse mackerel. Lab Leaflet MAFF Direct. Fish. Res. 38, 18 pp.

Machado, P. 1996. Aspectos da biologia e da ecologia do tubarão lamniforme *Scyliorhinus canicula* Linnaeus, 1758. Relatório de Estágio profissionalizante da Licenciatura em Biologia Aplicada aos Recursos Animais. Faculdade de Ciências de Lisboa. 60 pp. (In Portuguese.)

Martins, M.M., and F. Cardador. 1996. Abundance and distribution pattern of Spanish mackerel (*Scomber japonicus*) and mackerel (*Scomber scombrus*) in the Portuguese continental waters (ICES Div. Ixa). ICES C.M. 1996/H:24, 21 pp.

Mazhirina, G.P. 1994. Reproductive characteristics of blue whiting, *Micromesistius poutassou*, in the northeastern Atlantic. J. Ichthyol. 34(1):132-139.

Monstad, T. 1990. Distribution and growth of the blue whiting in the north-east Atlantic. In: T. Monstad (ed.), Biology and fisheries of the Norwegian spawning herring and blue whiting in the northeast Atlantic. Proceedings of the Fourth Soviet-Norwegian Symposium, Bergen, 12-16 June 1989, pp. 227-267.

Moura, O. 1995. Análise dos desembarques de algumas espécies de profundidade na Costa Continental Portuguesa. Relat. Cient. Técn. IPIMAR 12, 18 pp. (In Portuguese.)

Murta, A.G. 1992. Ecologia alimentar da sarda, *Scomber scombrus* (Linnaeus, 1758) e do carapau *Trachurus trachurus* (Linnaeus, 1758) na costa Portuguesa. Relatório final do Estágio Profissionalizante para conclusão da Licenciatura em Recursos Faunísticos e Ambiente. Faculdade de Ciências de Lisboa, Instituto Nacional de Investigação das Pescas. 129 pp. (In Portuguese.)

Murta, A.G., and M.F. Borges. 1994. Factors affecting the abundance and distribution of horse mackerel *Trachurus trachurus* (Linnaeus, 1758) in Portuguese waters. ICES C.M. 1994/H:20, 16 pp.

Olaso, I., F. Sanchez, and C.G. Piñeiro. 1994. Influence of anchovy and blue whiting in the feeding of northern Spain hake. ICES C.M. 1994/P:9, 14 pp.

Quéro, J.C. 1984. Les Lophiiformes. In: J. Graucher (ed.), Les poissons de mer des pêches françaises. Paris, pp. 146-148. (In French.)

Pierce, G.J., P.R. Boyle, L.C. Hastie, and M.B. Santos. 1994. Diets of squid *Loligo forbesi* and *Loligo vulgaris* in the northeast Atlantic. Fish. Res. 21:149-163.

Polonskiy, A.S. 1966. Blue whiting from Porcupine Bank. Rybn. Khoz. 4:5-9. (In Russian.)

Probatov, A.N., and B.I. Mikheev. 1965. Perspectives for industrial fisheries in the Atlantic. Rybn. Khoz. 41:3-5. (Marine Laboratory, Aberdeen, Translation no. 1306, February 1968.)

Rasero, M., A.F. Gonzalez, B.G. Castro, and A. Guerra. 1996. Predatory relationships of two sympatric squid, *Todaropsis eblanae* and *Ilex coindetti* (Cephalopoda: Ommastrephidae) in Galician waters. J. Mar. Biol. Assoc. U.K. 76:73-87.

Rellini, L.O., M. Capello, and R. Poggi. 1994. The stomach contents of some bottlenose dolphin (*Tursiops truncatus*) from the Ligurian Sea. In: P.G.H. Evans (ed.), European research on cetaceans, 8. Proceedings of the 8th Annual Conference, ECS, Montpellier, France, 2-5 March 1994. European Cetacean Society, Cambridge, pp. 192-195.

Rocha, F., B.G. Castro, M.S. Gil, and A. Guerra. 1994. The diets of *Loligo vulgaris* and *L. forbesi* (Cephalopoda: Loliginidae) in northwestern Spanish Atlantic waters. Sarsia 79:119-126.

Santos, M.B., G.J. Pierce, A. López, A. Barreiro, and A. Guerra. 1996. Diets of small cetaceans stranded in northwest Spain 1994-95. ICES C.M. 1996/N:11, 15 pp.

Sequeira, M.L., and A.M. Teixeira. 1988. Marine mammal surveys in Portugal. In: P.G.H. Evans (ed.), European research on cetaceans. Proceedings of the 6th Annual Conference, ECS, Portugal, 5-7 February 1988, pp. 9-12.

Sequeira, M.L., A.M. Inácio, and F. Reiner. 1992. Arrojamentos de mamíferos marinhos na costa Portuguesa entre 1978 e 1988. Serviço Nacional de Parques, Reservas e Conservação da Natureza, Lisboa. 48 pp. (In Portuguese.)

Silva, A. 1992. Contribuição para o conhecimento da pesca de Peixe-galo (*Zeus faber*, Linnaeus 1758) na costa continental Portuguesa. Relat. Téc. Cient. INIP 56, 19 pp. (In Portuguese.)

Silva, A. 1995. Feeding habits of john dory, *Zeus faber* (Linnaeus, 1758) off the Portuguese continental coast (ICES Div. Ixa). ICES C.M. 1995/G:17, 18 pp.

Silva, A., and M. Azevedo. 1995. Abundance and distribution of megrims, *Lepidorhombus boscii* and *L. whiffiagonis* in ICES Division Ixa (Portuguese waters). Bol. Inst. Port. Invest. Marít. 1:65-70.

Silva, A., G. Pestana, C. Dias, and S. Godinho. 1996. Preliminary results on the distribution and spawning of blue whiting, *Micromesistius poutassou*, off the Portuguese coast. ICES C.M. 1996/H:16, 22 pp.

Silva, M.A. 1996. Contribuição para o conhecimento do regime alimentar e biologia da reprodução do golfinho-comum, *Delphinus delphis* Linnaeus, 1758, na costa Portuguesa. Relatório de Estágio profissionalizante para a obtenção do grau de Licenciatura em Biologia Aplicada aos Recursos Animais, Faculdade de Ciências da Universidade de Lisboa, Lisboa. 64 pp. (In Portuguese.)

Thompson, K.R., and M.D. Riddy. 1995. Utilization of offal and discards from "finfish" trawlers around the Falkland Islands by the black-browed albatross *Diomedea melanophris*. Ibis 137(2):198-206.

Wiborg, K.F. 1987. Investigations on the squid, *Todarodes sagittatus* (Lamarck), in the Norwegian coastal and bank waters in September-December 1984, April and August-September 1985, at Shetland in July 1984 and at the Faeroes in August 1985. Fisken Havet 2:1-8. (In Norwegian.)

Würtz, M., and D. Marrale. 1993. Food of striped dolphin, *Stenella coeruleoalba*, in the Liguria Sea. J. Mar. Biol. Assoc. U.K. 73:571-578.

Zilanov, V.K. 1968. The biology and exploitation of the blue whiting. Murmansk Book Publishers. 76 pp. (Marine Laboratory, Aberdeen, Translation no. 2118, August 1980).

Zilanov, V.K. 1980. Short results of the Soviet study of blue whiting (*Micromesistius poutassou* Risso) ecology in the North Atlantic. ICES C.M. 1980/H:32, 24 pp.

Seabird Consumption in Sand Lance MSVPA Models for the North Sea, and the Impact of Industrial Fishing on Seabird Population Dynamics

R.W. Furness
Glasgow University, Applied Ornithology Unit, Glasgow, United Kingdom

M.L. Tasker
Joint Nature Conservation Committee, Aberdeen, United Kingdom

Abstract

The industrial fishery for sand lance, *Ammodytes marinus*, is the largest single-species fishery in the North Sea, with about 1 million tons harvested each year. Assessment of interactions among seabirds, sand lance stocks, and the industrial fishery in the North Sea has been a major recent concern of an International Council for the Exploration of the Sea (ICES) working group. Detailed seabird breeding population census data from the 1980s for the coasts of the North Sea and the European Seabirds at Sea database permit the assessment of energy requirements of seabirds by regions. From dietary data the quantities of sand lance consumed by seabirds can be estimated by seasons and regions. Seabirds consume an estimated 200,000 tons of sand lance, predominantly in summer, with consumption greatest in the northwestern North Sea. These data permit refinement of sand lance multispecies virtual population analyses (MSVPA), and indicate that exploitation of sand lance by seabirds and the fishery are spatially segregated due to constraints imposed by the distribution of seabird breeding sites and by sandy substrates for fishing.

Consumption of sand lance by seabirds can be high in the vicinity of major seabird colonies, such as around Shetland and Orkney, but is low in central regions of the North Sea and averages overall only about 4% of the North Sea sand lance stock. Thus the potential for the fishery to affect seabirds is much greater than the converse. The extent to which seabirds may suffer reductions in food supply as a consequence of the sand lance fishery depends especially on whether recruitment varies in relation to prevailing levels of spawning stock biomass, but also depends on the age classes of fish selected by birds. Recent major changes in sand lance abundance at Shetland permit us to analyze the shape of functional responses of breeding seabirds to variations in food supply over the period 1974-1995. This case study indicates the critical importance of a minimum abundance of lipid-rich fish for breeding seabirds, but also the complexity of seabird-fish interactions, with different seabird species at the same colony responding in different ways to changes in food supply.

Introduction

It is important to know the consumption of prey by seabirds if their impact on fish stocks is to be represented in models of natural mortality used by fisheries managers. Likewise, if management schemes are to account for the needs of seabirds, these must be estimated. To provide information on the consumption of prey by seabirds in the North Sea (Figure 1), we constructed a simple model, described in greater detail and with full input data in Tasker and Furness (1996). This model required the following information: seabird numbers in sections of the North Sea for each month of the year, energy requirements of these birds; diet composition by mass, energy content of foods, and food utilization efficiency (assimilation efficiency). In this paper estimates of consumption of prey by North Sea seabirds are provided using the best data currently available. We then examine the spatial pattern of consumption within the North Sea and consider the possible impact of industrial fishing on availability of sand lance *(Ammodytes marinus*) to seabirds. We take the recent sand lance stock decline at Shetland as a detailed case study.

Method of Modeling

Seabird numbers

Seabird numbers in the North Sea were obtained by combining data on densities of seabirds at sea throughout the year and data on numbers of breeding and nonbreeding individuals attending colonies around the North Sea in different months.

Seabirds at sea

Methods for counting birds at sea from ships in the North Sea are described by Tasker et al. (1984) and Webb and Durinck (1992). These methods, or slight variants, have been used by seabird counters from many countries around the North Sea. The data have been assembled

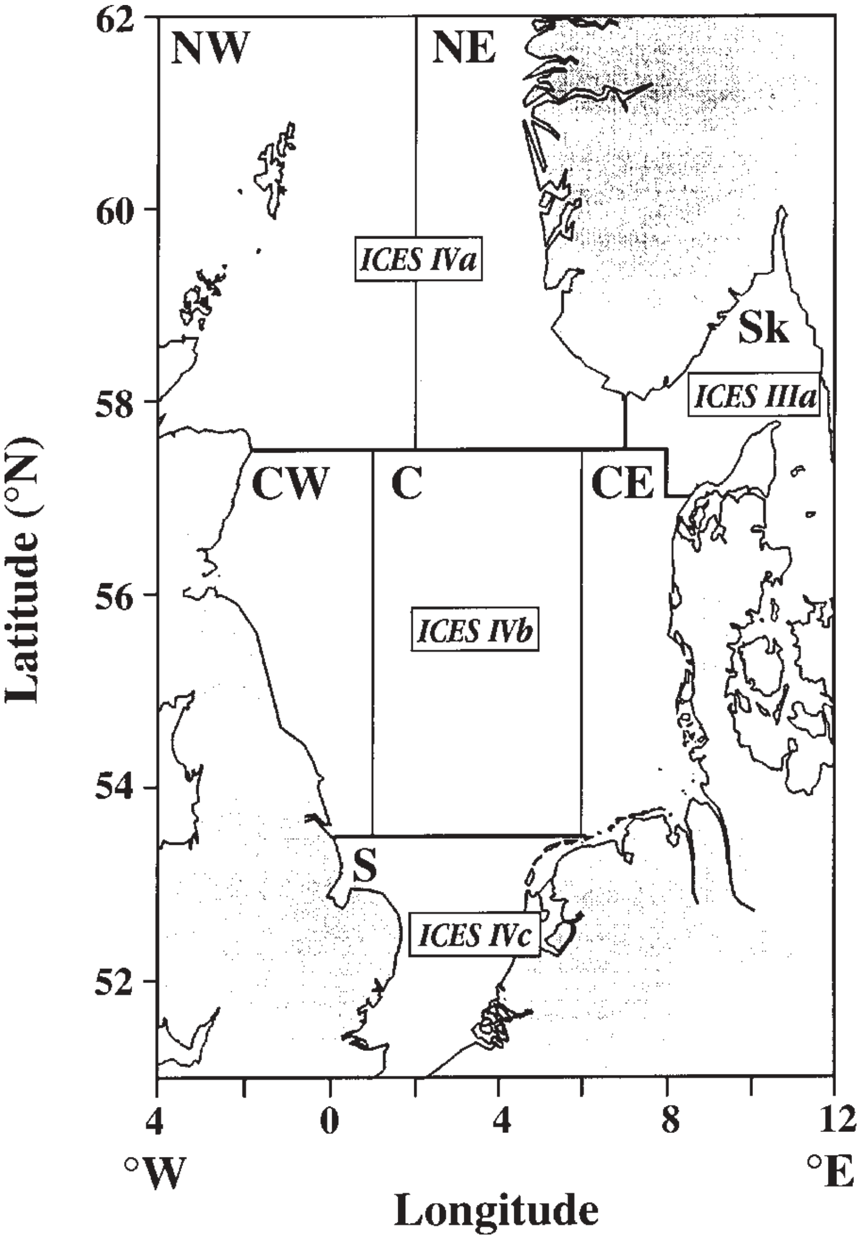


Figure 1. ICES areas of the North Sea as used in this study for estimation of seabird energy requirements and fish consumption.

into one database, the European Seabirds at Sea (ESAS) database, managed by the Joint Nature Conservation Committee in Aberdeen. The majority of the data within the North Sea were collected between 1980 and 1987 (Tasker et al. 1987) but we include more recent data. Temporal trends in seabird distribution within the period have been ignored (averaged).

Seabirds at colonies

Methods for counting birds at colonies vary with species (Lloyd et al. 1991). Accurate recent counts are available for most species in most areas of the North Sea (Tasker and Furness 1996). There have been few recent major changes in numbers in any area, but overall numbers of breeding seabirds are probably at or close to historical highs in most areas. To calculate total numbers of birds feeding in the region, the estimates of birds temporarily at colonies have to be added to those at sea, so the proportions of the birds that breed at a colony that are likely to be present on land during each month were estimated. In addition to breeding birds, colonies are also attended by nonbreeding and prebreeding birds. The proportions of numbers counted at colonies that need to be added to account for these nonbreeding birds were estimated from life table and colony attendance data (Tasker and Furness 1996). The timing of breeding activities, age at first breeding, and adult survival rates needed for input of the above parameters have been reviewed by Dunnet et al. (1990). These colony figures were added to estimates of numbers at sea before energetic modeling.

Diets of seabirds in the North Sea

Methods used to study seabird diets

Methods of sampling seabird diets and statistical considerations regarding necessary sample sizes and presentation of data have been reviewed by Duffy and Jackson (1986) and in the North Sea context by Dunnet et al. (1990). Food samples may be obtained by killing birds and dissecting the alimentary tract; by removing stomach contents from living birds using stomach pumps, emetics, or the natural tendency of some species to regurgitate when disturbed or handled; by examining waste products (feces or regurgitated pellets) containing identifiable hard parts of prey; or by observing or filming food being consumed, carried, fed to chicks, or dropped at colonies. Recent work on N-isotope ratios in seabird tissues has shown that analysis of isotopes can provide information on the trophic status, but not species composition, of diet (Hobson and Montevecchi 1991, Thompson et al. 1995).

All of these methods have their advantages and disadvantages. All can be used at breeding colonies during summer, but the study of diets in other seasons is restricted to analyzing pellets at resting places, to the killing of seabirds, or to directly observing the consumption of fish which is practicable behind fishery vessels and has been used in recent years (Hudson and Furness 1988, Camphuysen et al. 1993). The problem of determining diets and foraging ecology is aggravated by the fact that some seabirds feed extensively or even predominantly at night. Seabirds found dead on coasts in winter can be examined to obtain some information on the foods recently consumed, but probably provide a biased picture. In general, knowledge of the diets of North Sea seabirds is poor for the nonbreeding period (Blake 1983, 1984; Blake et al. 1985), but moderate to very good for the breeding season, except for nonbreeders.

Interspecific variation in diets

Many studies of the diets of seabirds have been made in recent years in the North Sea and adjacent areas. These show a strong selection for sand lance as food during the breeding season. North Sea seabirds eat many other kinds of animals. In addition to natural diets, anthropogenic sources such as discards, offal, and garbage are used by seabirds, particularly gulls. Fish is taken by most of the North Sea seabirds, and about 50% of the species take predominantly fish. In comparison, the percentage of fish in the diet often differs among closely related species; e.g., lesser black-backed gull (*Larus fuscus*) and herring gull (*L. argentatus*); common tern (*Sterna hirundo*) and Arctic tern (*S. paradisaea*); or common murre (*Uria aalge*) and black guillemot (*Cepphus grylle*).

The most important fish for the nutrition of seabirds in the North Sea are sand lance and clupeids, especially during the breeding season. Owing to a high fat content, sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) are of high caloric value per unit mass, and sand lance also have relatively high energy content (Harris and Hislop 1978, Massias and Becker 1990, Hislop et al. 1991). A few species of Gadidae are also important prey, but together with other fish groups, they are relatively rare in the diets of the smaller seabird species. They are supplementary prey to which the birds switch if sand lance and clupeids are not available in sufficient numbers to fulfill nutritional requirements.

The key prey of seabirds are also the object of industrial fisheries. As a consequence, North Sea seabirds are in potential competition with fisheries and at risk if the stocks of prey fish are depleted (e.g., Furness 1987a, Bailey et al. 1991). The quality of food can have major effects on the growth and survival of seabird chicks, although it appears to be less important for adults. In gulls and terns, chicks fed on fish grow better than those fed on marine invertebrates (Spaans 1971, Massias and Becker 1990), probably because fish have higher caloric and protein densities. Atlantic puffin (*Fratercula arctica*) chicks grow best on a diet of oily fish, their preferred prey, such as sprat or large sand lance (Harris and Hislop 1978, Harris 1984). Similarly, great skuas (*Catharacta skua*) feed their chicks on sand lance in preference to other food items and the proportion of the diet comprising sand lance is much higher in chicks than in breeding adults or nonbreeders at the same time in the season (Furness 1987b).

Variation in nutritional content is also found between individual sand lance, herring, and sprat at a given time and throughout the year (Hislop et al. 1991). The caloric values and body mass of sand lance larger than 10 cm show marked seasonal trends. As a consequence, the total energy content of a sand lance of a given length in summer is approximately double the spring value. Thus selection by North Sea seabirds of nutritionally superior prey within fish species may occur.

Length and shape of fish chosen by seabirds

The length of fish taken by seabirds corresponds to body and gape size of the bird; large species take larger fish, and small species take small fish to feed their young and themselves (Pearson 1968). In discard experiments this phenomenon can also be observed (Hudson and Furness 1988, Hüppop and Garthe 1993). Another factor to be considered is the shape of the fish. Discard experiments showed that, on average, only 30% (5-67%) of all flatfish (mainly dab, *Limanda limanda*; flounder, *Platichthys flesus*; and plaice, *Pleuronectes platessa*) but 80% (58-92%) of all round fish (mainly cod, *Gadus morhua*; whiting, *Merlangius merlangus*; and bib, *Trisopterus luscus*) were eaten by herring gulls, great black-backed gulls (*Larus marinus*), and lesser black-backed gulls (Garthe and Hüppop 1993). Most sand lance eaten by seabirds are 4-16 cm, but sizes can vary among years.

Geographic variation in diets

The diet composition of seabirds varies greatly between localities. Thus, obtaining an accurate picture of the diets of seabirds throughout the North Sea requires studies at a wide variety of localities. This is largely fulfilled for herring gull, common tern, common murre, and Atlantic puffin whose diets have been studied at several breeding sites on the North Sea coast (Tasker and Furness 1996). The diets of these seabird species vary geographically depending on the site-specific food availability. In general, sand lance are more important in diets of seabirds from the northern North Sea, while in the southern North Sea diet tends to be more diverse, including especially sprats and young herring.

Seasonal variation in diets

The diet composition of seabirds varies seasonally due to fluctuations in prey species availability (due to prey movements, weather, tides, predation) and to changing food demands during the different phases of the annual breeding cycle (e.g., Atlantic puffin: Barrett et al. 1987; black-legged kittiwake, *Rissa tridactyla*: Pearson 1968; sandwich tern, *Sterna sandvicensis*: Veen 1977). In terns, the food composition and length of fish fed varies between courtship feeding and the chick rearing period. Males feed females with fish longer than those they eat themselves (Taylor 1979) or than they later feed to chicks (Ewins 1985, Monaghan et al. 1989). Younger tern chicks get smaller fish or different prey species than older chicks (Lemmetyinen 1973, Ewins 1985, Uttley 1991, Frick 1993).

Interannual variation in diets

Interyear variability in diets is a common phenomenon among seabirds. This may be caused by annual fluctuations in prey stocks, by the food availability changing due to environmental factors such as weather and ocean temperatures, by differences in prey migration behavior, or by interspecific food competition. Owing to the different energetic values of the prey species, this variation can significantly affect breeding biology, chick growth and condition, as well as breeding success.

In common murres and Atlantic puffins, the percentage of clupeids or other fish in the diet correlates negatively with the percentage of sand lance. For many seabird species of Shetland, Bailey et al. (1991) show that the switching from sand lance to other prey species is in approximate proportion to the abundance of sand lance, and that there is no evidence of a nonlinear functional response. If sand lance dominate the food, the breeding success of seabirds is comparatively good (Shetland seabirds: Bailey et al. 1991; Atlantic puffin: Barrett et al. 1987; Arctic tern: Uttley 1991; common tern: Franck 1992).

Between 1972 and 1988, considerable changes in the species of fish fed to young puffins were found on the Isle of May (Harris and Wanless 1991). Sand lance were the most common prey except during 1974-1978, when sprats formed 50-86% of the diet (by mass). During the 1980s, the proportion of sprats declined and the importance of herring increased gradually.

Diets used in model

For estimation of fish consumed by seabirds in the North Sea, we reviewed the published information on diets of seabirds in the North Sea and adjacent areas, including both seabird community studies and those of individual species. From these data we present selected dietary information in a summary form (Table 1). This table includes for each major energy-consuming seabird species a best estimate of the fish species and sizes eaten. For some species it was necessary to separate sections IVa (west) and all other areas because diets clearly differed between areas. In general, sand lance were more strongly represented in the diet in IVa (west) than in other areas. The quality of the diet data varies considerably among species, being good for common murre but poor for northern fulmar (*Fulmarus glacialis*). Diets are only very poorly known outside the breeding season, and probably vary in detail from place to place and from year to year, especially in relation to changes in fish stocks (Hislop and Harris 1985, Barrett and Furness 1990, Bailey et al. 1991, Hamer et al. 1991, Wanless and Harris 1992). For this model we

Table 1. Diets of seabirds in the North Sea used in the model, for species with large energy requirements.

Species	Area	Months	Diet
Northern fulmar	All areas	May-Aug	30% sand lance (4-10 cm) 30% offal, 30% discards 10% zooplankton
Northern fulmar	All areas	Sep-Apr	0% sand lance 50% offal 25% discards 25% zooplankton
Herring gull	All areas	All year	30% discards 30% invertebrates 30% terrestrial foods 10% offal
Common murre	IVa (West)	Mar-Aug	100% sand lance (10-14 cm)
Common murre	IVa (West)	Sep-Feb	33% sand lance (10-14 cm) 33% sprat (10 cm) 33% gadids (12 cm)
Common murre	IVa (East), IVb, IVc	Mar-Aug	80% sand lance (10-14 cm) 20% sprat (10 cm)
Common murre	IVa (East), IVb, IVc	Sep-Feb	40% sand lance (1014 cm) 30% sprat (10 cm); 30% gadids (12 cm)
Shag	All areas	All year	100% sand lance (5-15 cm)
Great black-backed gull	All areas	Apr-Aug	60% discards 20% sand lance (12 cm) 20% other prey
Great black-backed gull	All areas	Sep-Mar	70% discards 30% other prey
Black-legged kittiwake	IVa (West)	May-Aug	100% sand lance (6-14 cm)
Black-legged kittiwake	IVa (West)	Sep-Apr	25% sprat (8 cm) 25% zooplankton 25% offal 25% discards
Black-legged kittiwake	IVb, IVc, IVa (East)	May-Aug	60% sand lance (6-14 cm) 20% sprat (8 cm) 20% zooplankton
Black-legged kittiwake	IVb, IVc, IVa (East)	Sep-Apr	25% sprat (8 cm) 25% zooplankton 25% offal 25% discards

For areas see Figure 1.

Table 1. (Con't.)

Species	Area	Months	Diet
Northern gannet	All areas	All year	30% sand lance 30% herring 30% mackerel 10% discards
Atlantic puffin	IVa (West)	May-Aug	90% sand lance (0-group) 10% rockling
Atlantic puffin	IVa (West)	Sep-Apr	30% sand lance 30% gadids 30% sprat 10% zooplankton
Atlantic puffin	IVa (East), IVb, IVc	All year	50% sand lance 30% sprat 20% gadids (all 0-group)
Razorbill	IVa (West)	Mar-Aug	100% sand lance (6-10 cm)
Razorbill	IVa (West)	Sep-Feb	60% sand lance 40% sprat
Razorbill	IVa (East), IVb, IVc	Mar-Aug	70% sand lance 30% sprat
Razorbill	IVa (East), IVb, IVc	Sep-Feb	60% sand lance 40% sprat

have used the dietary summary data as representing the best estimates of diets of North Sea seabirds at different times of year. We note here the uncertain nature of these data, especially with regard to seabird diet outside the breeding season. This is identified as one of the weakest aspects of the analysis. Another concern is the way in which many seabirds can switch diet according to food availability (Barrett and Furness 1990, Hamer et al. 1991). It is clear that in recent years many of the larger seabirds have obtained large amounts of food from fishing vessels, scavenging on offal and discards (Hudson and Furness 1988, 1989; Furness et al. 1992; Camphuysen et al. 1993). The possible effects on scavenging seabirds of increases in net mesh size, decreases in fishing effort and increases in minimum landing size regulations in North Sea fisheries have been reviewed by Furness (1992).

Energy content of foods

We have assumed the following caloric values of foods: sand lance, sprats, and young herring, 6.5 kJ/g; crustaceans, 4 kJ/g; squid, 3.5 kJ/g;

gadid and flatfish discards 4 kJ/g; offal, 10 kJ/g (Harris and Hislop 1978, Hudson 1986, Croxall et al. 1991, Camphuysen et al. 1993). We are aware of the enormous variation in caloric value of 0-group sand lance (a major part of the seabird diet in summer) but it seems that, unless sand lance are particularly scarce, seabirds select the larger 0-group fish which have high lipid content.

Assimilation efficiency varies among food types, and for fish it varies according to the lipid content of the fish, being higher when lipid content is higher. However, in general, assimilation efficiency is around 75-85% for fish diets and around 70% for other marine prey (Nagy et al. 1984, Jackson 1986, Gabrielsen et al. 1987, Brown 1989, Crawford et al. 1991). In view of the relatively small variation in assimilation efficiency, in relation to other errors in this calculation, use of a constant value of 75% seems satisfactory for our model.

Energetics model

Although there are more doubly labeled water studies of seabirds than there are for other avian groups, most species have been studied at only one location in one or a short series of years. Thus we lack information on the extent of variation in energy expenditures as a consequence of variations in food availability and other environmental factors. It would be unwise to assume that measured field metabolic rates (FMRs) for one site in one season represent figures that can be applied to that seabird species at all sites (Montevecchi et al. 1992). Indeed, Koteja (1991) was able to explain only 25% of variance in FMRs of birds (or of seabirds) as a consequence of species-specific physiology (reflected by deviations of basal metabolic rate (BMR) from the allometric prediction). Much of the remaining variance may be due to environmental conditions affecting the birds sampled for FMR determinations rather than to species-specific characteristics. For example, Furness and Bryant (1996) found that the at-sea metabolism of northern fulmars decreased with increasing wind speed (this accounting for nearly 50% of the variance in individual FMRs), while Gabrielsen et al. (1991) found that higher wind speed caused higher at-sea metabolism of little auks (*Alle alle*). Thus, it makes as much sense to use the mean of all labeled water studies with seabirds as a BMR multiplier, as to use each individual species FMR estimates in a model based on individual species determinations summed for the community. This is particularly so when the seabird community in question (that of the North Sea) shares few species in common with the set of seabird species for which doubly labeled water estimates of FMR have been made.

A total of 34 species-measurements of seabird energetics using labeled water or using allometric equations and activity budgets gave daily energy expenditures mostly in the region of 3 to 4 ×BMR during the breeding season, with medians of 2.9 BMR during incubation and 3.5

BMR during chick-rearing (Furness 1990). Examination of labeled water studies of seabird FMR and measured BMR of the same populations shows that the FMR/BMR ratio varied among studies from 1.8 to 6.6, with a mean of 3.6 for a sample of 27 studies (Tasker and Furness 1996). Three of these studies were of albatrosses, which have especially efficient flight and thus lower than average at-sea energy expenditures (Birt-Friesen et al. 1989), so that the appropriate multiples of BMR for North Sea seabirds are probably higher than these. For seabirds other than albatrosses the mean FMR/BMR ratio during the breeding period was 3.8, while for the small sample of six studies on seabirds that are numerous in the North Sea, the mean FMR/BMR ratio was 4.2. The FMR outside the breeding season must be greater than 1×BMR, but less than that during breeding (as shown by Bennett and Harvey 1987). Thus we have decided to use an FMR of 3.9 BMR during the breeding season and 2.5 BMR during other periods in the model. The BMR for each species was estimated from the allometric equation derived by Bryant and Furness (1995) for North Sea seabirds. In that study, the BMRs of individual species were found to deviate from the common regression by relatively small amounts, and some species considered to have "above average" BMRs fell below the regression and vice versa. Thus the view that the BMR of individual species should be taken into account in modeling was not strongly supported; for ease of computation the predicted BMRs have been used; this will have very little effect on the overall total energy demands of the community since some species fall above and others below the regression.

Results

Monthly figures for food consumption in terms of energy requirement in each area of the North Sea by 18 seabird species were computed from the above data. Two species, northern fulmar and common murre, are responsible for more than half of the energy requirements of the seabird species. Only one other species, herring gull, requires more than 10% of the total seabird energy requirement. The largest energy requirement is in ICES Division IVa (west).

These energy requirements were converted to food consumption needs. The results of this are presented in Table 2 for the eight greatest consumers of energy in the North Sea (responsible for 94% of the energy demand), and the shag (*Phalacrocorax aristotelis*). This latter species, although only requiring 1.2% of the total seabird energy demand, is included as it consumes mostly sand lance.

Consumption by seabirds is further summarized by food species and by quarter and area in Table 3. This shows a very large proportionate demand of Division IVa (west) and the large demand for sand lance (33% of total food of seabirds), and waste products from fisheries (30%, comprising 12% from offal and 18% discards).

Table 2. Annual energy requirements (kJ × 10^9) of 18 species of seabirds in the North Sea.

Species	Total	%
Northern fulmar	1,094.90	28.1
Northern gannet	273.22	7.0
Great cormorant	6.15	0.2
Shag	46.94	1.2
Great skua	21.08	0.5
Black-headed gull	39.37	1.0
Common gull	44.18	1.1
Lesser black-backed gull	69.52	1.8
Herring gull	451.40	11.6
Great black-backed gull	301.29	7.7
Black-legged kittiwake	307.01	7.9
Arctic tern	2.75	0.1
Common tern	2.70	0.1
Sandwich tern	2.38	0.1
Common murre	1,024.86	26.3
Razorbill	99.54	2.6
Black guillemot	7.86	0.2
Atlantic puffin	108.02	2.8
	3,903.17	

Table 3. Estimated quantities of food consumed by seabirds (tons) in each quarter of the year in each ICES statistical rectangle of the North Sea (as shown in Figure 1).

Area	Prey	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec	Total
IVa west	Sand lance	10,180	63,704	33,574	4,116	111,574
	Sprat/herring	4,202	689	2,907	3,038	10,836
	Live gadid	1,995	403	2,465	1,965	6,829
	Mackerel	867	1,448	1,652	554	4,522
	Adult herring	867	1,448	1,652	554	4,522
	Offal	10,949	13,992	8,646	10,034	43,621
	Discards	10,126	15,661	8,854	10,475	45,115
	Total	39,186	97,345	59,750	30,736	227,017

Table 3. (Cont'd.)

Area	Prey	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec	Total
IVa east	Sand lance	2,726	5,114	5,792	2,635	16,267
	Sprat/herring	1,590	867	895	1,800	5,152
	Live gadid	1,314	79	355	1,702	3,451
	Mackerel	367	381	214	208	1,170
	Adult herring	367	381	214	208	1,170
	Offal	2,010	1,616	9,604	1,988	15,218
	Discards	1,691	2,549	8,403	1,408	14,051
	Total	10,065	10,987	25,477	9,949	56,479
IVb west	Sand lance	3,894	17,915	19,567	4,781	46,157
	Sprat/herring	1,915	4,910	5,398	3,254	16,017
	Live gadid	1,026	539	1,733	2,335	5,633
	Mackerel	499	1,793	1,404	352	4,047
	Adult herring	499	1,793	1,404	352	4,047
	Offal	2,178	944	2,790	1,494	7,406
	Discards	5,841	2,081	5,547	3,385	16,854
	Total	15,852	29,975	37,843	15,953	99,623
IVb center	Sand lance	2,633	2,671	5,163	4,388	14,854
	Sprat/herring	1,663	687	1,096	3,118	6,564
	Live gadid	881	55	359	2,273	3,568
	Mackerel	488	161	561	900	2,110
	Adult herring	488	161	561	900	2,110
	Offal	2,284	873	2,920	2,995	9,070
	Discards	3,480	964	2,846	8,681	15,970
	Total	11,917	5,572	13,506	23,255	54,250
IVb east	Sand lance	1,376	1,230	1,424	1,135	5,165
	Sprat/herring	994	211	186	895	2,286
	Live gadid	501	0	51	675	1,228
	Mackerel	12	40	87	80	218
	Adult herring	12	40	87	80	218
	Offal	674	855	1,578	1,088	4,195
	Discards	1,722	1,982	2,353	1,456	7,513
	Total	5,291	4,358	5,766	5,409	20,824
IVc	Sand lance	834	509	868	833	3,044
	Sprat/herring	556	121	352	577	1,606
	Live gadid	254	1	255	359	868
	Mackerel	68	43	159	255	525
	Adult herring	68	43	159	255	525
	Offal	781	1,038	391	681	2,891
	Discards	2,899	2,842	978	2,967	9,686
	Total	5,460	4,597	3,162	5,927	19,146

Discussion

The results of the modeling can be compared with those by other studies of the North Sea, and from further afield. The results of all but one of these other studies have been based on populations of breeding seabirds in an area, with suitable extrapolation to allow for nonbreeding birds. In an area such as the North Sea, where there is substantial immigration, emigration, and passage of seabirds through the area the assumption that only local populations of birds use an area does not hold. This study and that of Tasker et al. (1989) are the only studies to use at-sea information from the North Sea to derive the bird population input.

Bailey (1986) used breeding population data from around the North Sea, and estimated about 1.9×10^{12}kJ of energy was required by seabirds. This is about half that estimated by the current model (3.9×10^{12}), but Bailey's seabird population data were from 1969-1970, and there has been a substantial increase in breeding numbers since then (Lloyd et al. 1991). Tasker et al. (1989) used at-sea data and estimated 2.7×10^{12} kJ was consumed by seabirds; this earlier data set did not adequately allow for numbers of birds in some unsurveyed areas of the North Sea.

All of the above studies, and those of Furness (1978, 1984), indicate that food consumption is not uniform across the North Sea, but is distinctly heterogeneous, with particular "hot-spots" in the western northwestern North Sea and around seabird colonies. These areas of high food consumption are not confined to colonies and their environs, but can occur elsewhere in the North Sea, particularly outside the summer breeding season. The present analysis was not sufficiently spatially disaggregated to fully identify these hot-spots.

Sand lance and waste products from fisheries clearly dominate as foods consumed. There are, though, from the seabird point of view, some important temporal and spatial variations in foods consumed. Temporally, sand lance fulfill just under a half of the total food supply of seabirds in the early part of the breeding seasons (April to June); this ratio declines to about 35% in July to September, and about 20% for the remainder of the year. During the period that sand lance are not taken, presumably through being unavailable while buried in the sediments, sprats, young herring, and gadids become much more important as food (from a total of 4% of total food in April-June to about 20% in October-December). Other studies have also shown substantial emigration of birds from the study area in winter. Common murres, for instance, are found in substantial numbers in the Skagerrak-Kattegat area in winter (Unpubl. data, H. Skov) and the English Channel (Unpubl. data, Webb et al.). These areas are not used by murres to any great extent during the summer. Use of offal and discards is also considerably more important during the winter than in spring or summer. In this case, most of the diet switching is by northern fulmars. However, the evidence for northern fulmar diet composition and seasonal variation is limited (Thompson and Furness 1995).

Estimated consumption by seabirds can be compared to the figure previously used in the MSVPA. Consumption by seabirds is quite small relative to fish stock biomass and annual production, and relative to the mass of prey taken by the main MSVPA predatory fish. Our estimate of total live prey consumed (270,000 tons per year) is similar to that previously estimated in the MSVPA (230,000 tons per year). However, the species composition of seabird prey is very different from that of the MSVPA predatory fish, and hence from the prey spectrum for seabirds assumed in the MSVPA (Table 4). The seabirds feed highly selectively, especially on sand lance and small clupeids, and consume virtually no benthic invertebrates ("an important other food of predatory fish" in Table 4). Thus, the mortality of sand lance due to seabirds is much greater than in the MSVPA model. Moreover, seabird predation on sand lance is highly concentrated in a small portion of the North Sea.

Competition with the industrial fishery

Given the high consumption of sand lance by seabirds, and the concentration of seabird demand in the northwest North Sea (ICES IVa west), the fact that most industrial catches of sand lance come from area IVb (Table 5), suggests one reason why there has not yet been much evidence of sand lance fishing affecting food supply to seabirds. Another is that mackerel stocks in the North Sea remain greatly depleted, and mackerel was previously one of the main predators of sand lance, so that consumption by the industrial fishery may simply have replaced that by mackerel. The most likely areas for adverse effects on seabirds seem to be recent relocation of sand lance fishing effort close to the east coast of Scotland where there are major wintering concentrations of shags and common murres that depend largely on sand lance as winter diet, and the removal of sand lance from fishing banks close to major breeding sites in ICES IVa in particular, as may have happened at Shetland (Tasker and Furness 1996).

Seabird responses to reduced sand lance abundance

Studies of Shetland seabirds have provided detailed information on responses to variation in food supply. Shetland is internationally important for breeding seabirds, with colonies of 13 species forming 25-100% of the population of the North Sea (Tasker et al. 1987). During the 1970s numbers of most seabirds in Shetland increased (Hunt and Furness 1996). Seabird colonies at Shetland appear to be strategically placed to make best use of local sand lance grounds and to avoid competition with birds from neighboring colonies (Furness and Birkhead 1984). Most seabirds in Shetland are largely dependent on the sand lance during the breeding season as for most seabird species there is no other suitably sized, energy-rich prey in Shetland (Bailey et al. 1991, Hislop et al.

Table 4. Diet of the five MSVPA predator species in 1981 according to the MSVPA keyrun (Hunt and Furness 1996) and diet of North Sea seabirds as estimated in this study.

Prey	Tons × 10^3 taken by MSVPA fish predators	% of total mass of prey taken by MSVPA fish	Tons × 10^3 taken by seabirds	% of total mass of prey taken by seabirds
Mackerel	—	—	13	2.2
Cod	29	0.4		
Whiting	117	1.8	22	3.7
Haddock	233	3.5		
Norway pout	812	12.3		
Herring	173	2.6	13	2.2
Sprat	190	2.9	30	5.0
Sandeel	624	9.4	197	32.8
Discards	—	—	109	18.2
Offal	—	—	71	11.8
Other food	4,443	67.1	146	24.3
Total	6,621	100.0	600*	100.1

* This total is derived from estimated energy needs (3.9 x10^{12} kJ per year) assuming an average caloric value of foods of 6.5 kJ/g.

Table 5. Area comparison between sandlance and sprat fishery landings and seabird consumption.

Area	Sand lance landings (× 1,000 t) 1984	1989	Sand lance consumption (× 1,000 t)	Sprat landings (t) 1985	Sprat consumption by seabirds (t)
IVa (West)	40.1	21.9	111.6	7,594	0
IVa (East)	32.4	234.9	16.3	24	5,200
IVb (West)	195.6	136.8	46.2	1,829	16,000
IVb (Central)	245.0	409.6	14.9	0	6,600
IVb (East)	99.1	189.1	17.6	36,640	2,300
IVc	44.7	26.1	3.0	2,922	900

Landings of sand lance for 1984 and 1989 and sprat for 1985 are derived from ICES statistics. Seabird consumption estimates are from Table 3. See Figure 1 for map of ICES areas of the North Sea.

1991). During the 1980s there was a marked decline in sand lance abundance in the supposedly local stock at Shetland shortly after the local industrial fishery reached a peak catch of 52,000 t in 1982 (Bailey et al. 1991). Seabirds are major predators of sand lance at Shetland. Furness (1990) estimated that seabirds consumed 49,000 t per year between 1981 and 1983. As sand lance recruitment failed and stock biomass declined, the species of seabirds showing the greatest reduction in breeding success were Arctic tern (Monaghan et al. 1989a), black-legged kittiwake (Hamer et al. 1993), Parasitic jaeger (*Stercorarius parasiticus*) (Phillips et al. 1996), great skua (Hamer et al. 1991), and Atlantic puffin (Martin 1989). Greater sensitivity of terns was predicted by Furness and Ainley (1984), and a common feature of all of these species is their tendency to feed only at or, in the case of puffins, close to the surface. By contrast, shag and common murre breeding success remained high throughout the period of sand lance scarcity. While breeding numbers of Arctic terns fell dramatically when breeding success crashed to zero, their breeding numbers jumped back up at least at some of the main colonies in 1991 when sandeel recruitment recovered. This implied that many birds had refrained from breeding in the poor years until food supply improved, as life history theory would predict. However, breeding numbers of great skuas did not drop much when breeding failures began, although adult mortality increased and recruitment increased until the nonbreeder clubs were almost empty (Hamer et al. 1991, Klomp and Furness 1992). Possibly great skuas need to retain their territory in order to have future prospects of breeding so are unable to behave as terns do. Great skuas showed considerable diet switching to alternative foods, whereas Arctic terns, puffins, murres, and kittiwakes continued to feed predominantly on sand lance but attempted to increase foraging effort to compensate for food shortage. Murres were able to do this whereas time-limited terns were not. Although common murre breeding success was not affected because adults were able to increase work rates (Monaghan et al. 1992), their breeding numbers did fall, showing a strong linear correlation with sand lance stock biomass estimates (Monaghan 1992), possibly due to winter mortality of murres, (Vader et al. 1990) as they continue to feed on sand lance around Shetland in winter and evidently did show increased mortality (Heubeck et al. 1991). Similarly, Arctic tern breeding productivity showed a significant correlation with sand lance abundance (Monaghan et al. 1989b). While both of those correlations are adequately described by linear functions, it is predicted that functional relationships with food supply will be sigmoidal (Cairns 1987, Montevecchi 1993). Above a certain abundance, further increases in fish density will not increase reproductive output or survival rate, and below a certain threshold density breeding cannot occur. Phillips et al. (1996) examined the breeding success of parasitic jaegers in relation to sand lance abundance and found a pattern much better described by a sigmoidal function than a linear one

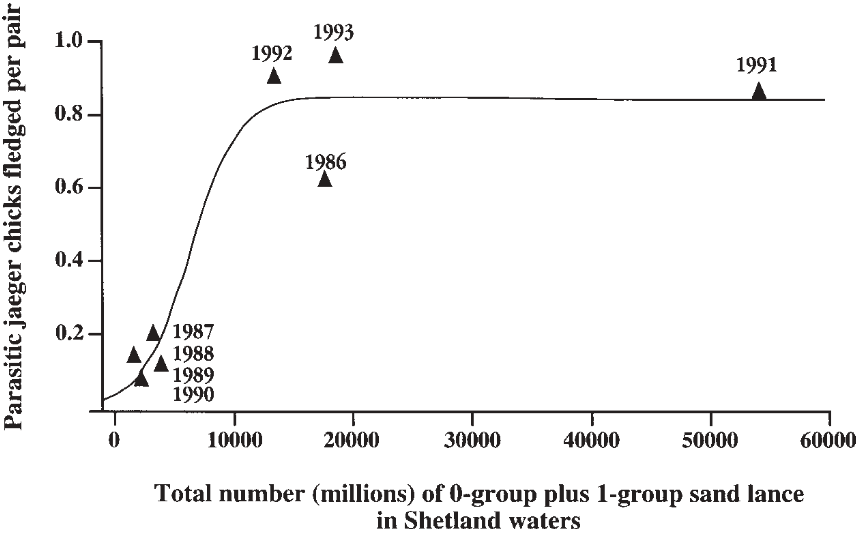


Figure 2. Logistic curve fitted to parasitic jaeger breeding success in relation to sand lance abundance at Shetland between 1986 and 1994 (from Phillips et al. 1996).

(Figure 2). It is not clear whether the industrial fishery affected sand lance abundance at Shetland or whether the fluctuations were natural, but the high local demand for sand lance by breeding seabirds close to major colonies, and the aggregation of wintering shag and murre populations on sand lance banks suggests that exploitation of certain locally important seabird foraging areas by industrial fisheries may impact birds whereas harvesting from central areas of the North Sea where seabird densities are low at all times of year, is less likely to cause problems for seabirds.

References

Bailey, R.S. 1986. Food consumption by seabirds in the North Sea in relation to the natural mortality of exploited fish stocks. ICES, Doc. C.M.1986/G:5.

Bailey, R.S., R.W. Furness, J.A. Gauld, and P.A. Kunzlik. 1991. Recent changes in the population of the sandeel (*Ammodytes marinus* Raitt) at Shetland in relation to estimates of seabird predation. ICES Mar. Sci. Symp. 193:209-216.

Barrett, R.T., and R.W. Furness. 1990. The prey and diving depths of seabirds on Hornoy, north Norway after a decrease in Barents Sea capelin stocks. Ornis Scand. 21:179-186.

Barrett, R.T., T. Anker-Nilssen, F. Rikardsen, K. Valde, N. Røv, and W. Wader. 1987. The food, growth, and fledging success of Norwegian puffin chicks *Fratercula arctica* in 1980-1983. Ornis Scand. 18:73-83.

Bennett, P.M., and P.H. Harvey. 1987. Active and resting metabolism in birds: Allometry, phylogeny and ecology. J. Zool. (Lond.) 213:327-363.

Birt-Friesen, V.L., W.A. Montevecchi, D.K. Cairns, and S.A. Macko. 1989. Activity-specific metabolic rates of free-living northern gannets and other seabirds. Ecology 70:357-367.

Blake, B.F. 1983. A comparative study of the diet of auks killed during an oil incident in the Skagerrak in January 1981. J. Zool. (Lond.) 201:1-12.

Blake, B.F. 1984. Diet and fish stock availability as possible factors in the mass death of auks in the North Sea. J. Exp. Mar. Biol. Ecol. 76:89-103.

Blake, B.F., T.J. Dixon, P.H. Jones, and M.L. Tasker. 1985. Seasonal changes in the feeding ecology of guillemots (*Uria aalge*) off north and east Scotland. Estuarine Coastal Shelf Sci. 20:559-568.

Brown, C.R. 1989. Energy requirements and food consumption of *Eudyptes* penguins at the Prince Edward Islands. Antarct. Sci. 1:15-21.

Bryant, D.M., and R.W. Furness. 1995. Basal metabolic rates of North Atlantic seabirds. Ibis 137:219-226.

Cairns, D.K. 1987. Seabirds as indicators of marine food supplies. Biol. Oceanogr. 5:261-271.

Camphuysen, C.J., K. Ensor, R.W. Furness, S. Garthe, O. Hüppop, G. Leaper, H. Offringa, and M.L. Tasker. 1993. Seabirds feeding on discards in winter in the North Sea. NIOZ Rep. 1993-8. Neth. Inst. Sea Res., Texel.

Crawford, R.J.M., P.G. Ryan, and A.J. Williams. 1991. Seabird consumption and production in the Benguela and western Agulhas ecosystems. S. Afr. J. Mar. Sci. 11:357-375.

Croxall, J.P., C. Ricketts, and A.G. Wood. 1991. Food consumption by predators in a CCAMLR integrated study region. Sci. Comm. Cons. Antarct. Mar. Living Resources Select. Sci. Paps. 1990:489-519.

Duffy, D.C., and S. Jackson. 1986. Diet studies of seabirds: A review of methods. Colonial Waterbirds 9:1-17.

Dunnet, G.M., R.W. Furness, M.L. Tasker, and P.H. Becker. 1990. Seabird ecology in the North Sea. Neth. J. Sea Res. 26:387-425.

Ewins, P.J. 1985. Growth, diet and mortality of arctic tern *Sterna paradisaea* chicks in Shetland. Seabird 8:59-68.

Franck, D. 1992. The influence of feeding conditions on food provisioning of chicks in common terns *Sterna hirundo* nesting in the German Wadden Sea. Ardea 80:45-55.

Frick, S. 1993. Nahrungsökologische Unterschiede von Fluß- und Küstenseeschwalbe (*Sterna hirundo* und *Sterna paradisaea*) im Wattenmeer. Diplomarbeit Universität zu Köln.

Furness, R.W. 1978. Energy requirements of seabird communities: A bioenergetics model. J. Anim. Ecol. 47:39-53.

Furness, R.W. 1984. Seabird biomass and food consumption in the North Sea. Mar. Pollut. Bull. 15:244-248.

Furness, R.W. 1987a. The impact of fisheries on seabird populations in the North Sea. In: G. Peet (ed.), The status of North Sea environment: Reasons for concern. Werkgroep Noordzee, Amsterdam, pp. 179-192.

Furness, R.W. 1987b. The skuas. T. and A.D. Poyser, Calton.

Furness, R.W. 1990. A preliminary assessment of the quantities of Shetland sandeels taken by seabirds, seals, predatory fish and the industrial fishery in 1981-83. Ibis 132:205-217.

Furness, R.W. 1992. Implications of changes in net mesh size, fishing effort and minimum landing size regulations in the North Sea for seabird populations. JNCC Rep. 133.

Furness, R.W., and D.G. Ainley. 1984. Threats to seabird populations presented by commercial fisheries. ICBP Tech. Publ. 2:701-708. ICBP, Cambridge.

Furness, R.W., and R.T. Barrett. 1991. Seabirds and fish declines. Natl. Geogr. Res. Explor. 7:82-95.

Furness, R.W., and T.R. Birkhead, T.R. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. Nature 311:655-656.

Furness, R.W., and D.M. Bryant. 1996. Effect of wind on field metabolic rates of breeding northern fulmars. Ecology 77:1181-1188.

Furness, R.W., K. Ensor, and A.V. Hudson, A.V. 1992. The use of fishery waste by gull populations around the British Isles. Ardea 80:105-113.

Gabrielsen, G.W., F. Mehlum, and K.A. Nagy. 1987. Daily energy expenditure and energy utilization of free-ranging black-legged kittiwakes. Condor 89:126-132.

Gabrielsen, G.W., J.R.E. Taylor, M. Konarzewski, and F. Mehlum. 1991. Field and laboratory metabolism and thermoregulation in dovkies (*Alle alle*). Auk 108:71-78.

Garthe, S. 1993. Quantifizierung von Abfall und Beifang der Fischerei in der südöstlichen Nordsse und deren Nutzung durch Seevögel. Hamburger Avifaun. Beitr. 25:125-237.

Garthe, S., and O. Hüppop. 1993. Gulls and fulmars following ships and feeding on discards at night. Ornis Svecica 3:159-161.

Garthe, S., C.J. Camphuysen, and R.W. Furness. 1996. Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. Mar. Ecol. Prog. Ser. 136:1-11.

Hamer, K.C., R.W. Furness, and R.W.G. Caldow. 1991. The effects of changes in food availability on the breeding ecology of great skuas *Catharacta skua* in Shetland. J. Zool. (Lond.) 223:175-188.

Hamer, K.C., P. Monaghan, J.D. Uttley, P. Walton, and M.D. Burns. 1993. The influence of food supply on the breeding ecology of kittiwakes *Rissa tridactyla* in Shetland. Ibis 135:255-263.

Harris, M.P. 1984. The puffin. Poyser, Calton.

Harris, M.P., and R.S. Bailey. 1992. Mortality rates of puffin *Fratercula arctica* and guillemot *Uria aalge* and fish abundance in the North Sea. Biol. Conserv. 60:39-46.

Harris, M.P., and J.R.G. Hislop. 1978. The food of young puffins (*Fratercula arctica*). J. Zool. (Lond.) 185:213-236.

Harris, M.P., and S. Wanless. 1991. The important of the lesser sandeel *Ammodytes marinus* in the diet of the shag *Phalacrocorax aristotelis.* Ornis Scand. 22:375-382.

Heubeck, M., P.V. Harvey, and J.D. Okill. 1991. Changes in the Shetland guillemot *Uria aalge* population and the pattern of recoveries of ringed birds, 1959-1990. Seabird 13:3-21.

Hislop, J.R.G., and M.P. Harris. 1985. Recent changes in the food of young puffins *Fratercula arctica* on the Isle of May in relation to fish stocks. Ibis 127:234-239.

Hislop, J.R.G., M.P. Harris, and J.G.M. Smith. 1991. Variation in the caloric value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. J. Zool. (Lond.) 224:501-517.

Hobson, K.A., and W.A. Montevecchi. 1991. Stable isotopic determinations of trophic relationships of great auks. Oecologia 87:528-531.

Hudson, A.V. 1986. The biology of seabirds utilising fishery waste in Shetland. Ph.D. thesis, University of Glasgow.

Hudson, A.V., and R.W. Furness. 1988. Utilization of discarded fish by scavenging seabirds behind whitefish trawlers in Shetland. J. Zool. (Lond.) 215:151-166.

Hudson, A.V., and R.W. Furness. 1989. The behaviour of seabirds foraging at fishing boats around Shetland. Ibis 131:225- 237.

Hunt, G.L., and R.W. Furness. 1996. Seabird-fish interactions, with particular reference to seabirds in the North Sea. ICES Cooperative Research Report No. 216. International Council for Exploration of the Sea, Copenhagen.

Hüppop, O., and Garthe, S. 1993. Seabirds and fisheries in the southeastern North Sea. Sula 7:9-14.

Jackson, S. 1986. Assimilation efficiencies of white-chinned petrels (*Procellaria aequinoctialis*) fed different prey. Comp. Biochem. Physiol. 85A:301-303.

Klomp, N.I., and R.W. Furness. 1992. Non-breeders as a buffer against environmental stress: Declines in numbers of great skuas on Foula, Shetland, and prediction of future recruitment. J. Appl. Ecol. 29:341-348.

Koteja, P. 1991. On the relation between basal and field metabolic rates in birds and mammals. Funct. Ecol. 5:56-64.

Lemmetyinen, R. 1973. Feeding ecology of *Sterna paradisaea* Pontopp. and *S. hirundo* L. in the archipelago of southwestern Finland. Ann. Zool. Fenn. 10:507-525.

Lloyd, C.S., M.L. Tasker, and K. Partridge. 1991. The status of seabirds in Britain and Ireland. T. and A.D. Poyser, London.

Martin, A.R. 1989. The diet of Atlantic puffin *Fratercula arctica* and northern gannet *Sula bassana* chicks at a Shetland colony during a period of changing prey availability. Bird Study 36:170-180.

Massias, A., and P.H. Becker. 1990. Nutritive value of food and growth in common tern (*Sterna hirundo*) chicks. Ornis Scand. 21:187-194.

Monaghan, P. 1992. Seabirds and sandeels: The conflict between exploitation and conservation in the northern North Sea. Biodiversity and Conserv. 1:98-111.

Monaghan, P., J.D. Uttley, and M.D. Burns. 1992. Effect of changes in food availability on reproductive effort in Arctic terns *Sterna paradisaea*. Ardea 80:71-81.

Monaghan, P., J.D. Uttley, and J. Okill. 1989b. Terns and sandeels: Seabirds as indicators of changes in marine fish populations. J. Fish. Biol. 35A:339-340.

Monaghan, P., J.D. Uttley, M.D. Burns, C. Thaine, and J. Blackwood. 1989a. The relationship between food supply, reproductive effort and breeding success in Arctic terns *Sterna paradisaea*. J. Anim. Ecol. 58:261-274.

Monaghan, P., P.J. Wright, M.C. Bailey, J.D. Uttley, and P. Walton. 1992. The influence of changes in food abundance on diving and surface feeding seabirds. In: W.A. Montevecchi, (ed.), Studies of high latitude seabirds 4, Trophic relationships of marine birds and mammals. Canadian Wildlife Service Occas. Paper.

Montevecchi, W.A. 1993. Avian indicators of marine fish conditions. In: R.W. Furness and J.J.D. Greenwood (eds.), Birds as environmental monitors. Chapman, London, pp. 217-266.

Montevecchi, W.A., V.L. Birt-Friesen, and D.K. Cairns. 1992. Reproductive energetics and prey harvest of Leach's storm-petrels in the northwest Atlantic. Ecology 73:823-832.

Nagy, K.A., W.R. Siegfried, and R.P. Wilson. 1984. Energy utilization by free-ranging jackass penguins, *Spheniscus demersus*. Ecology 65:1648-1655.

Pearson, T.H. 1968. The feeding biology of seabird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37:521-552.

Phillips, R.A., R.W.G. Caldow, and R.W. Furness. 1996. The influence of food availability on the breeding effort and reproductive success of Arctic skuas *Stercorarius parasiticus*. Ibis 138:410-419.

Spaans, A.L. 1971. On the feeding ecology of the herring gull *Larus argentatus* Pont. in the northern part of the Netherlands. Ardea 59:73-188.

Tasker, M.L., and R.W. Furness. 1996. Estimation of food consumption by seabirds in the North Sea. In: G.L. Hunt and R.W. Furness (eds.), Seabird-fish interactions, with particular reference to seabirds in the North Sea. ICES Cooperative Research Report, chapter 2.

Tasker, M.L., R.W. Furness, M.P. Harris, and R.S. Bailey. 1989. Food consumption of seabirds in the North Sea. ICES Symp. 66. Multispecies Models to Management of Living Resources. ICES, Copenhagen.

Tasker, M.L., P. Hope-Jones, T. Dixon, and B.F. Blake. 1984. Counting seabirds at sea from ships: A review of methods employed and a suggestion for a standardized approach. Auk 101:567-577.

Tasker, M.L., A. Webb, A.J. Hall, M.W. Pienkowski, and D.R. Langslow. 1987. Seabirds in the North Sea. Nature Conservancy Council, Peterborough.

Taylor, I.R. 1979. Prey selection during courtship feeding in common tern. Ornis Scand. 10:142-144.

Thompson, D.R., and R.W. Furness. 1995. Stable isotope ratios of carbon and nitrogen in feathers indicate seasonal dietary shifts in northern fulmars. Auk 112:493-498.

Thompson, D.R., R.W. Furness, and S.A. Lewis. 1995. Diets and long-term changes in δ^{15}N and δ^{13}C values in northern fulmars *Fulmarus glacialis* from two northeast Atlantic colonies. Mar. Ecol. Prog. Ser. 125:3-11.

Uttley, J. 1991. The influence of food supply on the parental investment of arctic terns *Sterna paradisaea*. Ph.D. thesis, University of Glasgow.

Vader, W., R.T. Barrett, K.E. Erikstad, and K.-B. Strann. 1990. Differential responses of common and thick-billed murres to a crash in the capelin stock in the southern Barents Sea. Stud. Avian Biol. 14:175-180.

Veen, J. 1977. Functional and causal aspects of nest distributions in colonies of the sandwich tern (*Sterna s. sandvicensis* Lath.). Behaviour Suppl. 20:1-193.

Wanless, S., and M.P. Harris. 1992. Activity budgets, diet and breeding success of kittiwakes *Rissa tridactyla* on the Isle of May. Bird Study 39:145-154.

Webb, A., and J. Durinck. 1992. Counting birds from ship. In: J. Komdeur, J. Bertelsen, and G. Cracknell (eds.). Manual for aeroplane and ship surveys of waterfowl and seabirds. International Waterfowl and Wetlands Research Bureau Special Publication No. 10. Slimbridge, p. 24-37.

Selection of Forage-Fish Schools by Murrelets and Tufted Puffins in Prince William Sound, Alaska

William D. Ostrand
U.S. Fish and Wildlife Service, Anchorage, Alaska

Kenneth O. Coyle
University of Alaska Fairbanks, Institute of Marine Science, Fairbanks, Alaska

Gary S. Drew
U.S. Geological Survey, Biological Resources Division, Anchorage, Alaska

John M. Maniscalco and David B. Irons
U.S. Fish and Wildlife Service, Anchorage, Alaska

Extended Abstract

Studies examining the distribution of seabirds and their prey have determined that seabird and forage abundances are correlated, but that the strength of this relationship generally weakens as the spatial scale decreases (for review see Hunt 1988). The poor correlation between seabirds and their prey abundances at finer scales suggests that seabirds do not have sufficient knowledge of the distribution of prey to consistently select the best prey patches (Hunt 1988). Hence, seabirds may be more effective if they supplement their searches for food by exploiting the efforts of other seabirds by joining foraging flocks (Hunt 1988). Mehlum et al. (1996) correlated Brünnich's guillemot (*Uria lomvia*) abundance to forage density at a fine scale by including a prey density threshold that excluded nonpreferred food items from their correlation analysis. In examining fine-scale relationships between common tern (*Sterna hirundo*) and forage fish, Safina and Burger (1985) did not find a relationship between predator and prey abundance, but did find a significant relationship between the number of birds, depth to prey, and the presence of predatory fish. These fine-scale studies suggest that birds may select patches by prey characteristics as well as abundance. We sought to explore the relationship between seabirds and forage-fish

Table 1. Logistic regression models of the likelihood that fish schools would be associated with birds, using characteristics of the schools as independent variables. Data were collected in Prince William Sound, Alaska, 21 July-11 August 1995.

Number of schools not associated with birds	Number of schools associated with birds	Model	Model *P*
545	70	$\text{BMurrelets}^{a} = -0.01\text{TDepth}^{b}(0.0004)^{c} + 0.00004\text{Area}^{d}(0.03) + 0.62\text{MDensity}^{e}(0.05) + 0.53\text{HDensity}^{f}(0.12)$	0.0002
606	9	$\text{TPuffins}^{g} = -0.00026\text{DColony}^{h}(0.02)$	0.0001

[a] The probability of selection by marbled or Kittlitz's murrelets.

[b] Total water depth.

[c] *P* value of the associated independent variable.

[d] The chord length × the mean height of the school.

[e] Selection for medium density fish schools over low density schools. If either medium or high density variables were significant then both were retained in the model.

[f] Selection for high density fish schools over low density schools.

[g] The probability of selection by tufted puffins.

[h] Distance to the nearest tufted puffin colony.

schools at fine scales within Prince William Sound, Alaska. To explicitly test for fine-scale selection of forage fish by tufted puffins (*Fratercula cirrhata*) and brachyramphine murrelets (*Brachyramphus* spp.), we analyzed our data using fish schools as the sampling unit.

We collected hydroacoustic and bird-observation data simultaneously along systematically arranged transects in three areas of Prince William Sound from 21 July to 11 August 1995. We derived depth, area, and density of forage-fish schools from the hydroacoustic data set. Total depth of water, distance to shore, and distance to the nearest seabird colony for each sampled forage-fish school was determine through geographic information system software. Subsequently we determined which schools were associated with tufted puffins or brachyramphine murrelets. The probability of the association of fish schools with birds was determined through the use of a resource selection function based on multivariate logistic regression (Manly et al. 1993).

Our analysis indicated that tufted puffins selected fish schools that were near their colony (Table 1). Brachyramphine murrelets selected larger, denser fish schools in shallower water (Table 1). The statistical models had Akaike's information criterion (Akaike 1973) and concordance values of 423.8 and 66.3% for the brachyramphine murrelets and 75.2 and 89.9% for the tufted puffin models, indicating a good fit for both models. The mean numbers (±1 SD) of brachyramphine murrelets and tufted puffins associated with a forage-fish school were 1.7 ± 1.1 and 1.2 ± 0.7, respectively.

Our results suggest that the species we examined used different foraging strategies to find different types of forage-fish schools. Also, tufted puffins and brachyramphine murrelets forage extensively as individuals or in small groups and infrequently participate in foraging flocks. These findings suggest that within Prince William Sound individual seabirds have sufficient knowledge of available forage to select prey patches in specific types of areas with specific physical characteristics. We believe that the differences in our findings and the foraging efficiencies and strategies implied from previous studies were due to local oceanographic features that concentrated or otherwise made prey more predictably available to the seabirds of Prince William Sound (Hunt 1988).

The multivariate approach was effective in investigating fine-scale relationships between seabirds and fish. We suggest that these methods can be useful in addressing questions about smaller-scale interactions between and within trophic levels.

References

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. In: B.N. Petrov and F. Csaki (eds.), Second International Symposium on Information Theory. Akademiai Kaido, Budapest, Hungary, pp. 267-281.

Hunt, G.L. 1988. The distribution of seabirds at sea: Physical and biological aspects of their marine environment. In: R. van den Elzen, J.K. Schuchmann, and K. Schmidt-Koenig (eds.). Current topics in avian biology. Deutsche Ornithologen-Gesellschaft, Bonn, Germany, pp. 167-171.

Manly, B.F.J., L.L. McDonald, and D.L. Thomas. 1993. Resource selection by animals: Statistical design analysis for field studies. Chapman and Hall, London. 177 pp.

Mehlum, F., G.L. Hunt, Z. Klusek, M.B. Decker, and N. Norlund. 1996. The importance of prey aggregations to the distribution of Brünnich's guillemots in Storfjorden, Svalbard. Polar Biol. 16:537-547.

Safina, C., and J. Burger. 1985. Common tern foraging: Seasonal trends in prey fish densities and competition with bluefish. Ecology 66:1457-1463.

Seabird Behaviors at Forage Fish Schools in Prince William Sound, Alaska

John M. Maniscalco
University of Alaska Fairbanks, Fisheries Division, Juneau, Alaska

William D. Ostrand
U.S. Fish and Wildlife Service, Anchorage, Alaska

Abstract

We studied the feeding behaviors of seabirds at mixed-species flocks in Prince William Sound, Alaska, during the summer of 1995. The largest and most persistent flocks were associated with postspawning male capelin. The presence of marbled murrelets and black-legged kittiwakes at the feeding flocks was positively correlated as was the presence of alcids and larids suggesting complementary feeding habits. Kittiwakes preferentially plunge-dived for fish while glaucous-winged gulls usually sat on the water and hop-plunged, possibly limiting access by kittiwakes. While feeding in mixed-species flocks, kittiwakes lost 6.7% of their food catches to interspecific kleptoparasitism and another 4.8% was lost intraspecifically. Kleptoparasitism against kittiwakes was most intense in tightly aggregated flocks and against alcids in loosely aggregated flocks. Jaegers were common kleptoparasites of kittiwakes in the largest flocks.

Introduction

Seabirds often gather in flocks to exploit patchily distributed prey (Brown 1980, Obst 1985, Heinemann et al. 1989). Behavioral studies of seabirds at mixed-species feeding flocks have added substantially to our view of how food is obtained by this group of animals searching in an environment which is mostly hidden from plain sight (e.g., Sealy 1973, Hoffman et al. 1981, Chilton and Sealy 1987, Mahon et al. 1992). Species composition of seabird flocks may vary widely depending on the feeding situation (Duffy 1983). Many seabirds play specific roles in the for-

---

Current affiliation for John M. Maniscalco is U.S. Fish and Wildlife Service, Anchorage, AK.

mation, continuation, or breakup of the flocks (Hoffman et al. 1981, Duffy 1983, Chilton and Sealy 1987, Mahon et al. 1992). The presence or absence of certain key seabirds can affect the availability of forage to a number of other species. For instance, cormorants which dive in the middle of fish schools may have the effect of breaking up the schools and making them unavailable to other seabirds (Hoffman et al. 1981). Duffy (1986) found that roseate terns (*Sterna dougalli*) were more successful when foraging alone in dispersed flocks than in tightly spaced flocks with common terns (*S. hirundo*). Yet, individual foraging success of certain species can increase with the number of birds involved (Gotmark et al. 1986).

Methods by which seabirds feed vary from dipping in birds such as petrels to pursuit diving in birds such as auks and penguins (Ashmole 1971). Depending upon their feeding circumstances at sea, gulls and kittiwakes may choose to surface seize, plunge-dive, hop-plunge, dip, or kleptoparasitize. These behaviors may depend upon the density of birds in the aggregation or upon how the forage is made available. Both of these factors were used to delineate different types of feeding flocks (Hoffman et al. 1981). The feeding method of a particular seabird species may make forage unavailable to other species through interference competition (Shealer and Burger 1993) or through dispersion of the prey (Hoffman et al. 1981).

Kleptoparasitism is one feeding strategy which is common in many gulls and is a way of life for jaegers (Brockman and Barnard 1979). The success of a kleptoparasite could be dependent on factors such as weather condition, size of prey carried by host, or stage of the breeding season (Furness 1987). Evidence suggests that instances of kleptoparasitism in many birds may increase with decreasing access to food (Brockman and Barnard 1979, Duffy 1980, Temeles and Wellicome 1992, Oro and Martinez-Vilalta 1994, Oro 1996). High rates of this feeding strategy in seabirds could adversely affect populations of the host (Furness 1987) and failure of one host species to breed could cause increased pressures on an alternate host (Arnason and Grant 1978).

In this paper, we examine species composition and seabird behaviors at feeding flocks in Prince William Sound, Alaska, in an attempt to determine how forage is made available or unavailable to certain seabird species.

Study Area

Prince William Sound (PWS) is a large estuarine embayment of the northern Gulf of Alaska which provides important foraging and breeding habitat for many seabirds (Isleib and Kessel 1973, Irons et al. 1988). Water depths extend to greater than 870 m and the numerous bays and fjords along with more than 150 islands form at least 5,000 km of shoreline.

High precipitation rates keep the sea-surface salinity low and catabatic winds flowing down the fjords transport this low-salinity water out of PWS, generally through Montague Strait and the smaller straits and passages of the southwestern region. The Alaska coastal current provides the major inflow of marine water through Hinchinbrook Entrance (Royer et al. 1990). Diurnal tidal changes in PWS can also create currents exceeding 5 km/hr through narrow passages.

Seabirds that commonly forage in flocks in PWS include black-legged kittiwakes (*Rissa tridactyla*), glaucous-winged gulls (*Larus glaucescens*), mew gulls (*Larus canus*), marbled murrelets (*Brachyramphus marmoratus*), tufted puffins (*Fratercula cirrhata*), and horned puffins (*F. corniculata*). Jaegers (*Stercorarius* spp.) kleptoparasitize at these flocks to an unknown extent. Murrelets and kittiwakes appear to have been declining in PWS beginning many years prior to the *Exxon Valdez* oil spill of 1989 (Klosiewski and Laing 1994). The extent to which seabird foraging behaviors change with massive environmental perturbations is not generally known. Three focal areas in PWS (northeastern, central, and southwestern) were chosen for study because of their habitat which is critical to these seabird species of interest.

Forage fish available to nesting seabirds in PWS include, but are not limited to, Pacific herring (*Clupea pallasi*), capelin (*Mallotus villosus*), Pacific sand lance (*Ammodytes hexapterus*), walleye pollock (*Theragra chalcogramma*), and eulachon (*Thaleichthys pacificus*) (Sanger 1987, Haldorson et al. 1995). Herring in PWS did not appear to be seriously affected immediately following the spill. However, in 1993, greatly reduced numbers of herring returned to spawn and many of them had ulcers and hemorrhages of the skin and fins (Meyers et al. 1994). Declines in sand lance delivered to nestling pigeon guillemots (*Cepphus columba*) following the spill may reflect a major change in the ecosystem (Oakley and Kuletz 1994, Hayes 1995).

Methods

Field procedures

From a random starting point, we selected transects in the three areas of primary interest along lines of latitude 2 nmi apart (for more details see Ostrand et al. 1997). Since many seabirds are often found nearshore or in shallow depth gradients (Vermeer et al. 1989, Stone et al. 1995), we also ran zig-zag transects near shore by monitoring on a straight line from shore to the halfway point between adjacent transects where water depth was 100 m. From this point, the ship continued monitoring to the beginning of the next transect. Our study period (July 20-August 12) was chosen to include the peak time of chick provisioning for many seabirds in PWS. We made observations using 8 × 40 binoculars, 6 m above the water line from a 26-m vessel while conducting hydroacoustic surveys to estimate forage fish and seabird distributions and abundances. We left our transect lines to more closely examine feeding flocks within 300 m of either side of our vessel.

Trawl data were collected from a separate vessel which was directed by the hydroacoustic vessel to trawl through patches in which there was the most uncertainty as to prey species and/or age class composition. A modified Canadian midwater herring trawl (100-m^2 opening), an improvised pair trawl, and a dip net were used to verify fish school compositions as estimated from the acoustic data. These trawls were only used on the larger fish schools and hence the fish collected from them were not representative of all schools.

We collected behavioral data on feeding flocks upon leaving the transect and continued to do so until the flock broke up naturally or became disturbed by our presence. A feeding flock was defined as an aggregation of three or more seabirds actively feeding as observed by diving alcids with fish in their bill or larids plunge-diving, dipping, or hop-plunging. While at a feeding flock, one observer videotaped the flock for later analysis while another recorded detailed information on the flock including: location (latitude and longitude), date, time, weather conditions, wind speed and direction, sea state, water and air temperatures, area covered by flock (m^2), any noticeable physical features (e.g., upwellings, fronts), flock composition with numbers and locations of each species within the flock, kleptoparasitic and aggressive interactions with as much detail as possible, other feeding methods used and their success, and the duration and fate of the flock if known. We categorized feeding methods as surface-seizing, dipping, surface-diving, plunging, pursuit-plunging, piracy (Ashmole 1971), and hop-plunging (Hoffman et al. 1981). Flock types were loosely classified following Hoffman et al. (1981): (I) small, short-duration flocks over tightly clumped prey; (II) large, persistent flocks over more broadly dispersed prey; and (III) flocks associated with sites where forage was concentrated by downwelling or other hydrophysical influence, determined by a subjective evaluation of oceanographic features.

Data analyses

Analysis of the videotapes included categorizing the feeding methods used, frequency of these methods, and frequency of kleptoparasitic and aggressive interactions. We used descriptive statistics to describe the various feeding methods employed by the seabirds at the flocks and to show the sizes of different feeding groups. We also described the relationship of kittiwakes and murrelets at feeding flocks and the relationship of kittiwake dive frequencies and gull presence in flocks using Spearman's rank correlation. These data were analyzed in S-Plus (Statistical Sciences, Inc. 1993). Chi-square and Fisher's Exact Test were used to compare and contrast the behaviors of different seabirds at the different flock types.

Results

Flock type and species composition

During 18 days of running 120 transects, we rarely encountered feeding flocks which ranged in size from 3 to 1,065 birds (mean = 135.8; N = 22). Fifteen bird species participated in feeding flocks with a maximum of 11 species at a Type II flock. Species participation in the three flock types was significantly different overall ($\chi^2 = 214.65$, df = 8, $P < 0.001$; Table 1). However, species compositions of Types I and II flocks were not significantly different ($\chi^2 = 7.025$, df = 4, $P = 0.135$).

Black-legged kittiwakes and marbled murrelets were the most numerous species in all three flock types (Table 1). A scatter plot of their presence in the flocks suggested rank ordering them before analysis. Kittiwake presence in flocks was positively correlated with murrelet presence (Spearman's rho = 0.613, $P = 0.005$). Tufted puffins and glaucous-winged gulls were also a predominant species in Type I and II flocks and the correlation results for all larids and alcids at the flocks were the same as those for kittiwakes and murrelets.

Marbled murrelets and tufted puffins were present together in great numbers in Type II flocks. However, in the only two Type I flocks in which tufted puffins participated, murrelets had a presence of zero and one. A significant negative correlation was not detected, perhaps because of the small sample size.

Type I flocks were composed of 7 to 174 birds (N = 14; Table 1) with the mean number of species being 3.3 (SD = 1.49). At these flocks, we often saw the fish held in tight balls by pursuit-diving birds which dived and resurfaced near the periphery of the flock, as also observed by Hoffman et al. (1981) and Mahon et al. (1992). Herring and capelin were found to be common prey at PWS Type I flocks as determined by trawling.

We encountered two Type II flocks of 984 and 1,065 birds with 11 and 8 species participating in them, respectively. These were much smaller in size than the Type II flocks described by Hoffman et al. (1981), who described such flocks as ranging in size from 5,000 to 50,000 individuals. However, we still considered them to be Type II flocks because: (1) they were significantly larger than flock types I and III ($\chi^2 = 1{,}696.1$, df = 2, $P < 0.001$); (2) both of them lasted for at least 2 days; and (3) they were loosely aggregated assemblages feeding on spawned out male capelin in one case and either capelin or herring in the second case.

Type III flocks were composed of 11 to 168 birds (N = 6; Table 1) with the mean number of species being 4.2 (SD = 2.40). Five of these flocks were concentrated around points of land and one at the mouth of a shallow passage. Herring of various age groups were found in a trawl at one of these flocks.

Larid behaviors at flocks

Alcids pursuit dived from the outskirts of Type I flocks and from throughout Types II and III flocks. We did not concentrate any part of our observations on these birds because of the difficulty of following these birds from where they dived to where they resurfaced.

Glaucous-winged gulls hop-plunged more frequently than any other foraging method at all flock types (Figure 1a). At Type I flocks, glaucous-winged gulls normally sat on the water directly over the fish school while kittiwakes sat on the water around the periphery of the school or circled above it. To maintain their position in this flock type, gulls hop-plunged as opposed to plunge-dived. The latter foraging method was used more often in Type II and Type III flocks (Fisher's exact test; $P < 0.001$). Kittiwakes also hop-plunged more often in Type I flocks than in Types II and III flocks combined ($\chi^2 = 14.356$; $P < 0.001$). Yet, in all flock types, plunge-diving was their preferred method of feeding (Figure 1b). We were able to detect a weak but insignificant negative correlation between the frequency of kittiwake plunges and the relative presence of larger gulls in the flock (Spearman rho = –0.5664, $P = 0.0587$).

Kleptoparasitism

Kittiwakes had an overall feeding success of 80.6% (N = 129) and lost 4.8% of their captures to intraspecific piracy and 6.7% to interspecific piracy. Glaucous-winged gulls had a feeding success of 55.3% (N = 38) and lost nothing to kleptoparasitism.

Kleptoparasitism against kittiwakes occurred more frequently in the tightly aggregated Type I flocks compared to Types II and III flocks combined ($\chi^2 = 83.55$, $P < 0.001$; Table 2, Figure 2). Intraspecific kleptoparasitic attempts by kittiwakes were observed most often in Type I flocks while attempts directed against alcids were more commonly seen in Type II flocks. Glaucous-winged gulls attempted to rob alcids only in Type I flocks. Gulls and kittiwakes kleptoparasitized alcids less than expected in Type I flocks ($\chi^2 = 15.32$, df = 1, $P < 0.001$) but not in Type III flocks ($\chi^2 = 1.780$, df = 1, $P = 0.182$).

Jaegers preferred to kleptoparasitize at the large Type II flocks (78% of observed attempts; Figure 2). Thirty-one out of 32 observed jaeger robbing attempts were directed toward kittiwakes and the other toward a juvenile glaucous-winged gull. One large capelin feeding flock had a group of 15 pomarine and 2 parasitic jaegers sitting on the water about 1 km away. They appeared to be making occasional sorties (usually alone) into the feeding flock. Their method of attack in Type II flocks was to concentrate efforts on kittiwakes which had recently caught a fish and those with fish visible in their bill.

Table 1. Total numbers of the most common seabirds and total birds at the different flock types with percent contribution of these species at each flock type (n = number of flocks).

	Type I (n = 14)		Type II (n = 2)		Type III (n = 6)	
Black-legged kittiwake	277	43%	860	42%	105	35%
Glaucous-winged gull	55	9%	250	12%	13	4%
Marbled murrelet	141	22%	420	20%	112	38%
Tufted puffin	143	22%	450	22%	12	4%
Other birds	26	4%	69	3%	54	18%
All birds	642	100%	2,049	100%	296	100%

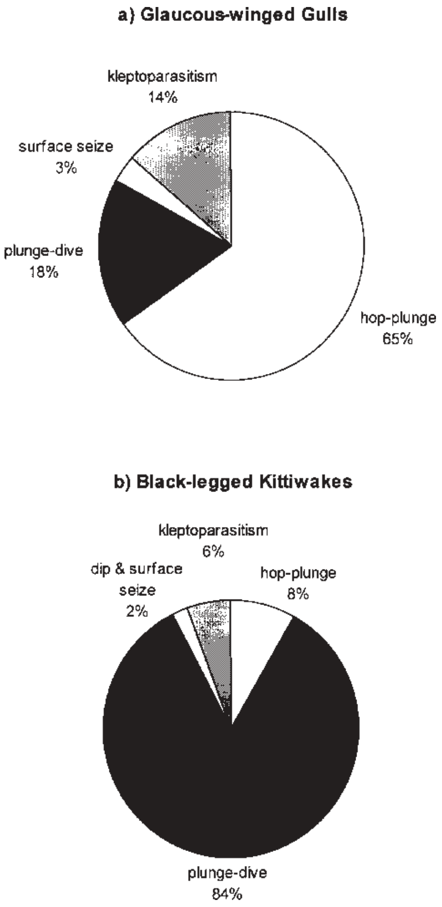


Figure 1. Frequency of feeding techniques used by (a) glaucous-winged gulls and (b) black-legged kittiwakes at all flock types combined.

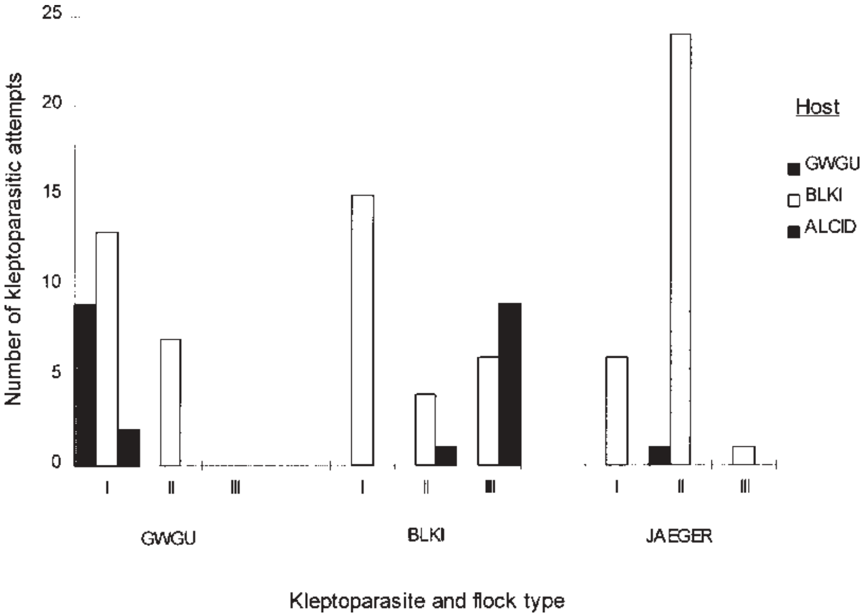


Figure 2. Number of kleptoparasitic attempts observed at the different flock types (GWGU = glaucous-winged gulls, BLKI = black-legged kittiwakes).

Table 2. Kleptoparasitism of alcids and kittiwakes by all larids combined in Types I and III flocks.

Flock type	Host	Host total abundance	Host relative abundance	Expected number of chases	Observed number of chases
I	Alcid	180	0.4286	12.43	2
I	Kittiwake	240	0.5714	16.57	27
III	Alcid	143	0.6272	10.66	8
III	Kittiwake	85	0.3728	6.34	9

Discussion

Flock types and species composition

In PWS flocks are generally smaller than those encountered in more oceanic regions (e.g., Hoffman et al. 1981, Duffy 1983). Feeding flocks of murrelets, kittiwakes, gulls, puffins, and guillemots fed on schools of herring, capelin, and sand lance that were near shore (Haldorson et al. 1995; Unpubl. data, Ostrand and Maniscalco). Conspecifics and congeners of these birds have also been found to be distributed near shore in other boreal environments (Vermeer et al. 1989, Stone et al. 1995), possibly to obtain easy access to their prey. Our observations on only 22 feeding flocks during 18 days was likely the result of spending a much greater proportion of time on offshore portions of transects.

Seabird prey can be concentrated by upwelling or downwelling in both oceanic and coastal regimes (e.g., Schneider et al. 1987, Wahl et al. 1989, Coyle et al. 1992). Such flow gradients are often found around islands and points of land (Hamner and Hauri 1981, Kinder et al. 1983). These processes may work in PWS during the summer to make herring more vulnerable to seabird predation and forming Type III flocks. Sand lance are also common in shallow waters and near shore which have sandy substrates and relatively high bottom current velocities (Auster and Stewart 1986). These conditions occur around many of the land masses in PWS. The capelin concentrations discovered near shore appeared to be postspawning aggregations, which are known to attract alcids (Piatt 1990) and many other seabirds (Hoffman et al. 1981). The hydroacoustic profiles suggest that the predominant concentration of capelin in these schools reside near the bottom of the water column. Alcids appear to be the driving force in Type I flocks where capelin are concentrated in tight balls near the surface and hence become accessible for gulls and kittiwakes (Grover and Olla 1983). In the large Type II flocks individual capelin appear to separate from the main school for unknown reasons and swim to near the surface where they are vulnerable to plunge-diving birds.

In British Columbia marbled murrelets may have been the catalyst in the formation of feeding flocks by forcing fish schools into tight balls and driving them to the surface (Mahon et al. 1992). This is a likely cause for the weak association between murrelets and kittiwakes at the flocks. Our observations of murrelet participation in flocks were consistent with observations made within intercoastal waters of British Columbia (Mahon et al. 1992) and inconsistent with the low murrelet participation in flocks of outside waters (Porter and Sealy 1981, Chilton and Sealy 1987). Hunt (1995) reviewed these and other studies and was unable to conclude why there was this difference in murrelet flock participation. The relative absence of murrelets in tightly aggregated flocks with many puffins in PWS does suggest, however, that murrelet feeding activity may be inhibited by larger alcids in this type of situation (see also Chilton and Sealy 1987, Piatt 1990).

Larid behaviors at flocks

Glaucous-winged gulls may deter smaller gulls and kittiwakes from feeding at densely aggregated flocks. Porter and Sealy (1982) observed that smaller California gulls usually hovered over flocks and plunge-dived while glaucous-winged gulls flew directly into the center and hop-plunged or dipped for prey. These behaviors are similar to what we have observed with kittiwakes and gulls in PWS feeding flocks. We encountered one feeding flock which had 12 glaucous-winged gulls sitting on the water over a tight ball of capelin and occasionally plunge-diving. Kittiwakes were entirely absent from this flock though many were seen within a few kilometers. Interference competition such as this has also been noted in brown noddies (*Anous stolidus*) which deterred the feeding attempts made by roseate terns near Puerto Rico and may have been stronger during periods of food shortage (Shealer and Burger 1993). We observed that kittiwakes partially compensated for the presence of glaucous-winged gulls at densely aggregated Type I feeding flocks by remaining on the water and hop-plunging more often in these flocks but always outside the central core of gulls. The negative correlation we found between kittiwake dive rates and gull presence in the flocks is further suggestive that interference competition does take place amongst larids in PWS. Unfortunately, keeping track of individual birds is difficult in Type I flocks, therefore correlations between feeding success of kittiwakes and gull presence were not possible to determine. Glaucous-winged gulls are unable to dominate the more loosely aggregated fish at Types II and III flocks and hence plunge-dived more often in those situations.

Kleptoparasitism

Densely aggregated Type I flocks promoted kleptoparasitism within the gulls and kittiwakes but did not facilitate piracy by jaegers perhaps because of their low success rate in this type of flock (Hoffman et al. 1981). Alcids were attacked less frequently in Type I flocks because of their ability to dive and resurface around the outer edge of these flocks and avoid the attacking kittiwakes (Hoffman et al. 1981, Chilton and Sealy 1987). The inability to keep fish tightly balled as in Types II and III flocks causes diving birds to resurface randomly. Without the focal point of a tight fish school, kittiwakes may cue on the resurfacing alcids for feeding opportunities. Our observations of greater numbers of alcid attacks at those flock types supports this hypothesis.

Parasitic and pomarine jaegers were most commonly observed in the largest (Type II) feeding flocks. Kittiwakes were preferentially chased rather than the larger gulls, probably because kittiwakes were smaller hosts or they delayed the swallowing of their prey or both. On the St. Lawrence River, smaller common terns were chased more often by parasitic jaegers than were black-legged kittiwakes and almost half of the chased terns had fish dangling from the bill, whereas none of the chased kittiwakes carried visible fish (Belisle and Giroux 1995). A review by Furness (1987), however, suggests that the parameters regarding a bird's susceptibility to chase remain equivocal.

Although most studies of jaeger piracy have been conducted near colonies (e.g., Andersson 1976, Birt and Cairns 1987) these birds are not common raiders at colonies in PWS (Pers. comm., D.B. Irons, U.S. Fish and Wildlife Service, Anchorage, AK). The relatively small colony sizes of PWS seabirds (Sowls et al. 1978) may limit kleptoparasitic opportunities at these locations. Foraging at large feeding flocks where there are both breeding and nonbreeding birds to steal from could be more beneficial especially when a host has been observed catching a fish (Hoffman et al. 1981).

Intraspecific kleptoparasitism as seen in kelp gulls (*Larus dominicanus*) at a rate of 15% may benefit this species (Steele and Hockey 1995). Although our data concerning kittiwakes are not directly comparable, they may suggest that kleptoparasitism among kittiwakes in PWS is not adversely affecting their populations. A significant change in rates of kleptoparasitism in PWS in the coming years may be indicative of changes in the abundance of seabirds and/or their prey.

Physical and biological processes which make forage easily available or difficult to obtain for seabirds in PWS are not necessarily the same as in other ecosystems, although there are some apparent similarities. Seabird behavior is much more complex than what is shown here and all of the aspects analyzed in this paper should be studied further in the coming years for a better understanding of seabird ecology in PWS and elsewhere.

Acknowledgments

We thank David Irons, David Duffy, and Thomas Shirley for their thoughtful review and helpful comments on this article. Lewis Haldorson and Jennifer Boldt kindly offered data concerning forage fish. The M/V *Pacific Star* served as our platform for the strip transects and we gratefully thank the crew for their assistance. The research described in this paper was supported by the *Exxon Valdez* Oil Spill Trustee Council. However, the findings and conclusions presented are ours and do not necessarily reflect the views or position of the Trustee Council.

References

Andersson, M. 1976. Predation and kleptoparasitism by skuas in a Shetland seabird colony. Ibis 118:208-217.

Arnason, E., and P.R. Grant. 1978. The significance of kleptoparasitism during the breeding season in a colony of arctic skuas *Stercorarius parasiticus* in Iceland. Ibis 120:38-54.

Ashmole, N.P. 1971. Sea bird ecology and the marine environment. In: D.S. Farner and J.R. King (eds.), Avian biology, Vol. 1. Academic Press, NY, pp. 223–286.

Auster, P.J., and L.L. Stewart. 1986. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic) — sand lance. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.66). U.S. Army Corps of Engineers, TR EL-82-4, 11 pp.

Belisle, M., and J.-F. Giroux. 1995. Predation and kleptoparasitism by migrating parasitic jaegers. Condor 97:771-781.

Birt, V.L., and D.K. Cairns. 1987. Kleptoparasitic interactions of Arctic skuas *Stercorarius parasiticus* and black guillemots *Cepphus grylle* in northeastern Hudson Bay, Canada. Ibis 129:190-196.

Brockman, H.J., and C.J. Barnard. 1979. Kleptoparasitism in birds. Anim. Behav. 27:487-514.

Brown, R.G.B. 1980. Seabirds as marine animals. In: J. Burger, B.L. Olla, and H.E. Winn (eds.), Behavior of marine animals, Vol. 4, Marine birds. Plenum Press, pp. 1-39.

Chilton, G., and S.G. Sealy. 1987. Species roles in mixed-species feeding flocks of seabirds. J. Field Ornithol. 58:456-463.

Coyle, K.O., G.L. Hunt Jr., M.B. Decker, and T.J. Weingartner. 1992. Murre foraging, epibenthic sound scattering and tidal advection over a shoal near St. George Island, Bering Sea. Mar. Ecol. Prog. Ser. 83:1-14.

Duffy, D.C. 1980. Patterns of piracy by Peruvian seabirds: A depth hypothesis. Ibis 122:521-525.

Duffy, D.C. 1983. The foraging ecology of Peruvian seabirds. Auk 100:800-810.

Duffy, D.C. 1986. Foraging at patches: Interactions between common and roseate terns. Ornis Scand. 17:47-52.

Furness, R.W. 1987. Kleptoparasitism in seabirds. In: J.P. Croxall (ed.), Seabirds: Feeding ecology and role in marine ecosystems. Cambridge University Press, pp. 77-100.

Gotmark, F., D.W. Winkler, and M. Andersson. 1986. Flock-feeding on fish schools increases individual success in gulls. Nature 319:589-591.

Grover, J.J., and B.L. Olla. 1983. The role of Rhinoceros Auklet (*Cerorhinca monocerata*) in mixed-species feeding assemblages of seabirds in the Strait of Juan de Fuca, Washington. Auk 100:979-982.

Haldorson, L., T. Shirley, K. Coyle, and R. Thorne. 1995. Biomass and distribution of forage species in Prince William Sound. Alaska Predator Ecosystem Experiment (APEX) 1995 annual report. University of Alaska Fairbanks, Juneau, AK.

Hamner, W.M., and I.R. Hauri. 1981. Effects of island mass: Water flow and plankton pattern around a reef in the Great Barrier Reef lagoon, Australia. Limnol. Oceanogr. 26:1084-1102.

Hayes, D.L. 1995. Recovery monitoring of pigeon guillemot populations in Prince William Sound, Alaska. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 94173), U.S. Fish and Wildlife Service, Anchorage, AK.

Heinemann, D., G. Hunt, and I. Everson. 1989. Relationships between the distributions of marine avian predators and their prey, *Euphausia superba*, in Bransfield Strait and southern Drake Passage, Antarctica. Mar. Ecol. Prog. Ser. 58:3-16.

Hoffman, W., D. Heinemann, and J.A. Wiens. 1981. The ecology of seabird feeding flocks in Alaska. Auk 98:437-456.

Hulsman, K. 1976. The robbing behavior of terns and gulls. Emu 76:143-149.

Hunt, G.L., Jr. 1995. Monospecific and mixed species foraging associations of marbled murrelets. In: C.J. Ralph, G.L. Hunt Jr., M.G. Raphael, and J.F. Piatt (eds.), Ecology and conservation of the marbled murrelet. USDA Forest Service Gen. Tech. Rep. PSW-GTR-152. Pacific Southwest Research Station, Albany, CA, pp. 255-256.

Irons, D.B., D.R. Nysewander, and J.L. Trapp. 1988. Prince William Sound waterbird distribution in relation to habitat type. Unpubl. rep., U.S. Fish and Wildlife Service, Anchorage, AK. 26 pp.

Isleib, P., and B. Kessel. 1973. Birds of the north gulf coast: Prince William Sound region, Alaska. Biol. Pap. Univ. Alaska 14. 149 pp.

Kinder, T.H., G.L. Hunt Jr., D. Schneider, and J.D. Schumacher. 1983. Correlations between seabirds and oceanic fronts around the Pribilof Islands, Alaska. Estuarine Coastal Shelf Sci. 16:309-319.

Klosiewski, S.P., and K.K. Laing. 1994. Marine bird populations of Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill. Exxon Valdez Oil Spill State and Federal Natural Resources Damage Assessment Final Reports. Bird Study Number 2, U.S. Fish and Wildlife Service, Anchorage, AK. 89 pp.

Mahon, T.E., G.W. Kaiser, and A.E. Burger. 1992. The role of marbled murrelets in mixed-species feeding flocks in British Columbia. Wilson Bull. 104:738-743.

Meyers, T.R., S.Short, K.Lipson, W.N. Batts, J.R. Winton, J. Wilcock, and E. Brown. 1994. Association of viral hemorrhagic septicemia virus with epizootic hemorrhages of the skin in Pacific herring *Clupea harengus pallasi* from Prince William Sound and Kodiak Island, Alaska, USA. Dis. Aquat. Org. 19:27-37.

Oakley, K.L., and K.J. Kuletz. 1994. Population, reproduction, and foraging ecology of pigeon guillemots at Naked Island, Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill. Exxon Valdez Oil Spill State and Federal Natural Resources Damage Assessment Final Reports. Bird Study Number 9, U.S. Fish and Wildlife Service, Anchorage, AK. 46 pp.

Obst, B.S. 1985. Densities of Antarctic seabirds at sea and the presence of the krill *Euphausia superba*. Auk 102:540-549.

Oro, D. 1996. Interspecific kleptoparasitism in Audouin's Gull *Larus audouinii* at the Ebro Delta, northeast Spain: A behavioral response to low food availability. Ibis 138:218-221.

Oro, D., and A. Marinez-Vilalta. 1994. Factors affecting kleptoparasitism and predation rates upon a colony of Audouin's gull (*Larus audouinii*) by yellow-legged gulls (*Larus cachinnans*) in Spain. Colon. Waterbirds 17:35-41.

Ostrand, W.D., K.O. Coyle, G.S. Drew, J.M. Maniscalco, and D.B. Irons. 1997. Selection of forage-fish schools by murrelets and tufted puffins in Prince William Sound, Alaska. In: Forage fishes in marine ecosystems. Alaska Sea Grant Report No. AK-SG-97-01. University of Alaska Fairbanks (this volume).

Piatt, J.F. 1990. The aggregative response of common murres and Atlantic puffins to schools of capelin. Stud. Avian Biol. 14:36-51.

Porter, J.M., and S.G. Sealy. 1981. Dynamics of seabirds multispecies feeding flocks: Chronology of flocking in Barkley Sound, British Columbia. Colon. Waterbirds 4:104-113.

Porter, J.M., and S.G. Sealy. 1982. Dynamics of seabird multispecies feeding flocks: Age-related feeding behavior. Behaviour 81:91-109.

Rice, J. 1985. Interactions of variation in food supply and kleptoparsitism levels on the reproductive success of common puffins (*Fratercula arctica*). Can. J. Zool. 63:2743-2747.

Rice, J. 1987. Behavioural responses of common puffins to kleptoparasitism by herring gulls. Can. J. Zool. 65:339-347.

Royer, T.C., J.A. Vermersch, T.J. Weingartner, H.J. Niebauer, and R.D. Muench. 1990. Ocean circulation influencing the *Exxon Valdez* oil spill. Oceanogr. 3:3-10.

Sanger, G.A. 1987. Trophic levels and trophic relationships of seabirds in the Gulf of Alaska. In: J.P. Croxall (ed.), Seabirds feeding ecology and role in marine ecosystems. Cambridge University Press, pp. 229-257.

Schneider, D., N.M. Harrison, and G.L. Hunt Jr. 1987. Variation in the occurrence of marine birds at fronts in the Bering Sea. Estuarine Coastal Shelf Sci. 25:135-141.

Sealy, S.G. 1973. Interspecific feeding assemblages of marine birds off British Columbia. Auk 90:796-802.

Shealer, D.A., and J. Burger. 1993. Effects of interference competition on the foraging acitivity of tropical roseate terns. Condor 95:322-329.

Sowls, A.L., S.A. Hatch, and C.J. Lensink. 1978. Catalog of Alaskan seabird colonies. U.S. Fish and Wildlife Service FWS/OBS-78/78.

Statistical Sciences, Inc. 1993. S-Plus for Windows user's manual and reference manual, version 3.1. Seattle, WA.

Steele, W.K., and P.A.R. Hockey. 1995. Factors influencing rate and success of intraspecific kleptoparasitism among kelp gulls (*Larus dominicanus*). Auk 112:847-859.

Stone, C.J., A. Webb, and M.L. Tasker. 1995. The distribution of auks and Procellariiformes in northwest European waters in relation to depth of sea. Bird Study 42:50-56.

Temeles, E.J., and T.I. Wellicome. 1992. Weather-dependent kleptoparasitism and aggression in a raptor guild. Auk 109:920-923.

Vermeer, K., K.H. Morgan, G.E.J. Smith, and R. Hay. 1989. Fall distribution of pelagic birds over the shelf off SW Vancouver Island. Colon. Waterbirds 12: 207-214.

Wahl, T.R., D.G. Ainley, A.H. Benedict, and A.R. DeGange. 1989. Associations between seabirds and water-masses in the northern Pacific Ocean in summer. Mar. Biol. 103:1-11.

Seabird Impacts on Forage Fish: Population and Behavioral Interactions

Elizabeth A. Logerwell
University of California, Ecology and Evolutionary Biology, Irvine, California

N. Brent Hargreaves
Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, Canada

Extended Abstract

We investigated the impact of piscivorous seabirds on the abundance and behavior of forage fish off Vancouver Island, British Columbia, Canada. To investigate the potential for population-level interactions, we estimated the annual consumption rate of seabirds. To examine behavioral-level impacts we investigated the effects of seabirds on the distribution of fish. This paper focuses on Pacific herring (*Clupea pallasi*), an important forage fish off Vancouver Island; and common murres (*Uria aalge*) and sooty shearwaters (*Puffinus griseus*), the most abundant piscivorous seabirds observed during our study.

Data on the distribution and abundance of fish and seabirds were collected on research surveys during 9-27 September 1991, 16 June-2 July 1992, and 7-27 July 1993 (Figure 1). The distribution of fish was sampled from the R/V *W.E. Ricker* using the recently developed Bernard Sigmund Beam Trawl designed to catch juvenile salmon in the top 10-15 m of the water column (Hargreaves and Hungar 1990). Although the nets were fished continuously, the samples were brought on board at 5- to 6-km intervals. To estimate the distribution of seabirds at sea, birds were counted while the ship was under way at speeds of 3-10 knots. All birds within a 300-m band transect to one side of the ship were counted and the data were entered into a field computer which assigned a time to each entry. This information was then used to calculate the position of all bird observations so that the distribution of seabirds could be related to the data on fish distributions.

To estimate seabird consumption rates, the following assumptions

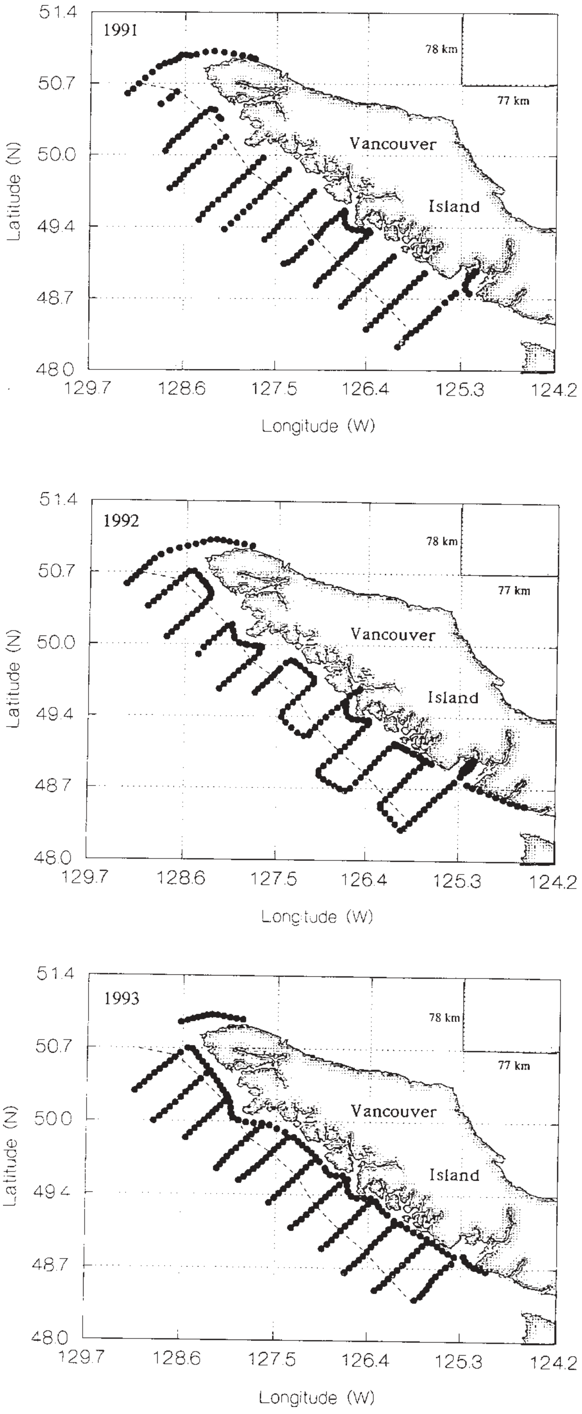


Figure 1. Transects surveyed off Vancouver Island during: (top) September 1991, (middle) June 1992, and (bottom) July 1993. Points represent locations of beam trawl net hauls. The location of the shelf break (the 200-m depth contour) is indicated by the dashed line.

were made: (1) murres and shearwaters consume 0- to 2-year herring, (2) herring make up half of the diet of the seabirds, (3) murres occupy the study area for 365 days a year, and (4) shearwaters occupy the study area for 180 days a year. The first two assumptions are based on seabird diet studies from British Columbia (Vermeer 1992) and other systems (Swennen and Duiven 1977). The third and fourth assumptions are drawn from Morgan et al. (1991). The daily energy requirements of a single murre or shearwater were estimated using a regression between body weights and seabird field metabolic rates measured with doubly labeled water (Koteja 1991). Daily energy requirements were converted to mass of fish consumed per day by dividing by the assimilation efficiency, assumed to be 75%, and by the energy content of fish, assumed to be 7.03 kJ/g (Cummins and Wuycheck 1971). The mass of fish consumed per day per bird was converted to mass of herring by multiplying by 0.5 (it was assumed that half the diet was herring). The mass of herring consumed per year by murres and shearwaters was then calculated by multiplying the daily herring consumption per bird by an estimate of the abundance of murres and shearwaters in the study area (based on the transect data) and the occupancy period of each species.

To estimate the biomass of 0- to 2-year herring off Vancouver Island, a spawning stock estimate of 23,000 tons was first assumed (Schweigert and Fort 1994). The number of spawners was estimated by dividing the total biomass by 124 g, the average weight of 3- to 8-year herring (Hart 1973). The number of 3-year fish was estimated by multiplying the total number of spawners by 0.20 (Stocker 1993). The number of 2-year fish was estimated by assuming an annual mortality rate of 0.393 (Pers. comm., Jacob Schweigert, Department of Fisheries and Oceans, Nanaimo, B.C., Canada), and the number of 0- to 1-year fish was estimated by assuming a daily mortality rate of 0.007024 (the latter was borrowed from a sardine population matrix; Pers. comm., Paul Smith, Southwest Fisheries Science Center, La Jolla, CA). Finally, the biomass of herring was calculated from these estimates of abundance by multiplying by average body weights for each age (Hart 1973, Bishop et al. 1993). Seabird consumption rates for each year of the survey were calculated by dividing the estimated biomass of herring the murres and shearwaters consumed by the estimated biomass of 0- to 2-year herring off Vancouver Island.

Based on our estimates, seabirds consumed 21% of the juvenile herring biomass in 1991, 17% in 1992, and 11% in 1993, for an average of 16%. Without further modeling, it is difficult to determine whether these consumption rates would have an appreciable effect on herring populations. However, our estimated consumption rate of 16% is similar to seabird consumption rates reported in other systems: 20% off the Oregon coast (Wiens and Scott 1975), 29% off Shetland Island (Furness 1978), and 23% in the Benguela Current (Furness and Cooper 1982).

To investigate the effects of seabirds on the distribution of fish, correlations between the density of seabirds observed and fish caught per net tow were estimated. Our expectation was that seabirds would forage to maximize energy intake and would thus be more abundant where fish were more abundant, resulting in a positive correlation between the two. However, we found a significant negative correlation between the density of murres and fish per net tow during both 1991 and 1992, the two years during which the fish and seabird data were collected simultaneously (Spearman rank correlations in 1991: $r_s = -0.305$, $P < 0.05$, N = 69; and 1992: $r_s = -0.252$, $P < 0.05$, N = 63). This suggests that murres were either depleting their prey at small scales, or that fish were swimming away from murres perhaps to depths below the 10-15 m sampled by the nets. We prefer the hypothesis that murres were driving fish away from the surface because the seabird aggregations observed were probably not large enough to locally deplete fish prey; maximum murre densities were around 20 birds per kilometer. In addition, murres are strong divers, routinely diving to depths of 30 m or more. If it is the surface waters that are most productive, and seabirds commonly drive fish away from the surface, then the presence of seabirds could negatively impact fish feeding and growth rates. In addition, researchers may want to keep in mind the possible effects of seabirds on the vertical distribution of fish when investigating habitat use by forage fish. In contrast to murres, there was no significant correlation between shearwaters and fish in either year. Shearwaters feed primarily at the surface and thus would not be expected to chase fish below the 10-15 m sampled by the nets.

References

Bishop, C.A., E.F. Murphy, M.B. Davis, J.W. Baird, and G.A. Rose. 1993. An assessment of the cod stock in NAFO Divisions 2J+3KL. Northwest Atlantic Fisheries Organization Scientific Council Report No. 93/86. NAFO, Dartmouth, NH.

Cummins, J.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitt. Int. Ver. Theor. Angew. Limnol. 18.

Furness, R.W. 1978. Energy requirements of seabird communities: A bioenergetics model. J. Anim. Ecol. 47:39-53.

Furness, R.W., and J. Cooper. 1982. Interactions between breeding seabird and pelagic fish populations in the southern Benguela region. Mar. Ecol. Prog. Ser. 8:243-250.

Hargreaves, B., and B. Hungar. 1990. Juvenile salmon abundance and distribution along the west coast of Vancouver Island in summer, 1990. In: The marine survival of salmon program, annual progress report. Biological Sciences Branch, Department of Fisheries and Oceans, Canada. Nanaimo, British Columbia, pp. 59-83.

Hart, J.L. 1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180.

Koteja, P. 1991. On the relation between basal and field metabolic rates in birds and mammals. Funct. Ecol. 5:56-64.

Morgan, K.H., K. Vermeer, and R.W. McKelvey. 1991. Atlas of pelagic birds of western Canada. Can. Wildl. Serv. Occas. Pap. 72.

Schweigert, J.F., and C. Fort. 1994. Stock assessment for British Columbia herring in 1993 and forecasts of the potential catch in 1994. Can. Tech. Rep. Fish. Aquat. Sci. 1971.

Stocker, M. 1993. Recent management of the British Columbia herring fishery. Can. Bull. Fish. Aquat. Sci. 226:267-293.

Swennen, C., and P. Duiven. 1977. Size of food objects of three fish-eating seabird species: *Uria aalge*, *Alco torda* and *Fratercula arctica* (Aves, Alcidae). Neth. J. Sea Res. 11:92-98.

Vermeer, K. 1992. The diet of birds as a tool for monitoring the biological environment. Can. Wildl. Serv. Occas. Pap. 75:41-50.

Wiens, J.A., and J.M. Scott. 1975. Model estimation of energy flow in Oregon coastal seabird populations. Condor 77:439-452.

Shrimp Fishery and Capelin Decline May Influence Decline of Harbor Seal (*Phoca vitulina*) and Northern Sea Lion (*Eumetopias jubatus*) in Western Gulf of Alaska

Donald J. Hansen
Minerals Management Service, Anchorage, Alaska

Abstract

The decline of the harbor seal, *Phoca vitulina richardsi*, in the western Gulf of Alaska was concurrent with the collapse of the shrimp-trawl fishery in the same area between 1976 and 1981. Over approximately the same time period (1976-1979 to 1985), the rate of decline of specific local breeding populations of the northern sea lion, *Eumetopias jubatus*, increased. Shrimp, slow-moving and relatively easy to catch, have been reported as the primary prey item of newly weaned harbor seal pups, and they may play a similarly important role in the diet of northern sea lion pups; young pinniped pups may need time and practice to acquire the speed and agility to catch fast-moving prey such as finfishes. Capelin, *Mallotus villosus*, a forage fish of harbor seals and northern sea lions, also declined in abundance in the early 1980s in the western Gulf of Alaska; capelin may be of importance to older pinniped pups, providing a high-lipid food source for the buildup of fat reserves for thermal insulation and growth. With the decline in abundance of both shrimp and capelin, young inexperienced harbor seals and sea lions may no longer be able to compete successfully with other predators for these food items. Thus, harbor seal and sea lion pups may be starving after they leave the rookeries.

Growth and Decline of Alaska Shrimp Fishery

The history of the pandalid, or pink, shrimp (*Pandalus borealis*) industry in Alaska has been summarized by Anderson and Gaffney (1977). The industry began in 1915 with a small fishery in southeast Alaska near

Wrangell and Petersburg. The harvest in this area remained small, peaking in 1958 at 3.45 million kg per year. In the 1950s, the shrimp fishery expanded to Kodiak Island and Cook Inlet, where the harvest increased rapidly, peaking in 1972 at 37.23 million kg per year. In the 1960s, fisheries were established along the south side of the Alaska Peninsula; there the harvest, 2.54 million kg per year in 1968, increased rapidly to 20.43 million kg per year in 1975 after quotas were instituted in the Kodiak area. During the 1970s, fishery districts expanded west to include the eastern Aleutians in the area of Dutch Harbor and Unalaska Island. Major shrimp fisheries are shown in Figure 1.

The decline of the fisheries was sudden and abrupt. Between 1976 and 1981, the statewide harvest of pandalid shrimp—including the harvests in the western Gulf of Alaska (Kodiak Island to the eastern Aleutian Islands)—crashed (Figure 2; Davis 1982). In Pavlof Bay, research surveys indicated that the population of pandalid shrimp declined by 95% over this period (Figure 3; Anderson 1991). In the Kodiak Island area, the decline began somewhat earlier: the commercial catch peaked in 1972, declined the following year, and crashed in 1978 (Figure 2; Alaska Sea Grant Program 1978). No improvement or recovery of the shrimp stocks was indicated from surveys between 1979 and 1986 of Pavlof Bay and the western Gulf of Alaska, even though the commercial fishery in Pavlof Bay had been closed since 1979 and the other fisheries closed in the early 1980s (Figure 3; Anderson 1991). Continued small-mesh surveys in the western Gulf of Alaska have shown no recovery of shrimp stocks through 1994 (Pers. comm., Anderson, Alaska Fisheries Science Center, NOAA, Kodiak, AK, Mar. 1996).

Pacific Harbor Seal Decline

The timing and geographic location of the shrimp crash were concurrent with the decline in abundance of the Pacific harbor seal, *Phoca vitulina richardsi*, in the western Gulf of Alaska. Maximum harbor seal counts during the molting season on southwest Tugidak Island, the major seal rookery in the western Gulf of Alaska, declined dramatically between 1976 and 1982 (Figures 4 and 5). Based on these counts, the harbor seal population declined by 19% per year (Pitcher 1990).

Because seal pregnancy rates (92%) at Tugidak Island during the mid-1970s were near normal levels (95-98%), a decline in female reproductive rate was not an apparent factor. The dramatic decline in seal numbers suggests substantial mortality and/or nearly complete recruitment failure as the primary cause (Pitcher 1990). A drastic decrease in juvenile seal survival after weaning could be responsible. A similar decrease in survival of northern sea lion juveniles after weaning is the currently accepted explanation for observed declines in the northern sea lion populations in Alaska (York 1994, Merrick et al. 1988).

The importance of shrimp to newly weaned harbor seals on the Pa-

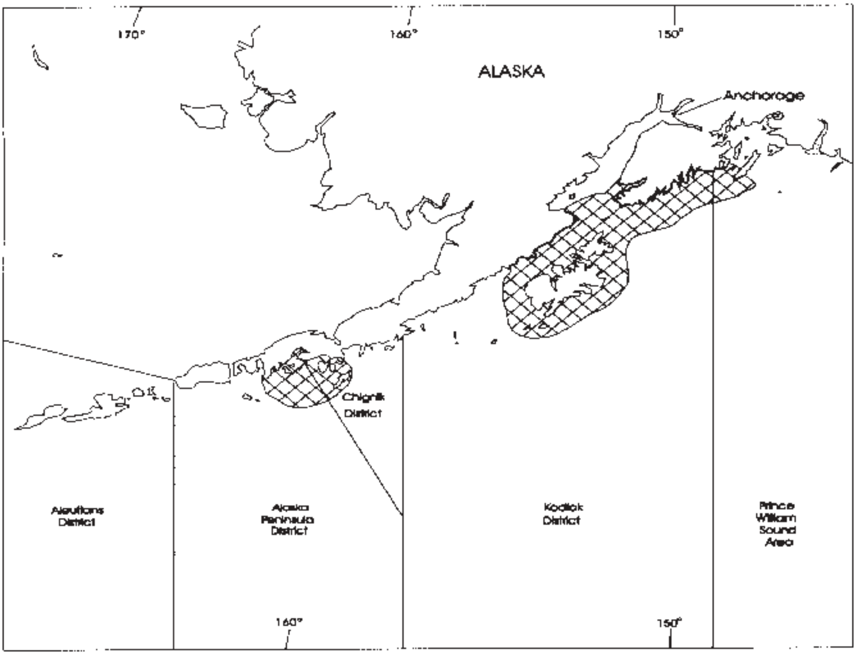


Figure 1. Location of major domestic shrimp fisheries (cross hatched) and districts within the western Gulf of Alaska. Sources: Davis 1982, Ingraham 1981.

cific and Atlantic coasts was reported by Bigg (1973) in his review of the literature on the food habits of young harbor seal pups. Carrick et al. (1962) and Bigg (1973) postulated that oestrus in female harbor seals is timed such that the weaning of pups will coincide with the local or regional shrimp spawning season, when these prey are concentrated and thus most available to pups. Pitcher (1980), in a study of harbor seals in the Gulf of Alaska, found that food items from 13 seal pups (<1 year old) included shrimps, capelin, Pacific tomcod, walleye pollock, and Pacific sand lance, with the predominant prey being small fishes. This sample, however, did not distinguish between newly weaned and older pups. The importance of crustaceans to pups of other seal species has also been documented: crustaceans (primarily shrimps, mysids, and amphipods) make up 98% of the diet of recently weaned ringed seal pups, *Phoca hispida* (Lowry and Frost 1981), and small crustaceans (euphausiids) are reported to be an indispensable food of newly weaned spotted seals, *Phoca largha*, a close relative of the harbor seal (Kato 1982).

Relatively slow-moving crustaceans such as shrimp represent an easy-to-catch food source for young pinniped pups, who need time and

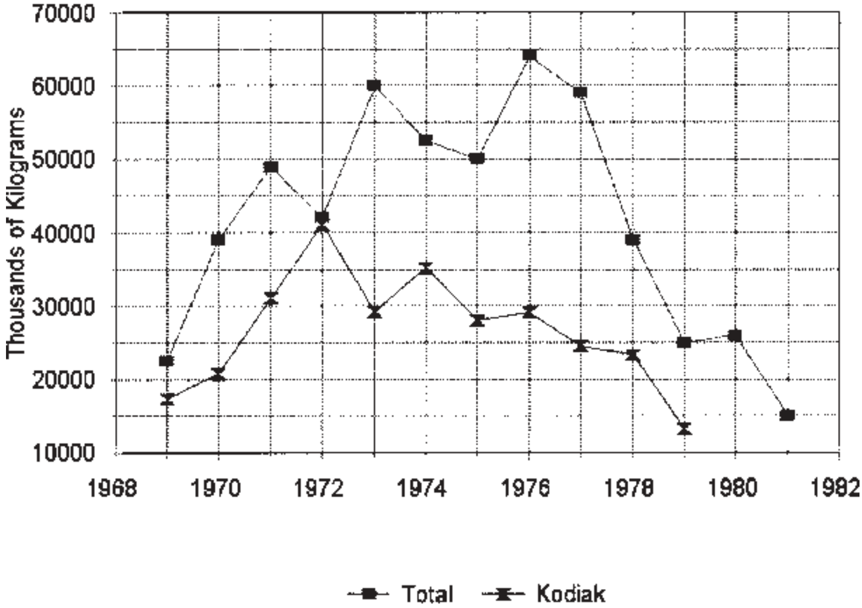


Figure 2. Total annual harvest of trawl shrimp from all areas in Alaska and from the Kodiak area, 1969-1981. Most of the Kodiak shrimp fisheries closed in 1979, while most other shrimp fisheries were closed by the early 1980s. Sources: Alaska Department of Fish and Game, Westward Region Shellfish Report, as cited by Anon. 1978; 32nd Annual Report of the Pacific Marine Fisheries Council, as cited by Davis 1982.

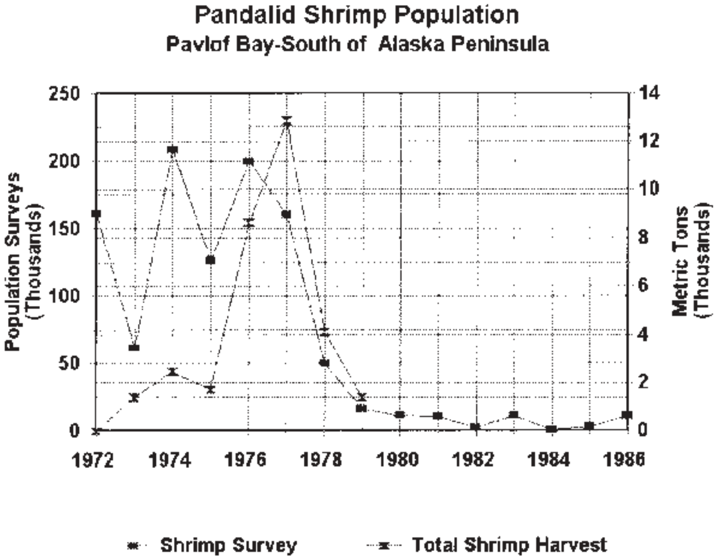


Figure 3. Average number of Pandalus borealis caught per tow 1982-1986 and commercial harvest from 1972 toclosure of fishery in 1979 (Anderson 1991, Jackson et al. 1983).

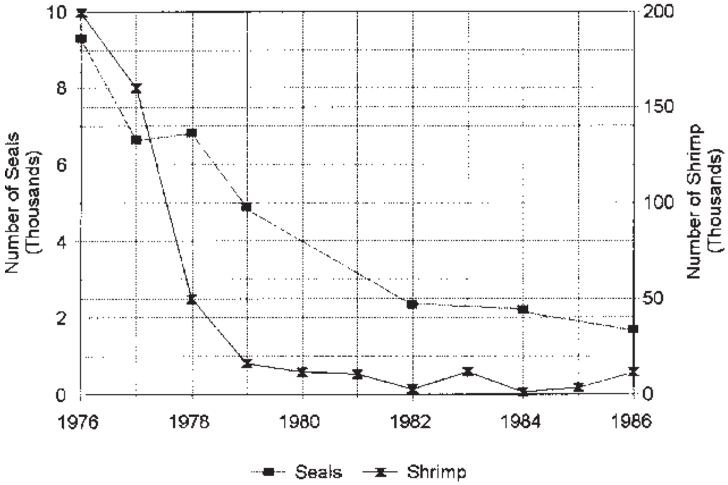


Figure 4. Maximum counts of harbor seals in the southwestern Tugidak Island hauling area during the molting period, 1976-1986, and the average number of Pandalus borealis caught per tow, 1976-1986 (Pitcher 1990, Anderson 1991).

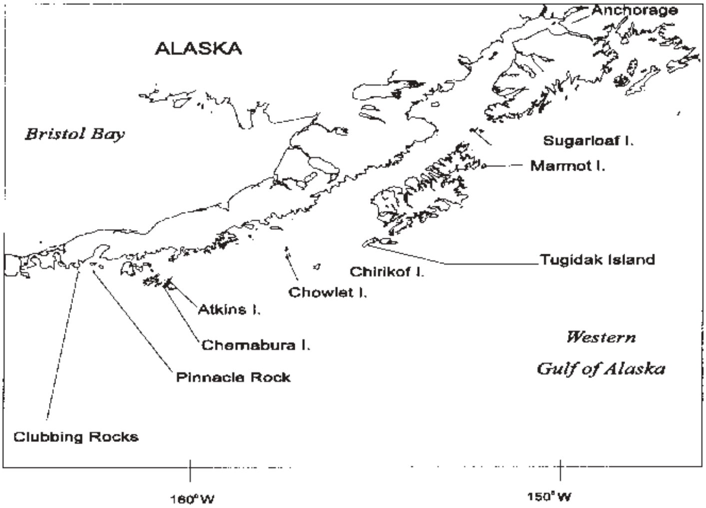


Figure 5. Location of the Pacific harbor seal rookery on Tugidak Island and of northern sea lion rookeries along the south side of the Alaska Peninsula and in the western Gulf of Alaska. Sources: Loughlin et al. 1992, Pitcher 1990.

practice to acquire the speed and agility to catch faster-moving prey such as finfishes. Unlike terrestrial mammalian predators that learn to hunt from their mothers, young pinnipeds are on their own after weaning and must rely on instinct and trial-and-error in learning to catch prey. The crash in the shrimp population in the western Gulf of Alaska may have resulted in the removal of a food source critical to newly weaned harbor seal pups, leading to starvation of most pups after 1976-1979 (Figure 4). Consequently, the continued decline of the harbor seal population in the western Gulf of Alaska may reflect the lack of recovery of the shrimp populations in this area.

Northern Sea Lion Decline

The overall population of the northern sea lion, *Eumetopias jubatus*, in the western Gulf of Alaska from the Kenai Peninsula to the central Aleutian Islands (Kiska Island) has been declining since the 1960s (Figure 6; Loughlin et al. 1990). However, sea lion counts at specific rookeries (local breeding populations) along the south side of the Alaska Peninsula (Figure 5) consistently declined sharply between 1976-1979 and 1985 (Figure 7), concurrent with the decline of the shrimp population in Pavlof Bay and along the south side of the Alaska Peninsula (Figure 3). In the eastern Aleutian Islands as well, the decline of the sea lion population and the crash of the commercial shrimp harvest occurred at the same time (Figure 8).

Although shrimp make up only a small portion of the diet of adult northern sea lions in the Gulf of Alaska—Calkins and Goodwin (1988) reported the frequency of dietary occurrence was 5.2% in the 1970s, declining to 2.7% in 1986 after the crash in the shrimp population—if they are an important or critical food source for newly weaned sea lion pups, as they appear to be for harbor seal and other pinniped pups, then the loss of shrimp to the food chain, or their greatly reduced availability, could be a contributing factor in the decline of the northern sea lion in the western Gulf of Alaska.

Decline in Capelin

The abundance of capelin, *Mallotus villosus*, in the western Gulf of Alaska declined in the 1980s, at approximately the same time as the shrimp populations (Figure 9; Anderson et al. 1996). Although the bycatch from shrimp trawls was generally low during the 1970s, forage fish such as capelin and walleye pollock were incidentally caught in shrimp nets more frequently during the late 1970s and early 1980s than during the early development of the fishery (Davis 1982; pers. comm., Anderson, Alaska Fisheries Science Center, NOAA, Kodiak, AK, Mar. 1996).

Capelin was reported to be an important or primary food source of both harbor seals and northern sea lions in the Kodiak area (Pitcher and Calkins 1979; Pitcher 1980, 1981; Calkins and Goodwin 1988). In particular, capelin was reported to be a primary forage fish of harbor seal pups aged 2.5-11 months, comprising 35.7% of their diet, compared to 9.2% for other age classes (Pitcher and Calkins 1979). Feeding capelin contain over 20% fat (Ashwell-Erickson and Elsner 1981). High-lipid foods such as herring and capelin may be particularly important for growing seal and sea lion pups that need to increase blubber reserves for insulation as their bodies grow. Pollock also occurs frequently in the diets of Gulf of Alaska harbor seals and sea lions—the frequency is 20% and 70%, respectively (Pitcher 1980, Calkins and Goodwin 1988)—but this prey item has a low fat content (0.8%) and probably represents a lower caloric-value food source than herring or capelin (Ashwell-Erickson and Elsner 1981).

Assuming that capelin is an important prey for harbor seals and sea lions, if this prey item is in short supply, then seal and sea lion pups and juveniles may be unable to compete successfully with other predators such as seabirds, whales, and large fish for this food source. Thus, the decline in the capelin population in the western Gulf of Alaska may also contribute to pinniped declines by decreasing the availability of a lipid-rich food source to young harbor seals and sea lions.

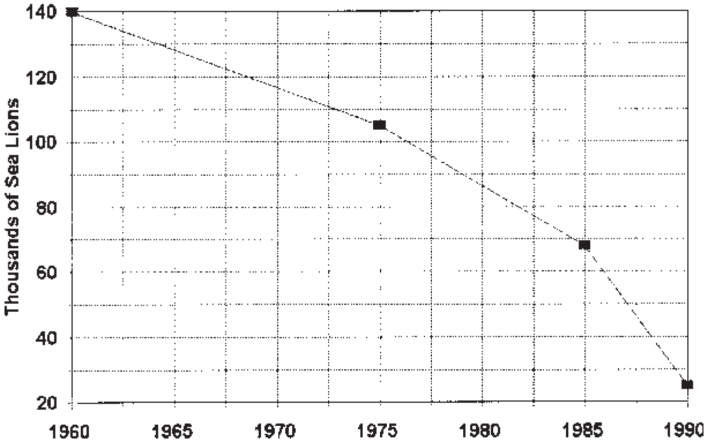


Figure 6. Overall trend in northern sea lion abundance from the Kenai Peninsula to Kiska Island of the western Aleutian Islands, 1960-1990. Source: Loughlin et al. 1990.

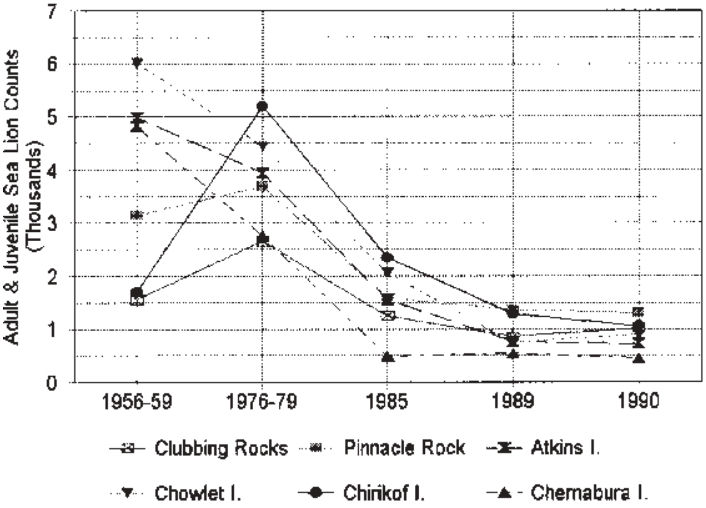


Figure 7. Counts of adult and juvenile northern sea lions in rookeries on the south side of the Alaska Peninsula for selected surveys from spring and summer, 1956-1990. Sources: Merrick et al. 1987, 1991.

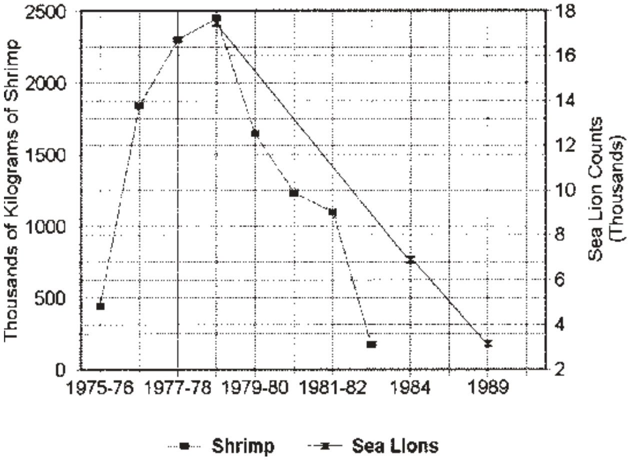


Figure 8. Total count of adult and juvenile sea lions from 1978 to 1989 and kilograms of shrimp harvested annually from 1975 to 1982 in the eastern Aleutian Islands. Sources: Merrick et al. 1987, Jackson et al. 1983.

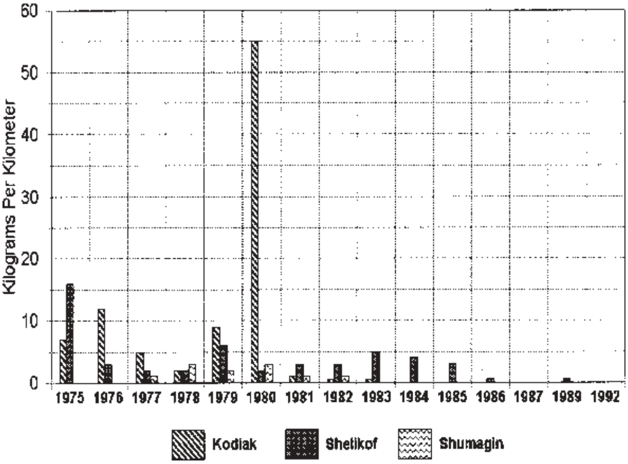


Figure 9. Capelin abundance from small-mesh trawl surveys expressed as kilograms per kilometer towed. Capelin abundance is shown for three regions: Kodiak Island, Shelikof Strait, and Shumagin Islands (Pers. comm., Anderson, Alaska Fisheries Science Center, NOAA, Kodiak, AK, Mar. 1996).

Conclusion

The crash in the shrimp populations in the western Gulf of Alaska between 1976 and 1981 and their lack of recovery may have been the result of over-harvest by the commercial shrimp fisheries and/or a natural population cycle. The decline in the availability of easy-to-catch shrimp to harbor seal and sea lion pups may have contributed to the concurrent decline in the area of both pinniped populations. Newly weaned pups, in the absence of easy-to-catch prey, may not be able to acquire sufficient food energy to sustain them long enough to learn and develop the skills and coordination needed to catch faster-moving finfishes. The decline in capelin, a high-lipid forage fish, which occurred at about the same time, may have reduced the ability of the pups to maintain or increase fat reserves for thermal insulation and growth. Thus, harbor seal and sea lion pups may be starving after they leave the rookeries.

References

Anon. 1978. Working paper number three. Past development of northern and western Gulf of Alaska fisheries. U.S. Department of Interior. Contract No. AA550-CT6-61, Task No. 9AF/BF. Information on Alaska shrimp fishery, vol. 1, pp. 260-291; vol. 2, pp. 407-418.

Anderson, P.J. 1991. Age, growth, and mortality of the northern shrimp *Pandalus borealis* Kroyer in Pavlof Bay, Alaska. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 89:541-553.

Anderson, P.J., and F. Gaffney. 1977. Shrimp of the Gulf of Alaska. Alaska Seas and Coasts 5(3):1-3.

Anderson, P.J., J.B. Blackburn, W.R. Bechtol, and B.A. Johnson. 1996. Synthesis and analysis of small-mesh trawl data 1953 to 1995. Draft report prepared for *Exxon Valdez* Oil Spill Restoration Trustees under auspices of the APEX Project 96163L. March 22, 1996, 40 pp.

Ashwell-Erickson, S., and R. Elsner. 1981. Energy cost of free existence for Bering Sea harbor seals and spotted seals. In: D.W. Hood and J.A. Calder (eds.), Eastern Bering Sea shelf: oceanography and resources. University of Washington Press, Seattle, WA, vol. 2, pp. 869-899.

Bigg, M.A. 1973. Adaptations in the breeding of the harbour seal, *Phoca vitulina*. J. Reprod. Fertil., Suppl. 19:131-142.

Calkins, D., and E. Goodwin. 1988. Investigation of the declining sea lion population in the Gulf of Alaska. Unpublished report, Alaska Department of Fish and Game, Anchorage, AK.

Carrick R., S.E. Csordas, S.E. Ingram, and K. Keith. 1962. Studies of the southern elephant seal, *Mirounga leonina* (L.) III. The annual cycle in relation to age and sex. Commonwealth Scientific and Industrial Research Organization (CSIRO) Wildl. Res. 7(2):119-160.

Davis, A.S. 1982. Commercial otter trawl shrimp fishery of Cook Inlet. Alaska Department of Fish and Game Information Leaflet 205, 52 pp.

Ingraham, W.J., Jr. 1981. Environment of pink shrimp in the western Gulf of Alaska. In: T. Frady (ed.), Proceedings of the International Pandalid Shrimp Symposium, February 13-15, 1979, Kodiak, AK. Sea Grant Report 81-3, University of Alaska, Fairbanks, AK.

Jackson, P.B., L.J. Watson, and J.A. McCrary. 1983. The westward region shrimp fishery and shrimp research program, 1968-1981. Alaska Department of Fish and Game Information Leaflet 216, 47 pp.

Kato, H. 1982. Food habits of largha seal pups in the pack ice area. Sci. Rep. Whales Res. Inst. Tokyo 34:123-136.

Loughlin, T.R., A.S. Perlov, and V.A. Vladimirov. 1990. Survey of northern sea lions *Eumetopias jubatus* in the Gulf of Alaska and Aleutian Islands during June 1989. National Marine Fisheries Service, Alaska Fisheries Science Center, National Marine Mammal Lab, Seattle, WA, 30 pp.

Loughlin, T.R., A.S. Perlov, and V.A. Vladimirov. 1992. Range-wide survey and estimation of Steller sea lions in 1989. Mar. Mammal Sci. 8(3):220-239.

Lowry, L.F., and K.J. Frost. 1981. Feeding and trophic relationships of phocid seals and walruses in the eastern Bering Sea. In: D.W. Hood and J.A. Calder (eds.), Eastern Bering Sea shelf: Oceanography and resources. University of Washington Press, Seattle, WA, vol. 2, pp. 813-824.

Merrick, R.L., T.R. Loughlin, and D.G. Calkins. 1987. Decline in abundance of the northern sea lion, *Eumetopias jubatus,* in Alaska, 1956-86. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 85(2):351-365.

Merrick, R.L., P. Gearin, S. Osmek, and D. Withrow. 1988. Field studies of the northern sea lions at Ugamak Island, Alaska during the 1985 and 1986 breeding seasons. NOAA Tech. Memo. NMFS F/NWC-143, 60 pp.

Merrick, R.L., L.M. Ferm, R.D. Everitt, R.R. Ream, and L.A. Lessard. 1991. Aerial and ship-based surveys of the northern sea lions (*Eumetopias jubatus*) in the Gulf of Alaska and Aleutian Islands during June and July 1990. NOAA Tech. Memo. F/NMFC-196, 34 pp.

Pitcher, K.W. 1980. Food of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 78(2):544-549.

Pitcher, K.W. 1981. Prey of the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 79(3):467-472.

Pitcher, K.W. 1990. Major decline in number of harbor seals, *Phoca vitulina richardsi*, on Tugidak Island, Gulf of Alaska. Mar. Mammal Sci. 6(2):121-134.

Pitcher, K.W., and D.G. Calkins. 1979. Biology of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska. Final Report, Research Unit 229, Contract 03-5-002-69, OCSEAP, U.S. Dept. Interior, Bureau of Land Management, 72 pp.

Sease, J.L. 1992. Status review: Harbor seals (*Phoca vitulina*) in Alaska. Alaska Fisheries Science Center Processed Report 92-15. National Marine Fisheries Service, Alaska Fisheries Science Center, National Marine Mammal Lab, Seattle, WA, 74 pp.

York, A.E. 1994. Population dynamics of northern sea lions, 1975-1985. Mar. Mammal Sci. 10(1):38-51.

Role of Fishes in Predator Diets of the Pacific Slope of the Northern Kuril Islands and Southeastern Kamchatka

Alexei M. Orlov
Federal Research Institute of Fisheries and Oceanography (VNIRO), Moscow, Russia

Abstract

The most abundant predatory fishes of the Pacific slope of the northern Kuril Islands are three pleuronectids: Kamchatka flounder (*Atheresthes evermanni*), Greenland halibut (*Reinhardtius hippoglossoides matsuurae*), and Pacific halibut (*Hippoglossus stenolepis*). Data on the diets of these species were collected during 1992-1996. In all, 1,441 stomachs of Kamchatka flounder, 1,283 stomachs of Greenland halibut, and 600 stomachs of Pacific halibut were analyzed. The species composition of the stomach contents was determined for 752, 411, and 468 stomachs, respectively. Forage fishes were frequently observed in stomachs of Greenland halibut (31.5%), which feed mainly on Commander squid, *Berryteuthis magister*. The frequency of forage fishes in stomachs of Kamchatka flounder was somewhat higher (36.8%). Pacific halibut, which feed mainly on cephalopods and macrobenthos, had the lowest frequency of forage fishes (25.4%). Greenland halibut had the most narrow range of fish in the diet. It included species of nine families, of which liparids and mesopelagic myctophids and microstomatids were most frequent. Kamchatka flounder fed mainly on sculpins, liparids, and myctophids. Pacific halibut fed most often on gadids (mainly pollock) and sculpins. All three predators ate walleye pollock, *Theragra chalcogramma* (Gadidae); *Elassodiscus* sp. (Liparidae); *Triglops* sp. (Cottidae); and the fathead sculpin *Malacocottus zonurus* (Psychrolutidae). The diets of all three predators differed according to size and sex, season, time of day, and depth of trawl.

Introduction

Predatory fishes of the continental slope in the Pacific Ocean off the northern Kuril Islands and southeastern Kamchatka are represented by Greenland halibut, *Reinhardtius hippoglossoides matsuurae*; Kamchatka flounder, *Atheresthes evermanni*; Pacific halibut, *Hippoglossus stenolepis*; sablefish, *Anoplopoma fimbria*; large rockfishes, *Sebastes borealis* and *Sebastes aleutianus*; liparid fishes of the genus *Liparis* and *Polypera simushirae*; sculpins of the genus *Myoxocephalus*; and the large skates *Bathyraja parmifera, B. aleutica, B. maculata*, and *B. matsubarai*; as well as Pacific cod, *Gadus macrocephalus*, migrating to the area periodically from shelf waters. Of all these fishes, the most abundant species are the three predatory pleuronectids. There is no specialized fishery on them in the region under consideration and they are caught there only as bycatch during bottom trawling (Dudnik et al. 1995). The biology of these species in Pacific continental shelf and slope waters off the northern Kuril Islands and southeastern Kamchatka is not well known. This is particularly true for diet. The one paper (Novikov 1974) giving data on the qualitative composition of their diet in the area is based on a very limited sample (187 stomachs of Greenland halibut, 75 stomachs of Kamchatka flounder, and 48 stomachs of Pacific halibut containing food). The main purpose of this paper is to provide a qualitative description of the diets of these three pleuronectids, including the importance of fish in their diets, and to analyze differences related to sex and size of the predators, depth of trawling, season, and period of day.

Materials and Methods

This paper is based on stomach content data from Greenland halibut, Kamchatka flounder, and Pacific halibut collected during cruises of Japanese trawlers (*Tomi Maru 53, Tomi Maru 82*, and *Tora Maru 58*) by specialists of VNIRO, SakhNIRO, KamchatNIRO, Zoological Institute of Russian Academy of Sciences (ZIN RAN), and Institute of Marine Biology of the Far East Branch of the Russian Academy of Sciences (IBM DVO RAN), during 1992-1996. Samples for analysis were taken from catches by bottom trawl with a soft ground rope, vertical opening of about 5 m, and horizontal opening of about 25 m. The investigations were carried out from May to December each year from 1992 to 1996. Trawling was conducted throughout the day. The area of research was located on the Pacific side of the northern Kuril Islands and southeastern Kamchatka (47°30′52°N) in a depth range of 100-900 m. To analyze stomach contents we used methods described by Lishev (1950) and Fortunatova (1951), as well as the *Manual for the Study of Fish Feeding Under Natural Conditions* (1961). Stomach contents were analyzed at sea. Consequently, all small food items (e.g., coelenterates, annelid worms, small crustaceans) were identified to the level of type, class, or order, while large crustaceans and fishes (depending on degree of their digestion in stomachs) were mainly identified to species. In all, during the period of investigation 1,441 stomachs of Greenland halibut, 1,283 of Kamchatka flounder, and 600 of Pacific halibut were analyzed. Food items were found in 752, 411, and 468 of these stomachs, respectively. Statistical treatment of the data was conducted with a special computer program written by VNIRO specialist Anatoly Gruzevich.

Results

General description of diet

The qualitative analysis of stomach contents of Greenland halibut, Kamchatka flounder, and Pacific halibut showed that all three species have broad diets which include lower invertebrates (sponges, coelenterates) which are occasionally eaten, and crustaceans, mollusks, and fishes which are the main components of the diet (Table 1).

The predominant food in the diet of Greenland halibut (frequency of occurrence [FO] = 47.79%) in the study area was mollusks, mainly Commander squid. Crustaceans were not important in the diet, and were consumed mainly by juveniles. Fish were second in FO (31.5%) and were represented by nine species. Liparids, myctophids, and microstomatids were found the most frequently in Greenland halibut stomachs.

Kamchatka flounder had the highest FO of fish (36.8%), represented by species from 10 families. The most common species were myctophids, liparids, and sculpins. Mollusks (mainly Commander squid) and crustaceans (mainly shrimps) were found in Kamchatka flounder stomachs at almost the same frequency (16.6% and 17.9%, respectively).

The greatest difference in the Pacific halibut diet was the high proportion of decapods (mostly pagurids and majids). Mollusks also had a high FO in stomachs. Squids and octopuses had almost the same FOs. Fish were in third place (25.4%) after mollusks and crustaceans. The range of fishes consumed by Pacific halibut was the widest and included species from 11 families. Gadids (mainly pollock) and sculpins were most frequent in occurrence.

The diets of all three predators differed depending on size and sex, season, time of day, and depth of trawl.

Differences by sex

Analysis of stomach contents showed some differences between males and females. Thus, the total FO of fishes in stomachs of Greenland halibut was 36.6% for females and 29.5% for males. The difference in FO of fish in stomachs of male and female Kamchatka flounder was insignificant; there were differences between the sexes in consumption of mollusks (21.1% for females and 15.3% for males) and crustaceans (13.9% and 17.9%, respectively). There were no significant differences in consumption of main food items between male and female Pacific halibut.

Table 1. Frequency of occurrence (%) of food items in the stomachs of predators collected in the Pacific Ocean off the northern Kuril Islands and southeastern Kamchatka in 1992-1996.

Food item	Greenland halibut	Kamchatka flounder	Pacific halibut
Porifera	—	0.78	—
Coelenterata	—	0.26	0.19
Hydrozoa	—	—	0.19
Actinaria	—	0.26	—
Annelida	0.13	0.52	1.31
Polychaeta	0.13	0.52	0.19
Oligochaeta	—	—	0.19
Echiurida	—	—	0.93
Crustacea	2.40	17.88	27.23
Mysidacea	—	0.26	—
Euphausiacea	0.80	1.04	—
Isopoda	—	—	1.85
Amphipoda	1.20	0.52	1.67
Decapoda	0.40	16.06	23.71
Pandalidae	0.27	14.25	2.78
Crangonidae	—	1.55	0.74
Paguridae	—	0.26	7.04
Lithodidae	0.13	—	2.41
Majidae	—	—	10.74
Chionoecetes opilio	—	—	7.22
Chionoecetes sp.	—	—	3.33
Hyas coarctatus	—	—	0.19
Unidentified crustaceans	0.40	1.04	—
Mollusca	47.79	16.58	30.20
Gastropoda	0.13	—	0.93
Nudibranchia	—	0.26	—
Cephalopoda	47.66	16.32	28.89
Teuthida	46.20	15.54	14.08
Berryteuthis magister	46.07	15.54	13.89
Unidentified squids	0.13	—	0.19
Octopoda (adults)	1.33	0.78	14.81
Octopoda (eggs)	0.13	—	—
Unidentified mollusks	—	0.52	0.38
Osteichthyes	31.54	36.82	25.42
Salmonidae	—	—	0.37
Oncorhynchus sp.	—	—	0.37
Osmeridae	—	—	0.19
Mallotus villosus	—	—	0.19
Microstomatidae	3.33	0.26	—
Leuroglossus schmidti	2.40	0.26	—
Bathylagus pacificus	0.13	—	—
Microstomatidae g. sp.	0.80	—	—

Table 1. Con't.

Food item	Greenland halibut	Kamchatka flounder	Pacific halibut
Myctophidae	2.66	4.66	0.74
Stenobrachius leucopsarus	0.13	—	—
S. nannochir	—	0.26	—
Lampanyctus jordani	0.13	—	—
Myctophidae g. sp.	2.40	4.40	0.74
Gadidae	0.53	1.81	7.60
Theragra chalcogramma	0.53	1.81	7.04
Gadus macrocephalus	—	—	0.56
Macrouridae	1.33	1.82	—
Albatrossia pectoralis	—	0.52	—
Coryphaenoides cinereus	0.40	0.78	—
Macrouridae g. sp.	0.93	0.52	—
Stichaeidae	—	—	0.56
Bryozoichthys lysimus	—	—	0.56
Zoarcidae	—	0.78	—
Lycenchelys sp.	—	0.78	—
Scorpaenidae	0.26	0.26	—
Sebastolobus macrochir	0.13	—	—
Sebastes sp.	0.13	0.26	—
Hexagrammidae	—	0.52	0.56
Pleurogrammus monopterygius	—	0.52	0.56
Cottidae	0.26	3.63	2.04
Triglops forficata	—	—	0.19
Triglops sp.	0.13	2.07	1.85
Icelus sp.	0.13	1.04	—
Artediellichthys nigripinnis	—	0.52	—
Psychrolutidae	0.27	2.07	0.56
Malacocottus zonurus	0.27	2.07	0.56
Agonidae	0.40	—	0.75
Aspidophoroides bartoni	—	—	0.19
Sarritor frenatus	—	—	0.56
Agonidae g. sp.	0.40	—	—
Liparidae	4.92	4.41	1.12
Allocareproctus jordani	—	—	0.19
Careproctus cypselurus	0.13	—	—
Careproctus sp.	—	0.26	—
Elassodiscus tremebundus	0.40	0.78	—
Elassodiscus obscurus	0.13	—	—
Elassodiscus sp.	0.53	0.52	0.19
Paraliparis grandis	0.27	—	—
Paraliparis sp.	0.13	—	—
Liparidae g. sp.	3.33	2.85	0.74
Pleuronectidae	—	—	0.37
Pleuronectes bilineatus	—	—	0.37
Unidentified Osteichthyes	18.11	16.06	10.56
Unidentified organic materials	17.04	26.17	15.74

We found some differences between males and females in fish species composition of diet characterized by presence of larger fish species in their stomachs (Table 2). Greenland halibut males ate mainly microstomatids and small sculpins, while liparids were observed more frequently in stomachs of females. Moreover, we found gadids, grenadiers (Macrouridae), and rockfishes in stomachs of females but these fishes were not noted in stomachs of males. While the FO of liparids and sculpins in stomachs of both males and female Kamchatka flounder was almost equal, males ate mainly myctophids and females more frequently consumed gadids, grenadiers, rockfishes, and Atka mackerel (*Pleurogrammus monopterygius*).

Size differences

To distinguish differences in diet with body length we identified the following size groups: for Greenland halibut, <50 cm, 51-70 cm, and >70 cm; for Kamchatka flounder, <40 cm, 41-60 cm, >60 cm; and for Pacific halibut, <60 cm, 61-90 cm, >90 cm.

For Greenland halibut of the smallest sizes the proportion of crustaceans in the diet (mainly amphipods) was the highest. With increase in size, the proportion decreased. Mollusks (mainly Commander squid) were the most important in the diet of fishes of 51-70 cm. This size group was also characterized by the minimum FO of fishes (28.5%), while fishes predominated in the diet of Greenland halibut >70 cm (41.4%).

Kamchatka flounder <40 cm ate mainly crustaceans (shrimps of the families Pandalidae and Crangonidae), and the FOs of mollusks and fishes were low. With increase in size the FO of crustaceans in stomachs decreased, while the FO of mollusks and fishes increased and reached the maximum for the largest individuals (>60 cm): 27.4% and 48.8%, respectively.

A somewhat different situation was characteristic of Pacific halibut. As in the other two predator species, crustaceans played the most important role in feeding of the smallest individuals. The FO of mollusks in stomachs increased from small to large individuals. However, the importance of squids decreased with increased size while that of octopuses increased. We found that fishes were consumed mainly by small Pacific halibut (31.9%).

With increase in size there were some differences in the fish species composition of the diet for all three predators. As a whole, the importance of small species decreased and that of larger species increased (Table 3). From juveniles to adults of Greenland halibut and Kamchatka flounder the proportion of myctophids and microstomatids in the diet decreased, while that of pollock, grenadiers, Atka mackerel, and liparids, on the contrary, increased.

Table 2. Frequency of occurrence (%) by sex of prey fish in stomachs of predators collected from the Pacific Ocean off the northern Kuril Islands and southeastern Kamchatka.

	Male			Female		
Prey fish	1	2	3	1	2	3
Salmonidae	—	—	0.56	—	—	—
Osmeridae	—	—	0.56	—	—	—
Microstomatidae	4.79	0.53	—	1.30	—	—
Myctophidae	1.83	8.95	1.13	3.92	0.55	0.88
Gadidae	—	1.05	7.91	1.31	2.78	7.46
Macrouridae	—	—	—	3.27	3.33	—
Stichaeidae	—	—	—	—	—	1.32
Zoarcidae	—	1.05	—	—	0.55	—
Scorpaenidae	—	—	—	0.66	0.55	—
Hexagrammidae	—	—	0.56	—	1.11	—
Cottidae	0.46	3.15	1.13	—	3.89	3.51
Psychrolutidae	—	1.58	0.56	0.65	2.78	0.88
Agonidae	—	—	1.13	0.98	—	0.88
Liparidae	3.20	4.74	1.69	7.53	4.44	0.88
Pleuronectidae	—	—	—	—	—	0.44
Unidentified fish species	19.18	15.26	11.30	16.99	18.33	12.28
Total stomachs with food	447	303	187	211	164	163

1 = Greenland halibut, 2 = Kamchatka flounder, 3 = Pacific halibut.

Table 3. **Frequency of occurence (%) by size group of prey fish in stomachs of predators collected from the Pacific Ocean off the northern Kuril Islands and southeastern Kamchatka.**

	Greenland halibut			Kamchatka flounder			Pacific halibut		
	<50 cm	51-70 cm	>70 cm	<40 cm	41-60 cm	>60 cm	<60 cm	61-90 cm	>90 cm
Salmonidae	—	—	—	—	—	—	0.46	—	—
Osmeridae	—	—	—	—	—	—	0.46	—	—
Microstomatidae	4.44	3.49	—	—	0.42	—	—	—	—
Myctophidae	3.70	2.71	1.01	—	7.56	—	1.85	—	—
Gadidae	—	—	4.04	—	2.10	2.38	6.94	7.14	11.43
Macrouridae	—	0.77	6.06	1.61	0.42	5.95	—	—	—
Stichaeidae	—	—	—	—	—	—	1.39	—	—
Zoarcidae	—	—	—	—	1.26	—	—	—	—
Scorpaenidae	—	—	2.02	—	—	1.19	—	—	—
Hexagrammidae	—	—	—	—	0.42	1.19	—	0.65	—
Cottidae	0.74	0.19	—	3.22	3.36	4.76	2.78	2.60	—
Psychrolutidae	—	—	2.02	—	2.10	3.57	1.39	—	—
Agonidae	0.74	0.19	1.01	—	—	—	0.92	1.30	—
Liparidae	0.74	3.89	14.14	—	4.20	8.33	1.85	—	2.86
Pleuronectidae	—	—	—	—	—	—	—	0.65	—
Unidentified fish species	23.70	17.28	15.15	3.22	17.23	21.43	14.81	7.14	8.57
Total stomachs with food	123	496	92	66	256	89	245	184	39

With increase in size of Pacific halibut, small species such as capelin, myctophids, stichaeids, sculpins, and poachers (Agonidae) disappeared from their diet, while the FO of pollock increased.

Seasonal differences

Seasonal differences in the diet of all three predator species resulted from changes in physiological state during the year. Seasonality in the diet of Greenland halibut was not pronounced: FOs of mollusks and fishes varied insignificantly (Figure 1A). They ate fish more frequently in summer, at which time the FO of grenadiers in the stomachs was rather high. In all seasons myctophids and microstomatids, as well as liparids, were important in the diet of Greenland halibut.

The most pronounced seasonal changes in diet were characteristic of Kamchatka flounder. In summer the FO of crustaceans (mainly shrimps) in their diet was very high. The FO of mollusks in stomachs did not change much during the year. Kamchatka flounder consumed fish most frequently in spring, when myctophids and sculpins predominated in its diet (Figure 1B); in summer liparids, and in autumn sculpins, liparids, and pollock were more important.

Seasonal differences in diet were also observed for Pacific halibut. The FO of crustaceans in stomachs was highest in spring and gradually decreased toward winter. During spring-autumn mollusks were consumed at almost the same frequency. In winter they (mainly octopuses) predominated in the diet of Pacific halibut (Figure 1C). The maximum FO of fishes was recorded in summer and autumn. In all seasons gadids (mainly pollock), and also sculpins in summer, predominated in the diet of Pacific halibut.

Feeding by Greenland halibut decreased in intensity from spring to summer (Figure 2) and increased toward autumn. This pattern was also characteristic of Kamchatka flounder. In contrast, Pacific halibut fed most intensively during summer and autumn.

Diurnal differences

The diet of Greenland halibut in the evening was markedly different from the daytime. In the evening the FO of mollusks was highest while that of fish was minimal (Figure 3A). Myctophids and microstomatids were the most frequently encountered fish in stomachs. The greatest consumption of fish was observed in the night and the morning, when FOs of liparids, myctophids, and microstomatids were the highest. During the night the diet consisted mainly of liparids and grenadiers.

Feeding by Kamchatka flounder was also characterized by clear diurnal changes. The maximum FO of crustaceans was recorded in the evening. During the rest of the day its value varied slightly. The FO of mollusks in stomachs decreased gradually from morning to night. Consumption of fish was approximately on the same level throughout the

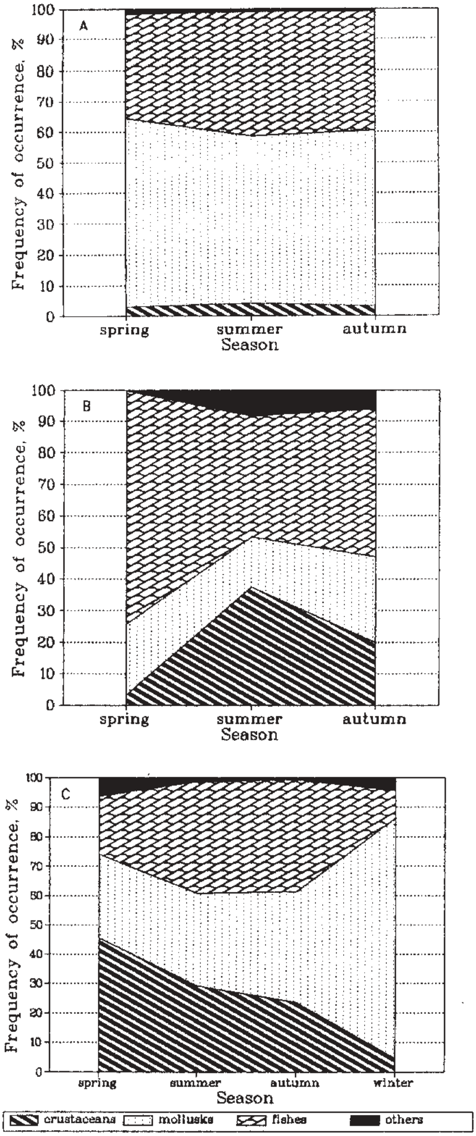


Figure 1. Seasonal differences in diet of Greenland halibut (A), Kamchatka flounder (B), and Pacific halibut (C) in the Pacific Ocean off the northern Kuril Islands and southeastern Kamchatka.

Total number of stomachs with food:

	Spring	*Summer*	*Autumn*	*Winter*
A	*83*	*146*	*523*	*—*
B	*40*	*169*	*202*	*—*
C	*160*	*112*	*175*	*21*

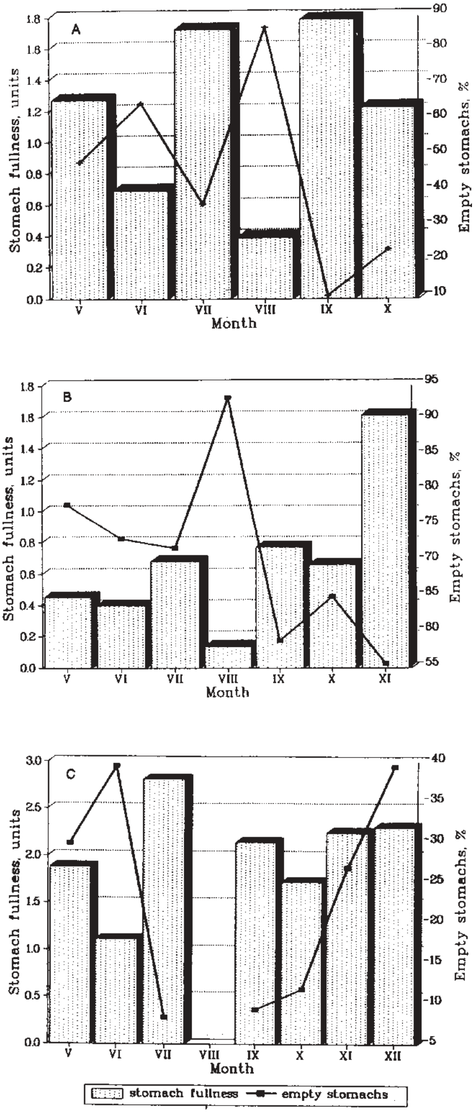


Figure 2. Monthly feeding intensity of Greenland halibut (A), Kamchatka flounder (B), and Pacific halibut (C) in the Pacific Ocean off the northern Kuril Islands and southeastern Kamchatka.
Number of stomachs opened:

	A	*B*	*C*		*A*	*B*	*C*
May	*162*	*183*	*223*	*Jun*	*247*	*361*	*123*
Jul	*57*	*208*	*36*	*Aug*	*190*	*194*	*—*
Sep	*351*	*261*	*76*	*Oct*	*276*	*216*	*68*
Nov	*—*	*18*	*41*	*Dec*	*—*	*—*	*33*

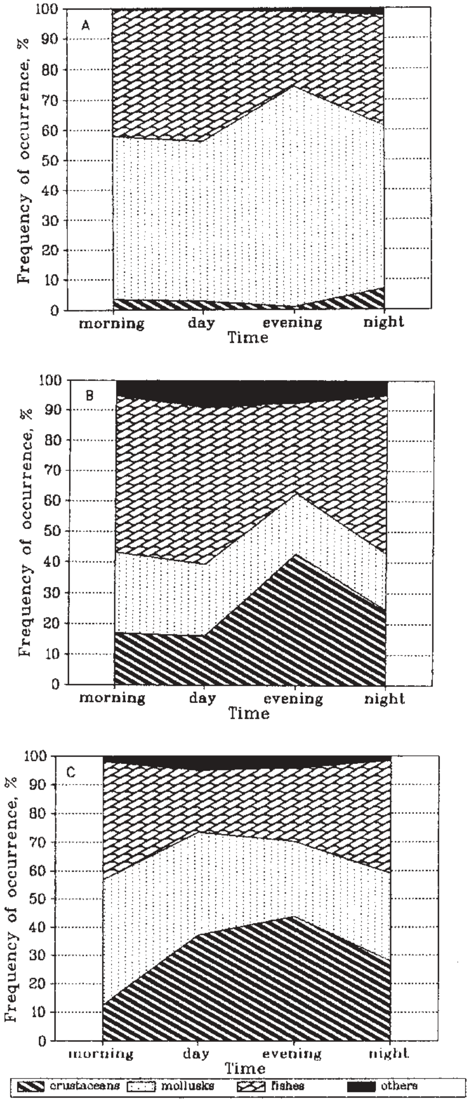


Figure 3. Diurnal changes in diet of Greenland halibut (A), Kamchatka flounder (B), and Pacific halibut (C) in the Pacific Ocean off the northern Kuril Islands and southeastern Kamchatka.

Total number of stomachs with food:

	Morning	*Day*	*Evening*	*Night*
A	*298*	*223*	*120*	*111*
B	*107*	*123*	*99*	*82*
C	*113*	*197*	*100*	*58*

day, except for evening hours when it was reduced by a factor of 2 (Figure 3B). At that time fish in the diet consisted mainly of sculpins. Myctophids and liparids occurred in stomachs in the morning, myctophids and sculpins during the day, and liparids during the night.

Pacific halibut ate crustaceans mainly in the evening hours (Figure 3C), while the maximum FO of mollusks in stomachs was noted in the morning. Morning was also characterized by the maximum consumption of fish, mainly pollock, sculpins, and salmon. The FO of fish gradually increased from daytime (lowest FO) to morning. Throughout the day pollock predominated in the fish portion of the diet of Pacific halibut. At night an increase in the FO of sculpins was also noted.

Analyzing diurnal changes in the diets of the species under consideration, one may note a clear decrease in feeding intensity for Greenland halibut from morning to night (Figure 4). Feeding of Kamchatka flounder was characterized by two peaks in decreasing feeding intensity (about 0900 and 2100 hours). The maximum unit of stomach fullness and the minimum number of empty stomachs were recorded at about 1800 hours. We observed two peaks of increased feeding intensity of Pacific halibut (about 0900 and 2100) when stomachs were fullest and the number of feeding individuals was lowest.

Depth differences

At depths less than 200 m gadids predominated in the diets of all three predators, and high FOs of sculpins and liparids were recorded for Kamchatka flounder and Pacific halibut (Table 4).

At a depth range of 200-399 m myctophids predominated in the diets of Greenland halibut and Kamchatka flounder, while, as at the shallower depths, pollock predominated in the Pacific halibut diet. We also observed high FOs of sculpins in stomachs of Kamchatka flounder.

At depths of 400-599 m liparids predominated in stomachs of all three predator species. At the same time, the importance of microstomatids in the diets of Greenland halibut and Kamchatka flounder, particularly Greenland halibut, increased. Grenadiers and rockfishes were also important in the diets of these two species.

At depths greater than 600 m liparids and grenadiers predominated in the stomachs of Greenland halibut and Kamchatka flounder. Microstomatids were also an important food for Greenland halibut feeding at these depths.

Discussion

Of the three species under consideration, the diet of the Pacific halibut was previously the most well known. Most data are from the Bering Sea and northeast Pacific (Gordeeva 1954; Novikov 1964, 1974; Fadeev 1971, 1984; International Pacific Halibut Commission [IPHC] 1978, 1987; Best and St.-Pierre 1986), where Pacific halibut are most abundant. In

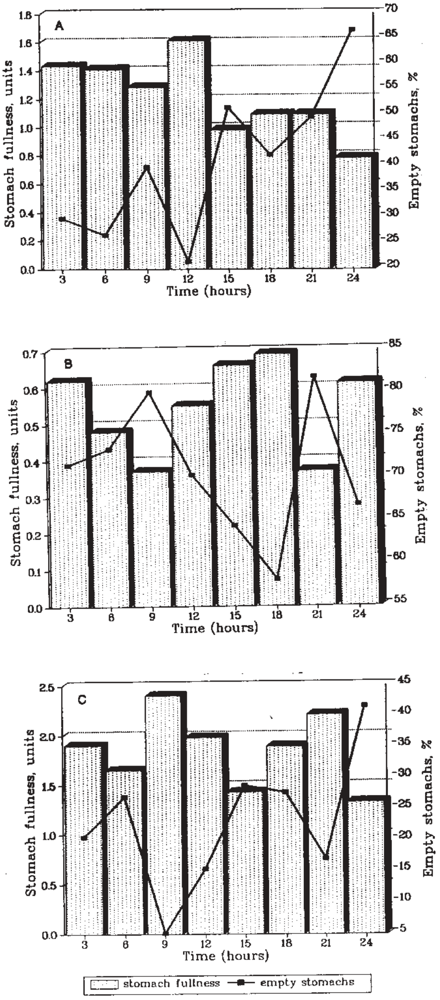


Figure 4. Diurnal changes in feeding intensity of Greenland halibut (A), Kamchatka flounder (B), and Pacific halibut (C) in the Pacific Ocean off the northern Kuril Islands and southeastern Kamchatka.

Number of stomachs opened:

Time	*A*	*B*	*C*
0000-0300	*63*	*196*	*30*
0300-0600	*99*	*103*	*49*
0600-0900	*252*	*250*	*80*
0900-1200	*153*	*194*	*46*
1200-1500	*200*	*154*	*187*
1500-1800	*227*	*162*	*81*
1800-2100	*178*	*190*	*102*
2100-2400	*111*	*192*	*25*

Table 4. Frequency of occurrence (%) by depth of prey fish in the stomachs of predators collected from the Pacific Ocean off the north Kuril Islands and southeastern Kamchatka.

	Depth										
	<200 m			200-399 m			400-599 m			>600 m	
Prey fish	1	2	3	1	2	3	1	2	3	1	2
Salmonidae	—	—	1.01	—	—	—	—	—	—	—	—
Osmeridae	—	—	—	—	—	0.31	—	—	—	—	—
Microstomatidae	—	—	—	—	—	—	3.57	0.44	—	6.56	—
Myctophidae	—	—	1.52	4.23	8.13	0.31	2.89	3.54	—	—	—
Gadidae	3.23	13.33	10.61	1.41	2.44	6.23	0.34	—	—	—	—
Macrouridae	—	—	—	—	0.81	—	1.02	2.21	—	6.56	14.29
Stichaeidae	—	—	1.52	—	—	—	—	—	—	—	—
Zoarcidae	—	—	—	—	—	—	—	1.33	—	—	—
Scorpaenidae	—	—	—	—	—	—	0.17	0.44	—	1.64	—
Hexagrammidae	—	—	1.01	—	0.81	0.31	—	—	—	—	—
Cottidae	—	6.67	4.55	—	5.69	0.62	0.34	2.21	—	—	—
Psychrolutidae	—	—	1.52	—	0.81	—	0.17	3.09	—	1.64	—
Agonidae	—	—	—	—	—	1.24	0.51	—	—	—	—
Liparidae	—	3.33	3.04	1.41	—	—	4.93	6.63	5.56	8.20	14.29
Pleuronectidae	—	—	—	—	—	0.62	—	—	—	—	—
Unidentified fish species	16.13	13.33	17.17	4.23	13.82	7.17	20.24	16.18	—	14.75	42.86
Total stomachs with food	29	29	149	70	127	304	586	249	15	67	6

1 = Greenland halibut, 2 = Kamchatka flounder, 3 = Pacific halibut.

the southwestern part of its range (along the Kuril Islands and off the coast of Japan) the Pacific halibut is a rather common species. However, information on its diet there was limited (Novikov 1974, Tsuji 1974). Our data filled this gap. Like in other regions, the diet of Pacific halibut in the Pacific off the northern Kuril Islands and southeastern Kamchatka consists mainly of crustaceans, mollusks, and fish. However, the proportions of these food items in this region differ from proportions reported for other parts of the species' range. Thus, in the Bering Sea and northeast Pacific fish play a leading role in its diet (Gordeeva 1954; Novikov 1964, 1974; Best and St.-Pierre 1986), whereas in our study area fish is on the third place after mollusks and crustaceans. Fish species composition of the diet varies depending on region. The species which is most abundant in the region predominates also in its diet (Fadeev 1971, 1984, 1986). Thus, Pacific halibut eat mainly walleye pollock, yellowfin sole, and sand lance in the Bering Sea and Gulf of Alaska (Moiseev 1953; Gordeeva 1954; Novikov 1963, 1964, 1974; Best and St.-Pierre 1986), and saffron cod in waters around Hokkaido (Tsuji 1974). Pacific waters off the northern Kuril Islands and southeastern Kamchatka are not an exception. There Pacific halibut also feed most frequently on pollock. The fact that fish is not the main basis of its diet is apparently associated with the narrowness of the continental shelf and slope where dense concentrations of the most abundant fish species are lacking.

The diet of Greenland halibut is less well known, and available information is from regions of its highest abundance in the Bering and Okhotsk seas. In all main areas of Greenland halibut inhabitation fish is a basis of its diet. Among fishes pollock is the most important food object (Gordeeva 1954; Shuntov 1966a, 1966b, 1970, 1971; Novikov 1974; Yang and Livingston 1988). In our region diet consists mainly of Commander squid, which reaches a very high abundance in waters off the Kuril Islands (Fedorets 1986). The importance of squid in the diet is also great in other regions (Shuntov 1966a, 1970, 1971; Novikov 1974; Fadeev 1984; Yang and Livingston 1988). However, there they do not play a leading role in the diet except in the Sea of Okhotsk (Fadeev 1971). Fish species composition in the diet of Greenland halibut in the investigated area also differs from other parts of its range. In our area liparids which inhabit near-bottom layers (Orlov 1993) are most important in the diet. Mesopelagic myctophids and microstomatids and benthopelagic grenadiers are also characterized by high FOs in stomachs. At the same time, the importance of typical bottom fishes for feeding of Greenland halibut is very low. Thus, we may conclude that the Greenland halibut feeds mainly in the water column and is typically a benthopelagic predator.

The diet of Kamchatka flounder is the least well known. It resembles the diet of Greenland halibut except that the occurrence of cephalopods in Kamchatka flounder stomachs is only a third of that found for Greenland halibut. At the same time, crustaceans (shrimps) are more important in the diet of Kamchatka flounder. Comparing stomach contents of Kamchatka flounder from different regions one can note the predominance of shrimps in its diet near the west coast of Kamchatka and in the western Bering Sea (Fadeev 1971, Novikov 1974). In those areas shrimps are in highest abundance. Pollock are the most predominant fish in the diet of Kamchatka flounder in all parts of their range (Moiseev 1953; Gordeeva 1954; Shuntov 1966b, 1970; Fadeev 1971, 1984). In the area of the northern Kuril Islands and southeastern Kamchatka pollock are not so important in the diet. There myctophids, liparids, and sculpins are more important in the diet, indicating the benthopelagic character of feeding by Kamchatka flounder. The high FO of squids in stomachs is possibly associated with their high abundance in the region under consideration. The importance of squids in the diet of Kamchatka flounder was noted by Moiseev (1953), except for the area of south Sakhalin and the southern Kuril Islands.

Differences in feeding between males and females of all three predator species practically are not studied. The differences revealed during our investigations are related to dimorphism in size. In all three species females are generally larger than males. Thus, the mean lengths of males were 58.0 cm for Greenland halibut, 50.4 cm for Kamchatka flounder, and 60.2 cm for Pacific halibut, while for females these values were 67.4, 58.2, and 67.5 cm, respectively. Differences in body weight were even more marked. Thus, the mean weight of males was 1,926 g for Greenland halibut, 1,294 g for Kamchatka flounder, and 3,068 g for Pacific halibut. For females these values were 3,563, 2,374, and 5,449 g, respectively. Due to the larger size of females they eat larger food objects, which is most characteristic of Greenland halibut and Kamchatka flounder. The diets of these species are rather similar, and this probably results in competition in their feeding. Differences in diet between males and females apparently favor weakening of this competition. The lack of such differences for Pacific halibut is obviously associated with the wider range of its diet and high plasticity of feeding. This results in weak intraspecies feeding competition.

Differences in diet composition depending on size are well studied for Greenland and Pacific halibuts. According to Yang and Livingston (1988) cephalopods and gadids (mainly pollock) are most important in the diet of Greenland halibut <50 cm in length in the Bering Sea. In the Sea of Okhotsk small Greenland halibut consume mainly squids (Shuntov 1966a). In our study area the diet of this size group was also characterized by a predominance of fishes (myctophids and microstomatids) and squids; however, the role of crustaceans (amphipods and euphausiids) was also important. In the Bering and Okhotsk seas individuals 51-70 cm in length consume basically fishes and squids, mainly pollock (Shuntov 1966a, Yang and Livingston 1988). Off the northern Kuril Islands and southeastern Kamchatka their diet consists of the same food items but among fishes, liparids, myctophids, and microstomatids predominate. The diet of large Greenland halibut consists mainly of fish in all regions. In our study area their frequency of occurrence in stomachs was the same as for cephalopods. But in contrast to the Bering and Okhotsk seas where pollock is the most important for large individuals of Greenland halibut, the investigated area is characterized by predominance of deepwater liparids and grenadiers in stomachs. The above changes are explained by the fact that, on the one hand, with increasing size Greenland halibut eat larger prey but, on the other hand, these changes are associated with peculiarities in the vertical distribution of different size groups of Greenland halibut: its juveniles inhabit shelf waters while adults live in slope waters.

Data on the diets of different size groups of Kamchatka flounder are almost lacking. It is known only that in the Bering Sea its juveniles feed mainly on shrimps, amphipods, mysids, squids, and small fishes (Shuntov 1966c). In the area of our investigation small Kamchatka flounder also consumed mainly shrimps and small sculpins. With increase in size the importance of crustaceans in the diet decreases, while that of cephalopods and fish increases. These differences in diet composition are explained by the same factors as for Greenland halibut, because different size groups of Kamchatka flounder inhabit different depth ranges.

Differences in diet with age are well known for Pacific halibut. In the Bering Sea and northeast Pacific crustaceans and small fishes: juveniles of flounders and pollock, capelin, sand lance, smelt, sculpins, poachers (Gordeeva 1954; Novikov 1964; IPHC 1978, 1987; Best and St.-Pierre 1986). Compared with juveniles the importance of fish in the diet of small and average-sized individuals of Pacific halibut increases. In the area of the northern Kuril Islands and southeastern Kamchatka fish were consumed most frequently by small individuals. Fish of 61-90 cm ate mainly cephalopods (about equal quantities of squids and octopuses). Large individuals fed mainly on octopuses. The described differences are mainly related to the low abundance of mass prey fishes and higher abundance of cephalopods there.

Seasonal changes in diet of halibuts are poorly known. As a whole, they are determined by features of seasonal distribution of both the predators and their food organisms. Moreover, these changes are affected by changes in physiological state of fish. Data available from the literature deal only with seasonal changes in feeding intensity of the species under consideration. Thus, according to Shuntov (1970), in the Bering Sea Greenland halibut feed less intensively in winter whereas in other seasons the intensity of feeding is on about the same level. We noted a decrease in the intensity of feeding by this species from summer to autumn (there were no observations in winter) that was associated with approaching the spawning period.

The intensity of Kamchatka flounder feeding in the Bering Sea is almost the same throughout the year (Shuntov 1970). In the area investigated for this study the intensity of feeding was similar to that of Greenland halibut and was explained by the same factors.

According to Novikov (1964), in the northwestern and central Bering Sea seasonal changes in intensity of Pacific halibut feeding are not pronounced. In the southeastern Bering Sea during summer and autumn they fed more intensively than in winter and spring, which is associated with winter spawning. In the investigated area the maximum intensity of feeding was observed in the summer-autumn period. Spawning of Pacific halibut there occurs from December to February (Rass 1959). According to our data, by December the intensity of feeding increased also. Possibly, they continue to feed actively during the spawning period.

Diurnal differences in the diets of Greenland halibut and Kamchatka flounder are associated with the character of their feeding. Being benthopelagic predators, they feed mainly in the water column. Their diet consists mainly of organisms which are characterized by daily vertical migrations (squids, mesopelagic fishes, shrimps). In the night, when mesopelagic fishes migrate to the surface layers, Greenland halibut feed mainly on liparids and grenadiers. Kamchatka flounder in the evening and night hours commonly feed near bottom when their diet consists mainly of shrimps, sculpins, and liparids. Myctophids were found in stomachs more often in the daylight hours when they migrate down to the near-bottom layers. Diurnal variations in the diet of Kamchatka flounder are apparently associated with changes in daily activity and availability of food organisms. In daylight hours when fishes obviously become less available, the importance of crustaceans in the diet of Kamchatka flounder increases. In the night the situation is reversed.

Considering diurnal changes in feeding intensity, one may conclude that Greenland halibut prefer to feed in the evening and at night. For other species daily variations are not so clear.

Changes in the diet of all three predator species with depth are associated with several factors. On the one hand, distribution of fish over the continental shelf and slope of the Far East seas is characterized by marked zonality (Andriyashev 1939) which is expressed in gradual replacement of one fish community by another. On the other hand, differences in diet result from the fact that different size groups of the species under consideration inhabit different depth ranges. The importance of pollock in the diets of Greenland halibut and Kamchatka flounder decreases with depth while the occurrence of deepwater myctophids, microstomatids, and grenadiers in stomachs increases. Thus, situations in our study area and the Bering Sea (Shuntov 1971, Yang and Livingston 1988) are quite similar. As for Pacific halibut, until now detailed investigations of this problem had not been conducted.

Acknowledgments

Many people helped collect samples for analysis of stomach contents.

My ichthyologist colleagues from SakhNIRO, KamchatNIRO, VNIRO, ZIN RAN, and IBM DVO RAN participated in collecting the primary data. Vasily Ul’chenko, VNIRO, assisted in developing the computer database on diet. Anatoly Gruzevich, VNIRO, developed special software for statistical analysis of the data.

References

Andriyashev, A.P. 1939. Ocherk zoogeografii i proiskhozhdeniya fauny ryb Beringova morya i sopredel’nykh vod (An outline of the zoogeography and origin of the fish fauna of the Bering Sea and neighboring waters). LGU, Leningrad. 187 pp. (In Russian.)

Best, E.A., and G. St.-Pierre. 1986. Pacific halibut as predator and prey. Int. Pac. Halibut Comm. Tech. Rep. 21:1-27.

Dudnik, Yu.I., A.M. Orlov, Kim Sen Tok, and S.N. Tarasiuk. 1995. Fish raw material resources in the continental slope of the Northern Kuril Islands. Rybnoye Khozyaistvo (Fisheries). 1:24-28. (In Russian.)

Fadeev, N.S. 1971. Biologiya i promysel tikhookeanskikh kambal (Biology and fishery of halibuts in the Pacific Ocean). Dal’izdat, Vladivostok. 100 pp. (In Russian.)

Fadeev, N.S. 1984. Promyslovye ryby severnoy chasti Tikhogo okeana (Commercial fishes of the North Pacific). Dokl. Vses. NC Akad. Nauk SSSR, Vladivostok. 271 pp. (In Russian.)

Fadeev, N.S. 1986. Flounders and turbots. In: M.E. Vinigradov, N.V. Parin, and V.P. Shuntov (eds.), Biologicheskiye resursy Tikhogo okeana (Biological resources of the Pacific Ocean). Nauka, Moscow, pp. 341-365. (In Russian.)

Fedorets, Yu. A. 1986. Biology and stocks of squid, *Berryteuthis magister* (Gonatidae), off the Commander Islands. In: B.G. Ivanov (ed.), Resursy i perspektivy ispol’zovaniya kal’marov Mirovogo okeana (Resources and fishery perspectives of squids in the World Ocean). VNIRO, Moscow, pp. 57-66. (In Russian.)

Fortunatova, K.R. 1951. Methods of study of predatory fish diet. Zool. Zh. 30(6):562-571. (In Russian.)

Gordeeva, T.K. 1954. Feeding of halibuts in the Bering Sea. Izv. Tikhookean. Nauchno-Issled. Rybn. Khoz. Okeanogr. 39:111-134. (In Russian.)

IPHC (International Pacific Halibut Commission). 1978. The Pacific halibut: Biology, fishery, and management. Int. Pac. Halibut Comm. Tech. Rep. 16:1-56.

IPHC. 1987. The Pacific halibut: Biology, fishery, and management. Int. Pac. Halibut Comm. Tech. Rep. 22:1-59.

Lishev, M.N. 1950. Methods of study of predatory fish diet. Izv. Tikhookean. Nauchno-Issled. Rybn. Khoz. Okeanogr. 32:121-128. (In Russian.)

Manual for the Study of Fish Feeding Under Natural Conditions. 1961. Izd. Akad. Nauk SSSR, Moscow. 264 pp.

Moiseev, P.A. 1953. Cod and flounders of Far Eastern seas. Izv. Tikhookean. Nauchno-Issled. Rybn. Khoz. Okeanogr. 40:1-287. (In Russian.)

Novikov, N.P. 1963. On the population of *Hippoglossus hippoglossus stenolepis* Schm. in the Bering Sea. Zool. Zh. 42(8):1183-1186. (In Russian.)

Novikov, N.P. 1964. Basic elements of biology of the Pacific halibut (*Hippoglossus hippoglossus stenolepis* Schmidt) in the Bering Sea. Izv. Tikhookean. Nauchno-Issled. Rybn. Khoz. Okeanogr. 51:167-207. (In Russian.)

Novikov, N.P. 1974. Promyslovye ryby materikovogo sklona severnoy chasti Tikhogo okeana (Commercial fishes of the continental slope of the North Pacific). Pischevaya Promyshlennost, Moscow. 308 pp. (In Russian.)

Orlov, A.M. 1993. Features of behavior of some bottom fishes on the northeastern shelf of the Okhotsk Sea. In: Biology and rational utilization of hydrobionts, their role in ecosystems. Tez. Dokl. Konf. Molodykh Uchenykh. TINRO, Vladivostok, pp. 26-27. (In Russian.)

Rass, T.S. 1959. Complex investigation of the waters of the northern Kuril Islands and Kronotsk Bay (Kamchatka). Tr. Inst. Okeanol. Akad. Nauk SSSR 36:282-292. (In Russian.)

Shuntov, V.P. 1966a. Data on the biology of Greenland halibut in the Sea of Okhotsk. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 60:271-279. (In Russian.)

Shuntov, V.P. 1966b. Some characteristics of distribution of Greenland halibut and Kamchatka flounder in the North Pacific. Ph.D. thesis, TINRO, Vladivostok. 20 pp. (In Russian.)

Shuntov, V.P. 1966c. Some characteristics of vertical distribution of Greenland halibut and Kamchatka flounder in the North Pacific. Vopr. Ikhtiol. 6(1):32-41. (In Russian.)

Shuntov, V.P. 1970. Seasonal distribution of Greenland halibut and Kamchatka flounder in the Bering Sea. Izv. Tikhookean. Nauchno-Issled. Rybn. Khoz. Okeanogr. 72:391-401. (In Russian.)

Shuntov, V.P. 1971. Some characteristics of distribution of Greenland halibut and Kamchatka flounder in the North Pacific. Izv. Tikhookean. Nauchno-Issled. Rybn. Khoz. Okeanogr. 75:3-36. (In Russian.)

Tsuji, S. 1974. A historical review of the halibut fishery in Japan, with some notes on the biology of the fish. Bull. Far Seas Fish. Res. Lab. (Shimizu) 11:77-109.

Yang, M.S., and P.A. Livingston. 1988. Food habits and daily ration of Greenland halibut, *Reinhardtius hippoglossoides*, in the eastern Bering Sea. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 86(4):675-690.

Using Pacific Halibut to Sample the Availability of Forage Fishes to Seabirds

David G. Roseneau and G. Vernon Byrd
U.S. Fish and Wildlife Service, Alaska Maritime National Wildlife Refuge, Homer, Alaska

Abstract

Evaluating the influence of fluctuating prey populations (e.g., forage fishes) is critical to understanding the recovery of seabirds injured by the T/V *Exxon Valdez* oil spill; however, it is expensive to conduct hydroacoustic and trawl surveys to assess forage fish stocks over broad regions. As part of the 1995 *Exxon Valdez* Oil Spill Trustee Council-sponsored Alaska Predator Ecosystem Experiment, we tested the feasibility of using sport-caught Pacific halibut (*Hippoglossus stenolepis*) to obtain spatial and temporal information on capelin (*Mallotus villosus*) and Pacific sand lance (*Ammodytes hexapterus*), two forage fishes important to piscivorous seabirds. We examined 586 halibut stomachs collected from vessels in a 100-150 vessel charter boat fleet fishing throughout Cook Inlet waters during late May-early September. Catch locations and dates provided information on geographic and seasonal variation in the incidence of capelin and sand lance in seven eastern inlet subunits between Ninilchik and Shuyak Island. We also obtained data on prey brought to chicks of black-legged kittiwake (*Rissa tridactyla*), common murre (*Uria aalge*), and tufted puffin (*Fratercula cirrhata*) at the Barren Islands to help evaluate the sampling technique. At the Barren Islands, capelin were the most numerous fish in halibut stomachs, and they were the most common prey fed to murre and kittiwake chicks by number and weight, respectively. They were also the largest prey group by weight in puffin chick diets. In the Point Adam area, where samples were collected during June through early August, we detected seasonal changes in the relative abundance of sand lance and capelin. Sand lance were most common in June, and capelin increased after early July. Based on our results, we concluded that this relatively simple cost-effective method can supply useful information on forage fish stocks in areas where seabird feeding and charter boat fishing activities overlap.

Introduction

This pilot study was developed as part of the *Exxon Valdez* Oil Spill Trustee Council-sponsored Alaska Predator Ecosystem Experiment (APEX) because there was need for a cheap, cost-effective means of assessing presence-absence and relative abundance of important prey species, particularly forage fishes, near seabird nesting colonies. Evaluating the influence of fluctuating prey populations (e.g., forage fishes) is a crucial element in understanding annual variations in the productivity of several fish-eating marine birds, including divers (e.g., common and thick-billed murres, *Uria aalge* and *U. lomvia*; tufted puffins, *Fratercula cirrhata*) and surface-feeders (black-legged kittiwakes, *Rissa tridactyla*). Knowledge of fluctuations in prey populations is also an important factor in understanding the recovery of seabirds injured by the T/V *Exxon Valdez* oil spill; however, it is expensive to conduct hydroacoustic and trawl surveys to assess forage fish stocks over such broad regions.

The presence of a large, 100-150 vessel charter boat fleet operating throughout Kachemak Bay and lower Cook Inlet during late May-early September offered a prime opportunity to explore the feasibility of using sport-caught Pacific halibut (*Hippoglossus stenolepis*) to obtain spatial and temporal information on capelin (*Mallotus villosus*) and Pacific sand lance (*Ammodytes hexapterus*), two forage fishes important to piscivorous seabirds (e.g., Piatt 1991, Springer 1991, Piatt 1995). Many of these vessels fish for halibut almost every fair-weather day in lower Cook Inlet between Ninilchik and the inlet shelf break and between Seldovia and Elizabeth Island. They also fish in Kennedy Entrance between the Kenai Peninsula and the Barren Islands, in the Barren Islands (as many as 20 boats were seen in the vicinities of West Amatuli, Ushagat, and Nord islands on some days in 1993-1994), and occasionally as far south as Shuyak Island (Pers. comm., R. Swenson; Pers. obs., D.G. Roseneau). Many of these areas are also used heavily by foraging seabirds, including those nesting in the Barren Islands and at the Gull and Chisik islands colonies (Piatt 1995; Pers. comm., J.F. Piatt; Pers. obs., D.G. Roseneau).

Halibut are opportunistic predators that take a wide range of both fish and invertebrate prey, and smaller individuals between about 30 and 70 cm in length tend to feed on a variety of miscellaneous fishes, including both sand lance and capelin (see Yang 1990). Halibut are usually associated with the bottom. However, fish weighing less than about 13-18 kg (commonly referred to as “chicken” halibut) have also been observed pursuing prey higher in the water column (Pers. comm., J. Martin and S. Meyers), and in some instances they have even been seen jumping out of the water in large surface schools of “bait fish” (e.g., capelin; Pers. comm., R. Swenson).

Based on the above information, and the spatial and temporal distribution of the charter vessel fleet, we designed and implemented a pilot program to collect halibut stomachs during late May-early September 1995 to test the concept that sport-caught fish could be used as a sampling tool to assess the relative abundance of capelin and sand lance in Kachemak Bay and lower Cook Inlet. Results from our initial effort indicated that this relatively simple, inexpensive technique can supply useful information on forage fish stocks in areas where seabird feeding and charter boat fishing activities overlap.

Objectives

Project objectives were to: (1) test the feasibility of using stomach contents from sport-caught Pacific halibut as a means of sampling forage fishes in the northern Gulf of Alaska; and (2) evaluate the effectiveness of this technique in obtaining information that could be useful to *Exxon Valdez* Oil Spill Trustee Council APEX studies of seabirds and forage fishes in the spill area (e.g., kittiwakes, murres, puffins, capelin, sand lance).

Methods

We set up the Kachemak Bay-lower Cook Inlet study area in early May 1995 and divided it into 12 subunits (Figure 1). During late May-early September, stomachs from 586 halibut averaging 39 cm in length (range = 71-213 cm) were collected from seven of the sampling areas by visiting several Homer-based sport fishing charter boat companies as vessel operators filleted fish for their customers at public and private port-side fish-cleaning facilities. Lengths, weights, and catch locations were obtained as halibut were processed, and when carcasses were discarded, stomachs were removed and weighed, and contents were emptied into plastic trays and identified using taxonomic keys and photographs. Fish that were whole and partly digested, but still recognizable, were sorted into seven categories: capelin, sand lance, herring, flatfish, sculpin, cod, and other species. Invertebrates were divided into six groups: crabs, shrimp, squid, octopus, other mollusks (gastropods and bivalves), and other species. Empty stomachs were weighed to obtain content weights, and undigested forage fish were also weighed and measured to obtain size information on target species (i.e., capelin and sand lance). Samples of whole capelin and sand lance were preserved in 10% buffered formaldehyde and 75% ethanol-2% glycerin solutions for later analysis by other investigators. Data, including dates and catch locations, were entered into computer spreadsheets. Analysis consisted of eliminating all potential bait items from the database (e.g., Pacific herring, *Clupea pallasi*), and calculating numbers and frequencies of occurrence of fish and invertebrates in different geographic areas and time periods.

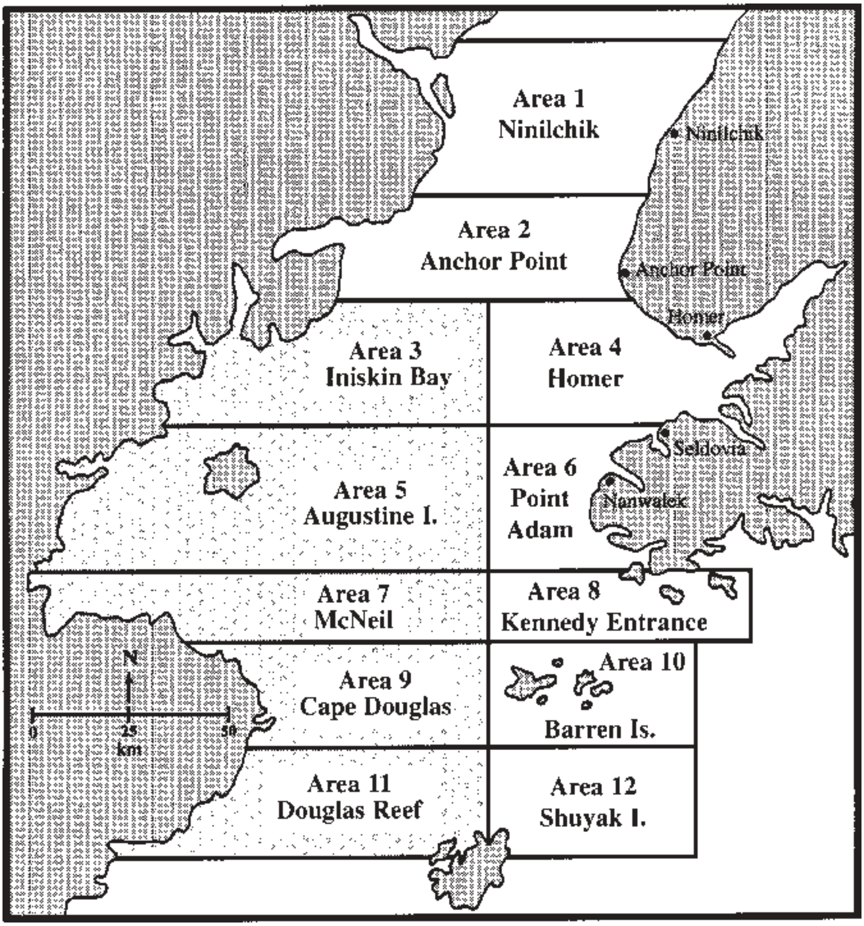


Figure 1. The Kachemak Bay-lower Cook Inlet study area (no samples were obtained from shaded areas).

Results

Fish were present in about 50% of the 586 stomachs (Figure 2), and capelin and sand lance were found in 30% and 11% of the 380 stomachs containing prey, respectively (Figure 3). As a group, fish dominated prey items by number (77%), and most of the fish were capelin and sand lance (73% and 24%, respectively; Figure 4). When numbers of fish were compared in six subunits (Figure 5; Area 1 was not included in the analysis because of inadequate sample size), sand lance appeared to be most numerous in the Homer and Kennedy Entrance vicinities (41% and 63% by number, respectively), and capelin appeared to be particularly abundant in the Point Adam area near the southern tip of the Kenai Peninsula (85% by number), and in the Barren Islands and Shuyak Island subunits (100% by number in both cases). By analyzing numbers of capelin and sand lance per stomach in the Point Adam area (the subunit with the best June-August data series), it was apparent that the relative abundance of these species changed over time (Figure 6). Sand lance averaged 1.2 fish per stomach in this area during June, but were nearly absent from the July-early August samples (<0.1 individual per stomach). In contrast, numbers of capelin increased markedly after late June, rising from an average of only 0.9 fish per stomach that month, to 2.4 individuals during July and 7.7 fish by early August.

Discussion

Results from the pilot study supported our general hypothesis that the contents of halibut stomachs could be used to obtain information on relative abundance of forage fishes in Kachemak Bay and lower Cook Inlet. Sand lance and capelin were regularly present in halibut up to 127 cm and 137 cm in length, respectively. The occurrence of these species in fish longer than 70 cm (see Yang 1990) suggests that they are taken by larger halibut, when they are abundant. These data also suggest that halibut up to about 125-135 cm in length can be used to sample and track sand lance and capelin populations in the Kachemak Bay-lower Cook Inlet region.

The high incidence of capelin in the Point Adam, Barren Islands, and Shuyak Island samples was consistent with reports from charter boat operators that large schools of “bait fish” were present in these areas. For example, in the Point Adam area (Area 6; Figure 1), schools of small fish more than 1 km long were noted on vessel fish finders during early June through mid-August, and on several occasions large concentrations of capelin were observed in surface waters (Pers. comm., R. Swenson). In several instances, small halibut (9-10 kg or less) jumped out of the water in the midst of these dense surface schools of fish. Similar large, dense concentrations of capelin were also seen in surface waters near the north end of Shuyak Island on 20 June, and at depth and on the sur-

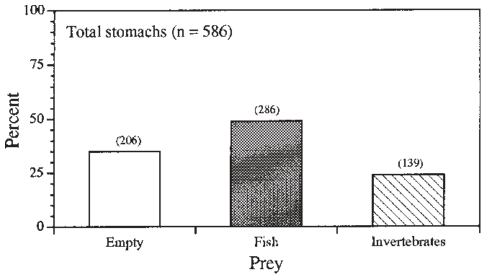


Figure 2. Frequency of occurrence of fish and invertebrates in halibut stomachs (numbers of stomachs shown in parentheses).

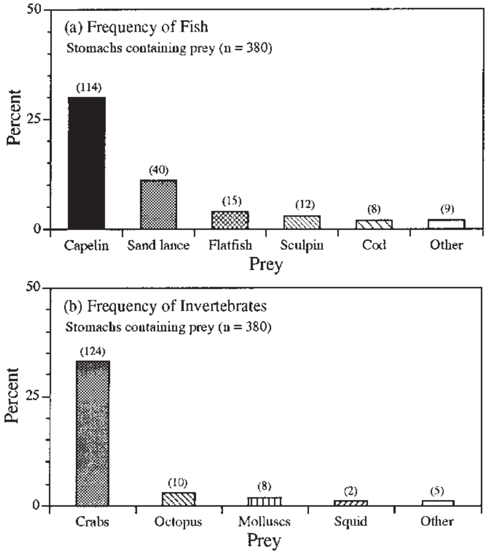


Figure 3. Frequencies of occurrence of (a) fish and (b) invertebrates in halibut stomachs containing prey (the mollusk category contains gastropods and bivalves; numbers of stomachs shown in parentheses).

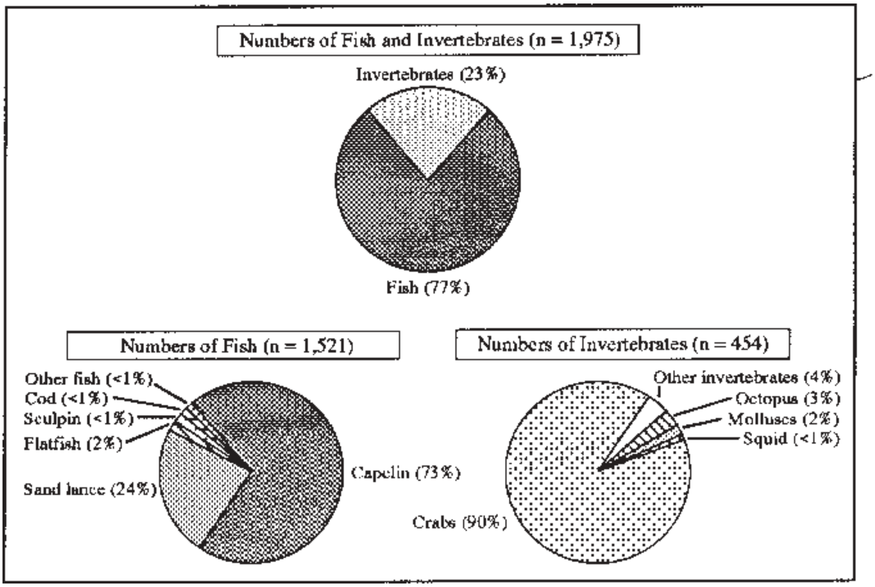


Figure 4. Numbers of fish and invertebrates that were identified to group or species in halibut stomachs containing prey (the mollusk category contains gastropods and bivalves).

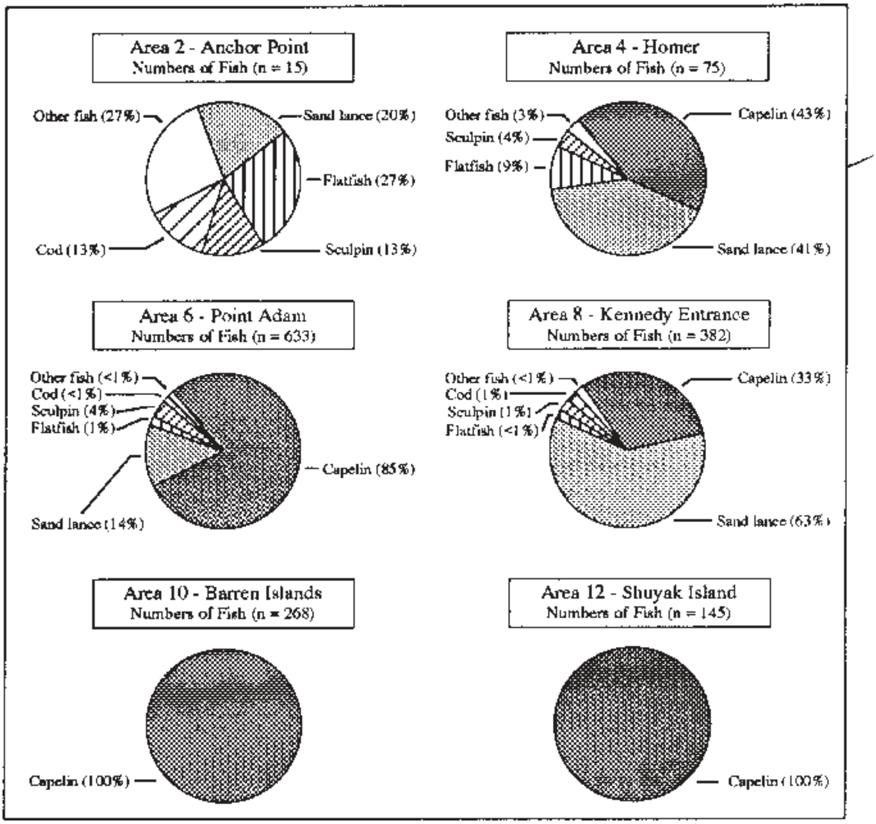


Figure 5. Numbers of fish that were identified to group or species in halibut stomachs from Areas 2, 4, 6, 8, 10, and 12.

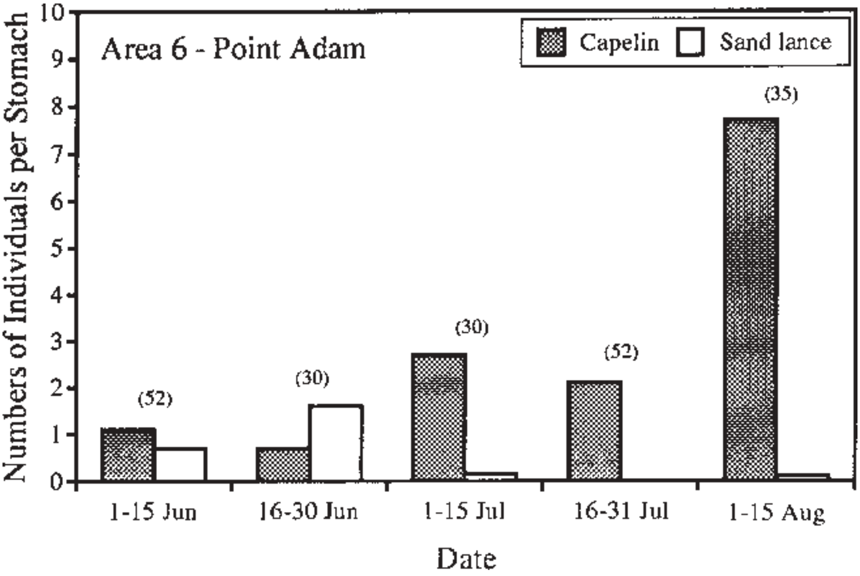


Figure 6. Average numbers of capelin and sand lance in halibut stomachs collected during 2-week intervals in Area 6 (numbers of stomachs shown in parentheses).

face near Nord, Ushagat, and West Amatuli islands in the Barren Islands during 17 June-2 July (Pers. comm., R. Swenson). In both of these subunits, large numbers of humpback whales (*Megaptera novaeangliae*) and seabirds were feeding on the schooling fish.

The high proportion of capelin in halibut stomachs from the Barren Islands area was also consistent with information obtained on types of prey fed to black-legged kittiwake, common murre, and tufted puffin chicks at the East Amatuli Island-Light Rock colony during late July-August (Roseneau et al. 1996). By number, 86% of all identifiable fishes (N = 356) brought to murre chicks were capelin, and by weight, capelin also dominated kittiwake chick diets (65%, N = 629 items). By weight, capelin were also the dominant prey fed to puffin chicks (28%, N = 346 items).

During the feasibility study, the level of cooperation received from Homer charter vessel operators was high; we could have easily obtained two to three times as many samples with little additional effort. Based on the operators' responses to the study and overall distribution of fishing activities in the region, a modest program with larger sample sizes (e.g., 20-40 stomachs containing prey per area per week) could be easily set up to monitor changes in relative abundance of capelin and sand lance in areas near seabird colonies in lower Cook Inlet and Kachemak Bay (i.e., the Barren Islands, Gull and Chisik islands).

Based on our initial results and the levels of cooperation received from Homer charter vessel operators, we recommend implementing a small program to continue collecting information on forage fish stocks via stomachs from 30-135-cm sport-caught halibut taken in the Kachemak Bay-lower Cook Inlet region. This low-cost approach will almost certainly provide useful data on overall presence-absence and relative abundance of capelin and sand lance for long-term APEX seabird studies in the Barren Islands and at the Chisik and Gull island colonies, and it will complement other ongoing APEX-sponsored forage fish projects in the same areas (e.g., hydroacoustic and trawl surveys by J.F. Piatt).

Conclusions

1. Results from the Kachemak Bay-lower Cook Inlet study area indicate that real-time analysis of stomachs from sport-caught halibut can provide useful low-cost information on the occurrence of forage fishes in areas where charter boat fleets operate on a regular basis.
2. Based on the apparent ability of the sampling method to detect changes in the relative abundance of capelin and sand lance in the Point Adam area, we also believe that this relatively simple cost-effective technique can provide useful information on seasonal and interannual variations in populations of forage fishes in areas where seabird feeding and charter vessel activities overlap (e.g., Barren Islands and Chisik Island vicinities).

Acknowledgments

This study was funded by the Exxon Valdez Oil Spill Trustee Council. We would like to thank our volunteers, Jill Aho and Daniel Boone, for helping make the 1995 pilot study a success. They consistently met returning vessels, collected halibut stomachs, sorted and identified prey items, and entered data into spreadsheets on schedules dictated by the charter fleet. We also extend special thanks to Captain Rick Swenson of Homer Ocean Charters. He provided a steady stream of halibut carcasses and facilities for processing them, encouraged other skippers to join in the study, and gave us important information on locations of capelin schools and halibut feeding in surface waters. Without Captain Swenson's help, collecting data would have been far more difficult and less efficient. Silver Fox Charters also deserves special mention. Several Silver Fox skippers participated in the project on a regular basis; their contributions rounded out sampling efforts and helped contribute to the success of the experimental program. John Martin, Alaska Maritime National Wildlife Refuge, and Scott Meyers, Alaska Department of Fish and Game, contributed observations of halibut pursuing prey in the upper water column. John F. Piatt, U.S. Geological Survey (formerly the National Biological Service), Anchorage; Alan M. Springer, Institute of Marine Sciences, University of Alaska Fairbanks; and Bruce A. Wright, National Marine Fisheries Service, Auke Bay, provided helpful suggestions during conceptual phases of the work.

References

Piatt, J.F. 1991. The aggregative response of common murres and Atlantic puffins to schools of capelin. Stud. Avian Biol. 14:36-51.

Piatt, J.F. 1995. Oceanic, shelf and coastal seabird assemblages at the mouth of a tidally-mixed estuary (Cook Inlet, Alaska). OCS Study MMS 93-0072. Minerals Management Service, Anchorage, AK. 33 pp. + appendices.

Springer, A.M. 1991. Seabird relationships to food webs and the environment: Examples from the North Pacific. Can. Wildl. Serv. Occas. Pap. 68:39-48.

Roseneau, D.G., A.B. Kettle, and G.V. Byrd. 1996. Barren Islands seabird studies. In: D.C. Duffy (compiler), APEX: Alaska Predator Ecosystem Experiment. Exxon Valdez Oil Spill Restoration Project Annual Rep. (Restoration Proj. 95163), Alaska Natural Heritage Program, University of Alaska Anchorage. Appendix J.

Yang, M.-S. 1990. Food habits of the commercially important groundfishes in the Gulf of Alaska in 1990. NOAA Tech. Memo. NMFS-AFSC-22, 150 pp. Available from National Technical Information Service, Springfield, VA 22161.

Predation-Competition Interactions of Yellow Perch (*Perca flavescens*) and Alewife (*Alosa pseudoharengus*) in Southern Lake Michigan: A Model Analysis

Sture Hansson
Stockholm University, Department of Systems Ecology, Stockholm, Sweden

David M. Post and James F. Kitchell
University of Wisconsin, Center for Limnology, Madison, Wisconsin

Thomas S. McComish
Ball State University, Department of Biology, Muncie, Indiana

Abstract

The Lake Michigan fish community has gone through dramatic shifts in species composition and abundance of key species. The abundance of yellow perch has fluctuated by over 20-fold since the 1950s, reaching high densities in the 1980s. To evaluate its role in those changes, we estimated predation rates by perch during periods of low and high abundance. Under both conditions young-of-the-year perch dominated total population consumption. Growth rates were inversely related to perch abundance, presumably related to intraspecific competition. Although decreased growth rates partially compensated for the increased yellow perch abundance, predation on important prey (zooplankton, the amphipod *Diporeia hoyi*, conspecific 0+ fish, and alewife eggs) probably decreased inshore food availability. When yellow perch were abundant, they depended on prey produced in offshore areas. Predation on alewife eggs may have contributed to the observed reduction in alewife populations during the early 1980s. Cannibalism on 0+ yellow perch may have reduced recruitment in the late 1980s and early 1990s.

Introduction

The Lake Michigan fish community has been strongly influenced by humans and by invasions of exotic species (e.g., Mills et al. 1993). Among the most widespread changes were those due to interactions with the alewife (*Alosa pseudoharengus*) which invaded in 1949 (Eck and Wells 1987) and reached very high abundances in the mid-1960s. As alewife abundance increased, many other fish species decreased. Among those were members of the native Percidae, Cyprinidae, and Cottidae; all of which had pelagic eggs or larvae and were zooplanktivorous at some stage in the life history (Crowder 1980). Beginning in the mid-1960s, salmon and trout were intensively stocked and created a biological control for alewife (Stewart at al. 1981).

When alewife declined in the late 1970s, the abundance of yellow perch (*Perca flavescens*) and a number of other species increased (Wells 1977, Jude and Tesar 1985, Kitchell and Crowder 1986, Crowder et al. 1987, Eck and Wells 1987). Several authors have considered the complexity of interactions between yellow perch and alewife: Were they caused by competition for zooplankton prey (Evans 1986, Crowder et al. 1987) or predation by alewife on perch larvae (Jude and Tesar 1985, Brandt et al. 1987, Crowder et al. 1987)? Perch also prey on alewife eggs and larvae (McComish 1992), producing a competition-predation interaction between perch and alewife. During the 1990s, intense fishery exploitation and a series of poor recruitment years have depressed the yellow perch population. Those changes were accompanied by a general increase in alewife. This interaction is important to fisheries management practices because: (1) yellow perch are the target of valuable commercial and sport fisheries, and (2) salmonid stocking policies are focused on the alewife as a key forage resource in support of a multimillion dollar sport fishery.

In this paper, we describe a bioenergetics modeling approach (Kitchell at al. 1977, Hewett and Johnson 1992) to assess food consumption by Lake Michigan yellow perch during the early 1970s and 1980s (Figure 1). Our results indicate that the strong yellow perch year classes in the 1980s influenced abundances of several prey species shared by perch and alewife. We also conclude that predation by perch could substantially reduce recruitment success by alewife.

Materials and Methods

Growth

Growth of yellow perch has varied considerably over time (Figure 2). We used year-class-specific growth data and length-to-weight conversions derived for each year separately (McComish 1992). For this paper, we classified fish from hatching to December 31 as young-of-the-year (YOY), and from January 1 to December 31 fish were age 1. Fish in their

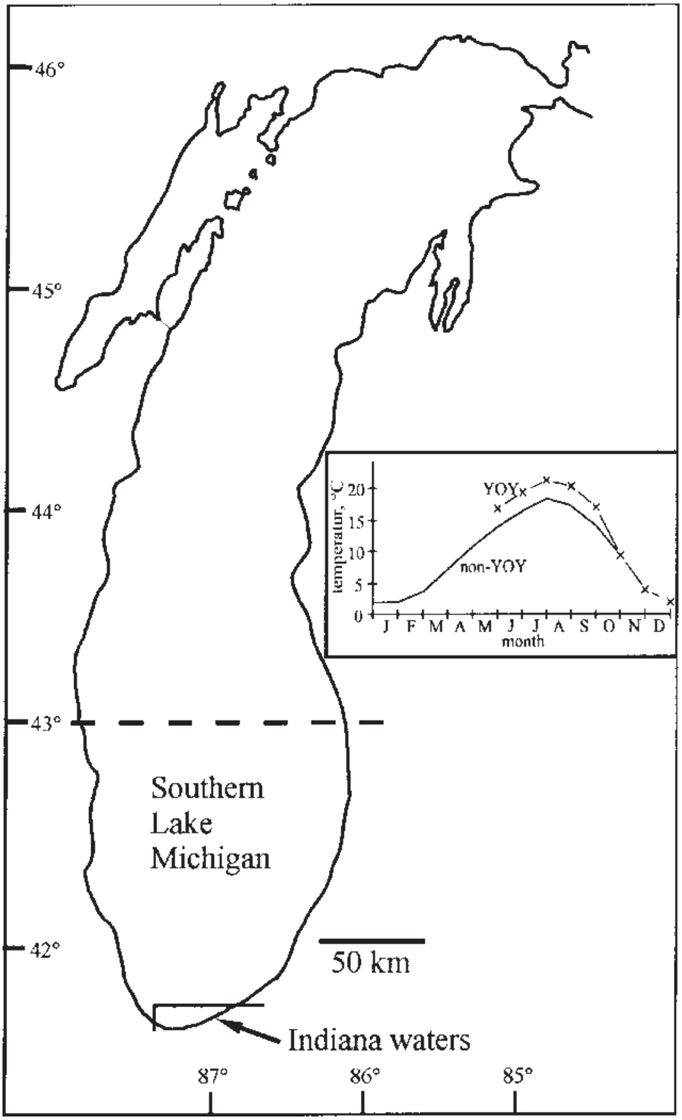


Figure 1. Lake Michigan, with the study area south of the broken line. The inserted graph shows the temperatures used in the bioenergetics. The YOY curve shows the temperatures used for YOY yellow perch and the non-YOY curve the temperatures used for older fish.

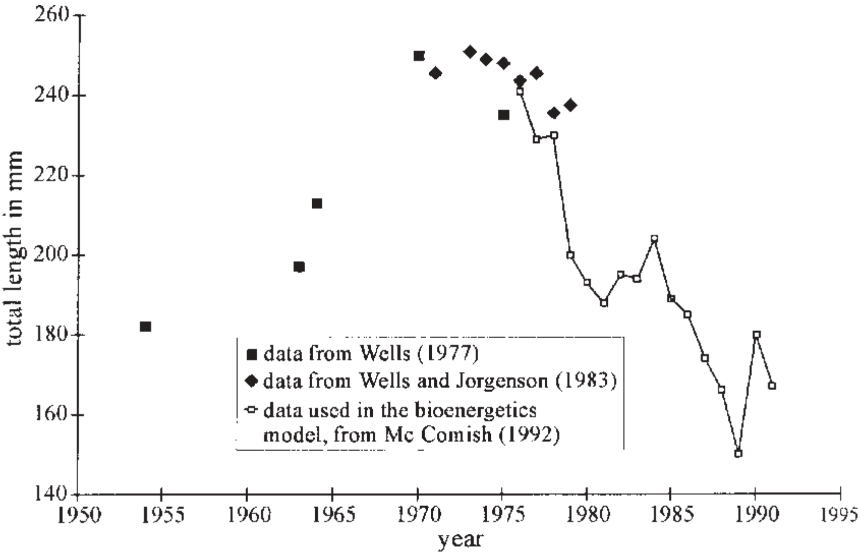


Figure 2. Length of age 3+ yellow perch at the end of the growing season in southern Lake Michigan. Data from before the period of our bioenergetics analysis are included to show growth variation over time. In the period before alewife flourished, the 1950s, the growth of yellow perch was relatively slow. Then, when alewife became abundant and yellow perch decreased (Wells 1977), the growth rate increased. The drop in growth started in the mid-1970s, while yellow perch abundance was still low. One could speculate that this was due to decreased abundances of two important prey items: alewife roe and age 0+ alewife. The first strong year class of yellow perch after the alewife decline was in 1980, which was followed by two even stronger year classes in 1983 and 1985 (Jude and Tesar 1985, Tesar et al. 1986, Eck and Wells 1987, McComish 1992). As a result of these strong year classes, intraspecific competition probably increased and growth declined.

first year of life (e.g., from hatching to the next spring) were considered 0+ and after than 1+ for a year.

Fish abundance

Yellow perch abundances were quantified by trawling at a depth of 5 m during June to August of 1983-1991 in Indiana waters of southern Lake Michigan (McComish 1989, 1992). For each year, areal abundances of age 2+ and older yellow perch were estimated from numbers of fish caught divided by the area swept by the trawl. The total number of yellow perch in southern Lake Michigan (Figure 1) was estimated by assuming that yellow perch inhabit the depth interval 0-15 m in June-August (Jude et al. 1981) and by multiplying the average abundance from the trawl catches by the area in this depth interval (1,563 km^2).

Mortality rates for each year class were estimated with linear regression using logarithms of fish numbers as dependent variable and their age as independent variable. The resulting slopes were the annual instantaneous mortality rate estimates (>4 age classes were included for each cohort, 2+ to >5+). Average R^2 was 0.90 and the range was 0.82-0.97. The estimated mortality rates (53-66% annually) were within the ranges reported for perch populations elsewhere (Kelso and Bagenal 1977, Thorpe 1977, Wells and Jorgenson, 1983, Szalai and Dick 1991). For the 1981-1986 cohorts, abundances of age 0+ fish on January 1 and older perch were estimated from cohort specific moralities and observed densities of adults.

Abundances of YOY fish were estimated from egg numbers. These were derived from size composition and abundance of spawners (fecundity: $\log_{10}Y = -3.712 + 3.451 \times \log_{10}X$, where X = length in mm and Y = egg number; Brazo et al. 1975) assuming a 1:1 sex ratio (Wells and Jorgenson 1983). For cohorts with data on parent stocks including only one or two age classes, YOY abundances were back calculated from numbers of 0+ fish at January 1 (details in Table 1). We assumed that yellow perch mature at age 3 (Brazo et al. 1975, Wells and Jorgenson 1983) and that the gonad production was 8% of the body weight for males (Becker 1983) and 20% for females (Brazo et al. 1975, Becker 1983). In the bioenergetics calculations, we assumed the weight spawned by an average adult to be 14% (1:1 sex ratio).

We assumed that yellow perch eggs hatch in May, that the larvae start exogenous feeding on June 1, and that 6.5% of the eggs develop to this stage (Mills et al. 1987). The number of YOY surviving to January 1 was back calculated from older fish, as described above. For the survival rate of larvae between June 1 and January 1 we ran two alternative mortality scenarios. In scenario 1 we assumed that the mortality rate was constant from June 1 to January 1. In scenario 2 we used two different mortality rates. From August 1 to January 1, the mortality was set equal to that estimated for older fish. From this, we calculated the number of YOY fish on August 1. This number, and the number of larvae on June 1 were used to estimate the daily mortality during the period June 1 to August 1. Our mortality rate estimates are in the range given by Thorpe (1977).

For the 1970s, we assumed that the cohorts had the same age structure as the 1983 cohort, but only 5% of its abundance. This was based on catches in standard trawlings in Indiana waters during 1985-1989. Those catches were more than 20 times higher than catches for the period 1975-1979 (McComish 1992). Similar increases in yellow perch in southern Lake Michigan were presented by Jude and Tesar (1985), Tesar et al. (1986), and Eck and Wells (1987).

Diets

The diet of southern Lake Michigan yellow perch is relatively well documented. We used 1972 data from Bergh (1977) and 1984 data from McComish (1989). Both of these studies were conducted at the same location using identical techniques and were consistent with other findings (Wells 1980, Crowder et al. 1981, Shroyer and McComish 1995). Diets were not available for YOY yellow perch prior to August, so we assumed a larval starting diet of 100% zooplankton (cf. Ney 1978) and allowed this diet to blend (linear interpolation) into the August diets. Winter diets (October 1-April 1) were derived by linear interpolation between fall and spring diets, but assuming that no fish eggs were consumed in this period (Figure 3; prey energy densities are in the figure legend).

Temperatures

We used data (1974-1987) from the 9-m water intake at Evanston, Illinois, for the temperature regime of yellow perch. Based on differences in depth distribution between YOY and older fish (Wells 1977), we assumed that YOY occupied shallower habitats where the summer temperature was 3 degrees warmer. Temperatures used in the bioenergetics model are shown in Figure 1.

Bioenergetics

Food consumption and production of yellow perch were estimated using the approach of Kitchell et al. (1977) and software by Hewett and Johnson (1992). For fish <1 gram wet weight, we used parameters from Post (1990) and those from Kitchell et al. (1977) for larger fish. All weights are given in wet weight. For zooplankton and *Diporeia hoyi* we assumed wet weights to be 10 times and 5 times the dry weights, respectively.

Results and Discussion

Yellow perch abundance and production

Depending on the mortality scenario used, the production of YOY in southern Lake Michigan was either 2.4 or 6.2 g/m^2 in 1985 and 0.9 or 2.3 g/m^2 in 1986 (scenarios 1 and 2, respectively; Table 1). Regardless of the YOY mortality scenario used, production of YOY was higher than that of any other age class. Chadwick (1976) also showed that yellow perch production was dominated by YOY fish. Production by all year classes together was 4.9-8.7 g/m^2 in 1985 and 3.1-4.5 g/m^2 in 1986. Annual harvest by fisheries was at least 1.5 and 2.1 g/m^2 in Indiana waters during these years (McComish 1992). This indicates high fishing pressure, where catches approximately equalled the production of age 1 and older yellow perch. Although uncertainties in our calculations should be

Figure 3. Yellow perch diet composition in southern Lake Michigan, as used in the bioenergetics. The prey energy densities used were: zooplankton, 600 cal/g wet weight (Hewett and Johnson 1992); Diporeia hoyi, 1,000 (Stewart and Binkowski 1986); insects, 800 (Cummins and Wuycheck 1971); alewife eggs, 1,400 (Flath and Diana 1985, Hewett and Johnson 1992); alewife, 800 (value for age 0+ fish; Hewett and Johnson 1992); rainbow smelt, linear increase from 800 at May 1 to 1,000 on Dec. 31 and then constant (Lantry 1991); yellow perch, linear increase from 600 at June 1 to 1,000 on Dec. 31 and then constant (Hewett and Johnson 1992).

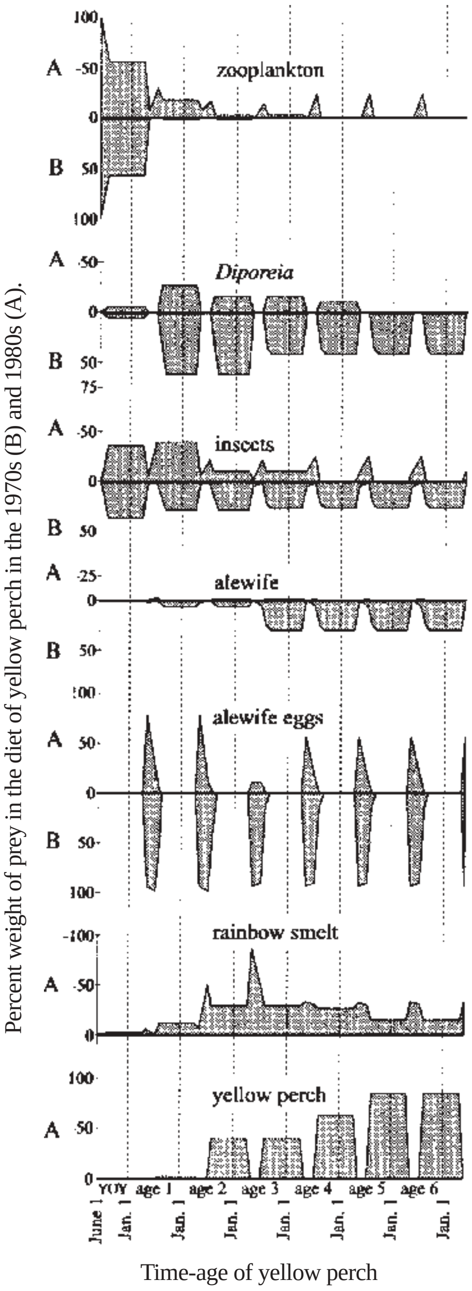


Table 1. Fish abundances (number per hectare) used to estimate food consumption and production by yellow perch in southern Lake Michigan (n.d. = no data). Two alternative values are given for August 1, representing YOY abundances estimated from two different scenarios. To illustrate the progression of a cohort, the 1983 cohort is underlined.

Year	1981*	1982*	1983*	1984*	1985*	1986	1987
Larvae, June 1	35,319	44,245	125,465	107,522	65,604	29,344	n.d.
YOY, Aug. 1							
scenario 1	10,571	13,242	37,550	32,180	19,634	8,782	n.d.
scenario 2	802	891	2,515	2,138	1,319	585	n.d.
age 0+, Jan 1	n.d.	513	642	1,822	1,561	953	426
age 1+, Jun 1	n.d.	330	465	1,325	1,145	691	312
age 2+, Jun 1	n.d.	n.d.	114	213	614	541	318
age 3+, Jun 1	n.d.	n.d.	n.d.	39	97	284	255
age 4+, Jun 1	n.d.	n.d.	n.d.	n.d.	13	45	132
age 5+, Jun 1	n.d.	n.d.	n.d.	n.d.	n.d.	4.6	20
age 6+, Jun 1	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	1.6

* YOY abundances back calculated from age 0+ abundances at January 1 and using the YOY mortality rates of the 1986 cohort.

acknowledged, the similarity between production estimates and catches indicate that our estimates of yellow perch prey consumption are reasonable, or at least not overestimations.

Yellow perch food consumption and effects on prey

Food consumption by YOY yellow perch varied considerably between the two mortality scenarios. For scenarios 1 and 2 in the 1970s, predation rates were 1,000 and 3,900 calories/m^2, respectively. Corresponding values for 1984-1986 were 5,700 and 21,400 calories/m^2. These estimates were substantially higher than those of all older fish combined: 740 calories/m^2 for the 1970s and 2,500 calories/m^2 for 1984-1986.

To assess predation intensity, we calculated ratios between consumption and prey production. If this ratio equalled 1, the entire production was consumed. The higher the ratio, the more likely it was that predation influenced the prey population. Estimated daily zooplankton consumption by yellow perch in July-August differed ~10 times between the two YOY scenarios. For the 1970s, zooplankton consumption was 0.003-0.02 g/m^2 while that for 1982-1984 was 0.02-0.3 g/m^2. In the periods July to August, zooplankton biomasses in shallow waters of southern Lake Michigan averaged 0.56 in 1971-1981 and 0.07 g/m^3 in

1982-1984 (Evans 1986). If we assume an average depth of yellow perch habitat of 8 m, and a daily zooplankton production to biomass (P/B) ratio of 0.01 (Sprules et al. 1991), then zooplankton production for the two periods is estimated to have been 0.045 and 0.006 g/m^2. Thus, the ratio of consumption to production was 0.07-0.4 for the 1970s, and 3-50 for 1982-1984. This indicates considerable predation differences between the 1970s and the 1980s and supports the hypothesis that in the 1980s predation by yellow perch reduced the nearshore zooplankton abundance (Evans 1986).

Effects of predation by yellow perch on benthos have also been discussed (Nalepa 1987, McDonald et al. 1990). The proportions of both *Diporeia hoyi* and insects in the diets of yellow perch decreased from the 1970s to the 1980s (Figure 3), but as perch abundance increased the total consumption of both prey types increased. Annual consumption of *D. hoyi* and insects in the 1970s was 0.8-1.0 and 0.8-2.2 g/m^2 (ranges due to the two scenarios for YOY). Corresponding values for 1984-1986 were 2.1-4.0 and 3.6-17 g/m^2. Data on abundance and production are available only for *D. hoyi*, for which Winnell and White (1984) estimated an annual production of 14 g/m^2 at a depth of 15 m for 1981. In water shallower than 10 m, abundance and production is probably much lower (Evans et al. 1990, McDonald et al. 1990) and *Diporeia* there may have been subjected to considerable predation by yellow perch. However, as suggested by McDonald et al. (1990) yellow perch predation on the *Diporeia* population was generally modest at the larger scale.

For the 1970s, we calculated that yellow perch in southern Lake Michigan consumed 0.2 g/m^2 or 350 tons of alewife annually. In 1984-1987, yellow perch consumed 0.05-0.09 g/m^2 or 80-140 tons. Even if only age 0+ alewife were eaten, consumption was small relative to the production of this age group (170,000-455,000 tons in the 1970s and 55,000-250,000 tons in 1984-1987; Pers. comm., G.W. Eck, U.S. Fish and Wildlife Service, National Fisheries Center, Ann Arbor, MI, and L.A. Eby, Center for Limnology, University of Wisconsin, Madison, WI).

The weakly negative effects of yellow perch on alewife survival found by Mansfield and Jude (1986) cannot, therefore, be explained by predation on large YOY alewife. However, if the predation focused on early life stages, these consumption to production ratios might be misleading. Early in the life of a prey cohort, the per-individual biomass and production is small and large numbers of individuals are needed to meet the demands of the consumers. For example, the yellow perch population consumed more alewife eggs than other alewife life stages (1970s: 1,000 tons; 1984-1987: 1,500-2,500 tons). The production of alewife eggs during these periods were 4,300-12,000 tons in 1973-1978 and 2,200-6,300 tons in 1984-1987 (Pers. comm., Eck and Eby, addresses above). This gives a consumption to production ratio of 0.2 to 1.1 in 1984-1987. However, our estimates are conservative because egg production estimates are for all of Lake Michigan while our consumption estimates are for southern Lake Michigan only. This suggests that much of the egg production in the 1980s was eaten by yellow perch. Predation by yellow perch on alewife eggs could, therefore, have contributed to the decline of the alewife population in the mid-1980s and could have been responsible for sustaining low alewife recruitment in the years that followed.

When alewife decreased, it was replaced in the yellow perch diet by conspecifics and rainbow smelt (Figure 3). The annual consumption of smelt was 2,000-5,600 tons in 1984-1987, compared to an annual production of 1,700-21,000 tons of age 0+ smelt (Pers. comm., Eck and Eby, addresses above; Lantry and Stewart 1993). These smelt production values are for the whole Lake Michigan, while consumption estimates are for the southern part only. It is thus possible that smelt population dynamics were also influenced by yellow perch predation during the 1980s.

Cannibalism was common among yellow perch in 1984-1987 (Figure 3; 1,000-4,000 tons annually). Our estimates of the production of age 0+ yellow perch during this period were 3,700-16,900 or 1,500-6,700 tons depending on the YOY scenario used and the ratio of consumption (by conspecifics) to production was 0.06-1.1 or 0.15-2.7. Thus, cannibalism may have contributed to the weak yellow perch year classes in the beginning of the 1990s (Hess 1994, Francis et al. 1996). For Eurasian perch (*Perca fluviatilis*), but less so for yellow perch, cases of intensive cannibalism have been reported before (e.g., Alm 1952, Tarby 1974, Collette et al. 1977, Koonce et al. 1977, MacLean and Magnuson 1977, Thorpe 1977, Treasurer et al. 1992).

Interactions with the offshore pelagic community

The increased production of yellow perch in the mid-1980s was heavily dependent on food produced in offshore habitats (alewife, alewife roe, rainbow smelt, and probably also *Diporeia* and zooplankton). Yellow perch predation on eggs may have also influenced the offshore food web by decreasing the recruitment of alewife. Egg predation by strong year classes of yellow perch, in combination with predation on adult alewife by salmonids, may both have contributed to low alewife abundance. One would then expect that a combination of decreased predation by both yellow perch and salmonids would result in increased abundance of alewife. This prediction is being tested now, as yellow perch year classes have been weak or very weak since 1990 (Shroyer and McComish 1995) while the stocking rate of salmonids has been relatively stable. In concert with this chain of conditions, alewife catches in Indiana waters have been relatively higher in the 1990s (Shroyer and McComish 1995).

Conclusions

Yellow perch abundance in southern Lake Michigan increased by more than an order of magnitude from the 1970s to the 1980s. Two important consequences of this were: (1) increased intraspecific food competition, as indicated by substantial decreases in growth, and (2) intense predation on eggs and possibly larvae of the alewife. Much of the food required by the abundant yellow perch in the 1980s originated from offshore areas. For four important prey groups (zooplankton, the amphipod *Diporeia hoyi*, conspecific age 0+ fish, and alewife eggs), consumption rates by yellow perch in the mid-1980s were similar to the estimated production, supporting the inference that predation rates and intraspecific competition had substantial effects on prey populations.

Yellow perch predation on alewife eggs may have contributed to the low alewife populations during the 1980s. Cannibalism on age 0+ yellow perch in the 1980s may have been a population bottleneck. Recent recovery of the alewife population corresponds with reduced perch populations owing to high fishery exploitation of adult fish and poor recruitment in perch. This combination of intense predation-competition interactions makes both perch and alewife populations subject to rapid, reciprocal changes. These complex nonlinear dynamics provide further evidence that salmonid stocking and management practices for Lake Michigan must be based on: (1) a basic understanding of the ecological interactions among members of this community, and (2) an effective and continuing forage stock assessment program.

Acknowledgments

This study was supported by grants to S.H. from the Swedish Natural Science Research Council (NFR) and to J.F.K. from the University of Wisconsin Sea Grant Program. Gary Eck and Lisa Eby provided us with their unpublished data. Ed Rutherford and Brett Johnson gave valuable comments on an earlier version of the manuscript.

References

Alm, G. 1952. Year class fluctuations and span of life of perch. Inst. Freshwater Res. Drottningholm Rep. 33:17-38.

Becker, G.C. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison.

Bergh, C.M. 1977. Food habits of the yellow perch in Indiana waters of Lake Michigan near Michigan City, Indiana, in 1971-72. M.S. thesis, Ball State University, Muncie, Indiana.

Brandt, S.B., D. M. Mason, D.B. MacNeill, and T. Coates. 1987. Predation by alewives on yellow perch in Lake Ontario. Trans. Am. Fish. Soc. 116:641-645.

Brazo, D.C., P.I. Tack, and C.R. Liston. 1975. Age, growth, and fecundity of yellow perch, *Perca flavescens*, in Lake Michigan near Ludington, Michigan. Trans. Am. Fish. Soc. 104:726-730.

Chadwick, E.M.P. 1976. Ecological fish production in a small Precambrian shield lake. Environ. Biol. Fishes 1:13-60.

Collette, B.B., M.A. Ali, K.E.F. Hokanson, M. Nagiec, S.A. Smirnov, J.E. Thorpe, A.H. Weatherley, and J. Willemsen. 1977. Biology of the percids. J. Fish. Res. Board Can. 34:1890-1899.

Crowder, L.B. 1980. Alewife, rainbow smelt and native fishes in Lake Michigan: Competition or predation? Env. Biol. Fish. 5:225-233.

Crowder, L.B., J.J. Magnuson, and S.B. Brandt. 1981. Complementarity in the use of food and thermal habitat by Lake Michigan fishes. Can. J. Fish. Aquat. Sci. 38:662-668.

Crowder, L., M. McDonald, and J. Rice. 1987. Understanding recruitment of Lake Michigan fishes: The importance of size-based interactions between fish and zooplankton. Can. J. Fish. Aquat. Sci. 44 (suppl. 2):141-147.

Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitt. Int. Ver. Limnol. 18:1.

Eck, G., and L. Wells. 1987. Recent changes in Lake Michigan's fish community and their probable causes, with emphasis on the role of the alewife (*Alosa pseudoharengus*). Can. J. Fish. Aquat. Sci. 44 (Suppl. 2):53-60.

Evans, M.S. 1986. Recent major declines in zooplankton populations in the inshore region of Lake Michigan: Probable causes and implications. Can. J. Fish. Aquat. Sci. 43:154-159.

Evans, M.S., M.A. Quigley, and J.A. Wojcik. 1990. Comparative ecology of *Pontoporeia hoyi* populations in southern Lake Michigan: The profundal region versus the slope and shelf regions. J. Great Lakes Res. 16:27-40.

Flath, L.E., and J.S. Diana. 1985. Seasonal energy dynamics in the alewife in southeastern Lake Michigan. Trans. Am. Fish. Soc. 114:328-337.

Francis, J.T., S.R. Robillard, and J. E. Marsden. 1996. Yellow perch management in Lake Michigan: A multi-jurisdictional challenge. Fisheries 21:18-20.

Hess, R. 1994. Report of Lake Michigan Technical Committee. Lake Michigan Committee. Photocopy.

Hewett, S.W., and B.L. Johnson. 1992. Fish bioenergetics model 2. An upgrade of a generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Tech. Rep. WIS-SG-92-250, 2nd edn., 79 pp.

Jude, D.J., and F.J. Tesar. 1985. Recent changes in the inshore forage fish of Lake Michigan. Can. J. Fish. Aquat. Sci. 42:1154-1157.

Jude, D.J., H.T. Tin, G.R.S.P.J. Heufelder, C.P. Madenjian, T.L. Rutecki, P.A. Mansfield, N.A. Auer, and G.E. Noguchi. 1981. Adult, juvenile and larval fish populations in the vicinity of the J.H. Campbell power plant, eastern Lake Michigan, 1977-1980. Great Lakes Research Division, University of Michigan, Ann Arbor, Special Rep. 86.

Kelso, J.R., and T.B. Bagenal. 1977. Percids in unperturbed ecosystems. J. Fish. Res. Board Can. 34:1959-1963.

Kitchell, J.F., and L.B. Crowder. 1986. Predator-prey interactions in Lake Michigan: Model predictions and recent dynamics. Environ. Biol. Fishes 16:205-211.

Kitchell, J.F., D.J. Stewart, and D. Weininger. 1977. Application of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34:1922-1935.

Koonce, J.F., T.B. Bagenal, R.F. Carline, K.E.F. Hokansson, and M. Nagiec. 1977. Factors influencing year-class strength of percids: A summary and a model of temperature effects. J. Fish. Res. Board Can. 34:1900-1909.

Lantry, B. 1991. Ecological energetics of rainbow smelt in the Laurentian Great Lakes: An interlake comparison. M.S. thesis, State University of New York, Syracuse.

Lantry, B.F., and D.J. Stewart. 1993. Ecological energetics of rainbow smelt in the Laurentian Great Lakes: An interlake comparison. Trans. Am. Fish. Soc. 122:951-976.

MacLean, J., and J.J. Magnuson. 1977. Species interactions in percid communities. J. Fish. Res. Board Can. 34:1941-1951.

Mansfield, P.J., and D.J. Jude. 1986. Alewife (*Alosa pseudoharengus*) survival during the first growth season in southeastern Lake Michigan. Can. J. Fish. Aquat. Sci. 43:1318-1326.

McComish, T.S. 1989. Selected characteristics of the yellow perch stock in Indiana waters of Lake Michigan, 1984-88. Federal aid project 3-387-R. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

McComish, T.S. 1992. Yellow perch population characteristics in Indiana waters of Lake Michigan. 1991 Project Performance Report 1. Federal Aid Project F-18-R, Segment 4.

McDonald, M.E., L.B. Crowder, and S.B. Brandt. 1990. Changes in *Mysis* and *Pontoporeia* populations in southeastern lake Michigan: A response to shifts in the fish community. Limnol. Oceanogr. 35:220-227.

Mills, E.L., J.L. Forney, and K.J. Wagner. 1987. Fish predation and its cascading effect on the Oneida Lake food chain. In: W.C. Kerfoot and A. Sih (eds.), Predation: Direct and indirect impacts on aquatic communities. University Press of New England, Hanover and London, pp. 118-131.

Mills, E.L., J.H. Leach, J.T. Carlton, and C.L. Secor. 1993. Exotic species in the Great Lakes: A history of biotic crises and antropogenic introductions. J. Great Lakes Res. 19:1-54.

Nalepa, T.F. 1987. Long-term changes in the macrobenthos of southern Lake Michigan. Can. J. Fish. Aquat. Sci. 44:515-524.

Ney, J. 1978. A synoptic review of yellow perch and walleye biology. Am. Fish. Soc. Spec. Publ. 11:1-12.

Post, J.R. 1990. Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): In situ estimates and bioenergetic models. Can. J. Fish. Aquat. Sci. 47:554-560.

Shroyer, S.M., and T.S. McComish. 1995. Characteristics of the near-shore non-salmonine fish community in Indiana waters of Lake Michigan, with emphasis on yellow perch. Report from Aquatic Biology and Fisheries, Department of Biology, Ball State University.

Sprules, W.G., S.B. Brandt, D.J. Stewart, M. Munawar, E.H. Jin, and J. Love. 1991. Biomass size spectrum of the Lake Michigan pelagic food web. Can. J. Fish. Aquat. Sci. 48:105-115.

Stewart, D.J., and F.P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: An energetics-modeling synthesis. Trans. Am. Fish. Soc. 115:643-661.

Stewart, D.J., J.F. Kitchell, and L.B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Trans. Am. Fish. Soc. 110:751-763.

Szalai, A.J., and T.A. Dick. 1991. Role of predation and parasitism in growth and mortality of yellow perch in Dauphin Lake, Manitoba. Trans. Am. Fish. Soc. 120:739-751.

Tarby, M.L. 1974. Characteristics of yellow perch cannibalism in Oneida Lake and the relation to first year survival. Trans. Am. Fish. Soc. 103:462-471.

Tesar, F., D.J. Jude, H. Tin, and P. Mansfield. 1986. Ecology of fish in nearshore southeastern Lake Michigan, 1973-1982. In: R. Rossman (ed.), Southeastern nearshore Lake Michigan: Impact of the Donald C. Cook nuclear plant. University of Michigan, Ann Arbor, Great Lakes Research Division, Publ. 22:353-399.

Thorpe, J. 1977. Synopsis of biological data on the perch *Perca fluviatilis* Linnaeus, 1758 and *Perca flavescens* Mitchill, 1814. FAO Fisheries Synopsis 113.

Treasurer, J.W., R. Owen, and E. Bowers. 1992. The population dynamics of pike, *Esox lucius*, and perch, *Perca fluviatilis*, in a simple predator-prey system. Environ. Biol. Fishes 34:65-78.

Wells, L. 1977. Changes in yellow perch (*Perca flavescens*) populations of Lake Michigan, 1954-75. J. Fish. Res. Board Can. 34:1821-1829.

Wells, L. 1980. Food of alewives, yellow perch, spottail shiners, trout-perch, and slimy and fourhorn sculpins in southeastern Lake Michigan. U.S. Fish Wildl. Serv., Tech. Pap. 98:1-12.

Wells, L., and S.C. Jorgenson. 1983. Population biology of yellow perch in southern Lake Michigan, 1971-79. U.S. Fish Wildl. Serv., Tech. Pap. 109:1-19.

Winnell, M.H., and D.S. White. 1984. Ecology of shallow and deep water populations of *Pontoporeia hoyi* (Smith) (Amphipoda) in Lake Michigan. Freshwater. Invertebr. Biol. 3:118-138.

Confirming Forage Fish Food Web Dependencies in Prince William Sound Using Natural Stable Isotope Tracers

Thomas C. Kline, Jr.
Prince William Sound Science Center, Cordova, Alaska

Abstract

Natural abundances of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ were measured in plankton and nekton samples collected in 1994 and 1995 throughout Prince William Sound, Alaska (PWS), and selected locations in the northern Gulf of Alaska (GOA).

Values of $\delta^{15}N$ were used to determine realized trophic levels (TL) of potential forage and predator nekton species using the copepod *Neocalanus cristatus* as a reference.

A $\delta^{13}C$ gradient is suggested for carbon in the study area plankton, with high ^{13}C in PWS and low ^{13}C in the GOA. The interplay of these carbon sources is hypothesized to play a role in PWS food web nutrition. The initial focus of analytical work was addressed to resolving the relationship of $\delta^{13}C$ to GOA versus PWS carbon sources. These analyses consisted of extensive isotopic analyses of individuals of the herbivorous copepod *N. cristatus* taken from bulk net plankton samples collected during oceanographic surveys in 1994 and 1995. Copepods feeding in the GOA were significantly ^{13}C-depleted compared to those feeding in PWS consistent with a source isotope effect.

After removing lipid- and trophic-level isotope effects from nekton $\delta^{13}C$, it was possible to assess significance of the GOA and PWS carbon sources. This approach was used to determine the relative importance of GOA-origin carbon, which was found to vary among “forage fish” species. By combining isotopic with energetic analyses, it is possible to ascertain which locations in PWS are most dynamic with respect to transfer of energy into food webs via forage fishes.

Introduction

The failure of several Prince William Sound, Alaska, vertebrate species to recover from population crashes following the 1989 T/V *Exxon Valdez* oil spill (EVOS), has raised concerns that shifts in food web structure may have occurred. Of particular concern is recruitment of *Clupea pallasi* (Pacific herring), presently at a historical low in abundance in PWS, a fjord-like inland sea that receives oceanic water from the Gulf of Alaska via the Alaska coastal current (Niebauer et al. 1994). The emergent hypothesis is that when large herbivorous copepods of the genus *Neocalanus* and other macrozooplankton, primary sources of food for predatory fishes (Parsons 1987), are in low abundance, these fishes resort to piscivory. Prey include *Clupea*, *Oncorhynchus* spp. fry including *O. gorbuscha* (pink salmon, also impacted by the oil spill), and other age 0+ fishes that can be regarded as "forage fish" species. Predator species were expected to be dominated by gadid species in the pelagic system. The switch to piscivory is hypothesized to be a factor in recruitment of fishes, many of which are also important as forage for birds, and mammal species that were also affected by EVOS in PWS.

Confirmation of the hypothesis that macrozooplankton availability and related processes control fisheries recruitment is being tested in a large-scale multidisciplinary project known as Sound Ecosystem Assessment (SEA). Because of their predictable nature, stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) are providing an effective method for testing this hypothesis. Natural stable isotope ratio analyses of fishes, their prey, and their predators serve as effective tracers of energy supply thus providing insight into habitat usage and assisting in quantifying amounts of carbon and by extension, energy, derived from various areas of production. Nitrogen stable isotope ratios provide excellent definition of relative trophic level (Fry 1988, Wada et al. 1991, Hobson and Welch 1992, Kiriluk et al. 1995). The heavy isotope of nitrogen, ^{15}N, is enriched by about 0.34% (or 3.4 per mil in conventional delta units, see Materials and Methods) with each trophic level (Minagawa and Wada 1984) and has been shown to accurately indicate the realized trophic level of species within an ecosystem (Kling et al. 1992, Cabana and Rasmussen 1994). Carbon isotope signatures can effectively be used to trace multiple sources of carbon into food webs once it can be established that these sources have distinctive isotopic signatures (Fry and Sherr 1984, Wada et al. 1991). The data obtained from stable isotope measurements are unique in that they trace assimilated material and thus can be used for accurate ecosystem process modeling (e.g., Wada et al. 1991, Conway et al. 1994, Macko and Ostrom 1994, Michener and Schell 1994, Nadelhofeffer and Fry 1994).

Because of their predictable relationship when comparing consumers to diet, stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) effectively provide empirical evidence of trophic relationships in marine food webs. Natural abundance of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ of Prince William Sound pelagic biota were measured in samples collected from 1994 to 1995. Values of $\delta^{15}N$ were used to determine trophic level (TL) relative to *N. cristatus* whereas $\delta^{13}C$ values were used to differentiate carbon derived from Gulf of Alaska production versus carbon produced within Prince William Sound.

Materials and Methods

Sampling

Nekton and zooplankton were sampled from a variety of vessels ranging from a 25-m trawler, F/V *Alaska Beauty*, equipped with a 40- by 28-m midwater wing trawl (2.0 cm stretch-mesh web codend) to small fry skiffs and seine boats that participated as part of the SEA project. Zooplankton samples were collected with a 335 µ-mesh, 0.5-m-diameter ring net towed vertically to the surface from station depth and 50 m at designated SEA project stations. Life history stage copepodid-V (C5) *N. cristatus* were picked from zooplankton samples and analyzed as individuals. Sampling of nekton for stable isotope analysis consisted of a section (~1 g) of epaxial muscle (fishes) or mantle (squid) for those with lengths > ~100 mm or the whole organism for those <100 mm. Samples were frozen (–20°C) on board the vessel for later laboratory preparation for natural stable isotope abundance analysis.

Laboratory preparation

The gastrointestinal tract was removed from whole fish samples to remove dietary material from samples.

All samples were stored frozen until freeze dried (Labconco) and ground to a fine powder with a dental amalgamator (Crescent Dental Wig-L-Bug). Replicate aliquots of ~1.5 mg (except for individual samples of *Neocalanus* which were too small for more than one analysis) were weighed to the nearest microgram and then loaded into combustion boats for mass spectrometric analysis.

Isotopic determination

A Europa Scientific model 20/20 stable isotope analyzer equipped with a Europa Scientific Roboprep sample preparation and purification unit was used. Analytical results include $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios in standard delta units, $\delta^{13}C$ and $\delta^{15}N$, respectively, and %C and %N.

Standard delta notation is used to express stable isotope ratios, which are reported relative to international standards (air for N and Vienna Peedee belemnite for C) and defined by the following expression:

$$\delta^{15}\mathrm{N} \text{ or } \delta^{13}\mathrm{C} = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000 \text{ per mil} \qquad (1)$$

where $R = {}^{15}\mathrm{N}/{}^{14}\mathrm{N}$ or ${}^{13}\mathrm{C}/{}^{12}\mathrm{C}$ (after Craig 1957). The isotope standards have delta values of 0 by definition, i.e., $\delta^{15}\mathrm{N} = 0$ for atmospheric N_2. Naturally occurring $\delta^{15}\mathrm{N}$ and $\delta^{13}\mathrm{C}$ values observed in biota range from ~0 to ~ +20 and from ~ 0 to ~ −50, respectively. The negative $\delta^{13}\mathrm{C}$ values reflect the relative enrichment of ${}^{13}\mathrm{C}$ in the limestone standard compared with biota.

Samples were rerun when replication was poor (difference in delta units >0.6). Typically, replication is <0.2 delta units. The %C and %N data were used to calculate C/N. Mean of $\delta^{13}\mathrm{C}$, $\delta^{15}\mathrm{N}$, and C/N replicates were used for further analysis.

Lipid normalization

Normalization for lipid composition was by the method of McConnaughey and McRoy (1979) using their C/N lipid proxy:

$$L = \frac{93}{\left(1 + \frac{1}{0.246\,\mathrm{C/N} - 0.775}\right)} \tag{2}$$

used to calculate lipid-normalized $\delta^{13}\mathrm{C}$ (expressed as $\delta^{13}\mathrm{C}'$):

$$\delta^{13}\mathrm{C}' = \delta^{13}\mathrm{C} + 6\left(\frac{3.9}{1 + \frac{287}{L}} - 1\right) \tag{3}$$

Trophic level and normalization

The enrichment of ${}^{15}\mathrm{N}$ that results from a feeding process (Minagawa and Wada 1984) enables one to use $\delta^{15}\mathrm{N}$ as a good proxy for trophic level (Fry 1988, Kling et al. 1992, Cabana and Rasmussen 1994). *Neocalanus* spp. are the dominant herbivores in the plankton community of the North Pacific (Miller et al. 1984). Although *N. cristatus* are facultatively carnivorous on planktonic Protozoa, they cannot be sustained on such a diet (Gifford 1993). Thus, the a priori trophic level (*TL*) of 2 (i.e., herbivores) was applied to the $\delta^{15}\mathrm{N}$ of *N. cristatus* as a baseline for estimation of *TL* of other taxa. The $\delta^{15}\mathrm{N}$ values corresponding to higher *TL*s were estimated by adding the ${}^{15}\mathrm{N}$ trophic fractionation factor, $\varepsilon_\mathrm{N} = 3.4$, to the value obtained for next lower *TL*; e.g., 3.4 was added to the $\delta^{15}\mathrm{N}$ of *N. cristatus* to estimate the $\delta^{15}\mathrm{N}$ of *TL* = 3.

Values of $\delta^{13}\mathrm{C}$ were normalized for TL as well as lipid content so as to have the residual variation reflect $\delta^{13}\mathrm{C}$ of the carbon source. Normalization for trophic enrichment of ${}^{13}\mathrm{C}$ using the trophic enrichment factor, $\varepsilon_\mathrm{C} = 1$, to the reference *TL* (the *TL* of *N. cristatus*) was made using the following relationship:

$$\delta^{13}\mathrm{C}'_{TL} = \delta^{13}\mathrm{C}' - \varepsilon_C(\delta^{15}\mathrm{N}_{sample} - \delta^{15}\mathrm{N}_{Neocalanus}) / \varepsilon_N \tag{4}$$

where $\delta^{13}C'_{TL}$ is the *TL* normalized $^{13}C/^{12}C$ value of $\delta^{13}C'$, $\varepsilon_C = 1$ (DeNiro and Epstein 1978, McConnaughey and McRoy 1979, Rau et al. 1983, Fry and Sherr 1984, Hobson and Welch 1992), the $\delta^{15}N$ values are those of the sample and *Neocalanus*, and $\varepsilon_N = 3.4$ (Minagawa and Wada 1984, Owens 1987). This normalization makes it possible to make direct $\delta^{13}C$ comparisons between the sample in question with *Neocalanus*, which is being used as representative of the organic carbon pool at the herbivore level.

Results and Discussion

Neocalanus herbivore (TL = 2) reference

The 938 individual *N. cristatus* sampled from 1994 through 1995 had a mean $\delta^{15}N = 8.0$ (SD = 1.8). This $\delta^{15}N$ value of 8.0 was used as the *TL* = 2 (herbivore) reference value. The $\delta^{15}N$ values for *TL* = 3 and 4 calculated using (4) were 11.4 and 14.8, respectively. Values of $\delta^{13}C$ of stage C5 *N. cristatus* feeding (only those sampled from upper 50 m during March-June 1995) in the northern GOA just south of the entrance to PWS were found to be consistently dichotomous when compared to those from within PWS (Kline 1996). Feeding C5 *N. cristatus* from the GOA had $\delta^{13}C = -24.4$ (SD = 1.4, N = 33) and $\delta^{13}C' = -23.1$ (SD = 1.1, N = 33) whereas those from PWS had $\delta^{13}C = -20.2$ (SD = 1.1, N = 99) and $\delta^{13}C' = -19.7$ (SD = 0.9, N = 99). Thus organic carbon in the form of zooplankton from the northern GOA is ^{13}C-depleted by ~4 per mil compared with PWS. This gradient is similar to the ~2.5 per mil gradient in $\delta^{13}C$ between the Bering Sea and the GOA at the Aleutian passes (Schell 1996) and the 7 per mil $\delta^{13}C$ gradient found across Drake Passage (Rau et al. 1991).

Nekton database

Data from 1,592 nekton samples consisting principally of fishes collected in 1994 and 1995 from PWS and analyzed for $\delta^{15}N$ and $\delta^{13}C$ are presented in this paper. Invertebrate nekton included squid (*Berryteuthis magister*) and glass shrimp (*Pasiphaea pacifica*). Nekton $\delta^{15}N$ values were plotted against length to suggest how nekton shift in *TL* as a function of size (Figure 1A). This plot also provides an indication of the nekton size distribution in the database. The large cluster of nekton ≤180 mm in Figure 1A has a $\delta^{15}N$ of ~ +12 suggesting a *TL* ~ 3 consistent with the concept of a forage class *TL*. Higher *TL*s are indicated by higher $\delta^{15}N$. Thus $\delta^{15}N$ defines a forage class by realized *TL* (Kling et al. 1992) and size class. Larger nekton, more likely to be predators, show considerable *TL* variability (from ~ *TL* = 3 to *TL* > 4) consistent with some zooplankton foraging which is expected to vary according to the SEA hypotheses. Values of $\delta^{13}C$ and $\delta^{15}N$ are expected to increase with *TL* (DeNiro and Epstein 1978, McConnaughey and McRoy 1979, Rau et al. 1983, Fry and Sherr 1984, Minagawa and Wada 1984, Owens 1987, Hobson and Welch 1992, Kiriluk et al. 1995) at a ratio of 1/3.4 (the ratio of $\varepsilon_C/\varepsilon_N$, the trophic fractionation factors). The scatterplot and linear regression of the nekton database (Figure 1B) has a slope inconsistent with this ratio. This fact, the low correlation coefficient of $r^2 = 0.37$, and the wide scatter of $\delta^{13}C$ suggest that a significant source of variation is independent of *TL*. Note, however, that normalization for *TL* (Figure 1C) resulted in a decrease in the correlation ($r^2 = 0.14$). *TL*-normalized $\delta^{13}C$ values when plotted against C/N (Figure 1D) show the effect of increased C/N on $\delta^{13}C$ (McConnaughey and McRoy 1979, Rau et al. 1992). When C/N was used to normalize for lipid content, in addition to *TL* normalization, the slopes of the regressions of the net result, $\delta^{13}C'_{TL}$, with $\delta^{15}N$ (Figure 1E) and C/N (Figure 1F) was eliminated, validating the use of the C/N correction for lipid content (Rau et al. 1992). The *TL*- and lipid-normalized values when replotted vs. length (Figure 1G) also had no slope. The variance in $\delta^{13}C'_{TL}$ shown in Figure 1G thus reflects isotope effects other than lipid content or *TL*.

The coincidence of the large *Neocalanus* $\delta^{13}C'$ gradient between the GOA and PWS with the nekton $\delta^{13}C'_{TL}$ (recall that the *TL* normalization normalizes the $\delta^{13}C'$ value to the same *TL* as *Neocalanus*, making the $\delta^{13}C'$ values comparable) value distribution suggests that GOA-derived productivity is important for nekton. Periodic flow reversals at Hinchinbrook Entrance (Niebauer et al. 1994), downward diapause migration of C5 *Neocalanus* spp. during the late spring (Miller 1993) coinciding with deep water renewal in PWS (Niebauer et al. 1994), and simultaneous transport of zooplankton by the landward movement of coastal waters (Cooney 1986) suggest mechanisms that could transport secondary productivity into PWS. Low $\delta^{13}C'_{TL}$ values (e.g., values $< \sim -21$) measured in the nekton are consistent with the flux of carbon from outside PWS making its way into food chains there. Thus $\delta^{13}C'_{TL}$ values of nekton provide direct evidence for the hypothesis of plankton flow into PWS influencing nekton production. From the $\delta^{15}N$-based *TL* determination (Figure 1A), nekton $< \sim 180$ mm can be defined as “forage fishes.” Figure 1H shows the data from Figure 1G, but restricted to nekton ≤180 mm, where it can be seen that a substantial portion of the forage class nekton has $\delta^{13}C'_{TL}$ consistent with utilization of carbon derived from the GOA. However, most data points in Figure 1G appear between $\delta^{13}C'_{TL} = -20$ and -22 suggesting a significant overlap in use of both PWS as well as GOA carbon. Further analysis examines the forage fishes (and other nekton) by species (Figure 2).

Forage class nekton by species

Box and whisker plots of $\delta^{15}N$ data of nekton ≤180 mm (Figure 2A) suggest species-level differences in realized *TL* (Kling et al. 1992). Whereas most species had $\delta^{15}N$ consistent with $TL = 3$, i.e., primary carnivores, northern lanternfish were about 0.5 *TL* higher. Conversely, walleye pollock (these consisted of <100-mm young of the year) were consis-

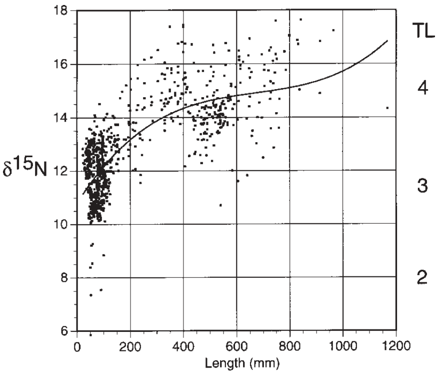


Figure 1A. Isotopic analysis of Prince William Sound nekton. Nekton δ^{15}N values suggesting trophic level (TLs indicated on right axis) change as a function of length; based on the herbivorous copepod, Neocalanus cristatus, reference (r^2 = 0.56, P = 0 .0001; β coefficient X, P = 0.0001, β coefficient X^2, P = 0.0001, β coefficient X^3, P = 0.0001).

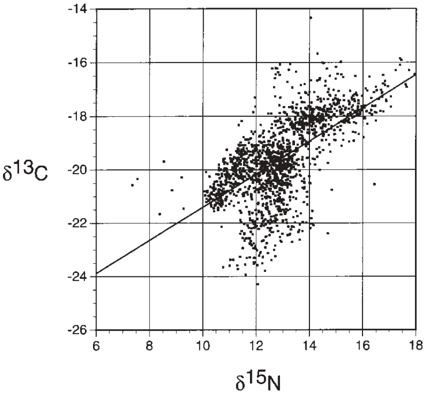


Figure 1B. Nekton δ^{13}C as a function of δ^{15}N. Regression line (r^2 = 0.37, P = 0.0001) slope = 0.62 (SE = 0.02, P = 0.0001) which differed from the ratio of the trophic fractionation factors $\varepsilon_C/\varepsilon_N$= 1.0/3.4 = 0.29.

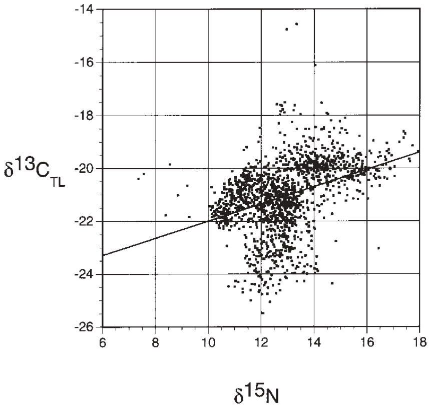


Figure 1C. Data in Figure B replotted following normalization of δ^{13}C for trophic level which reduced the correlation, r^2, to 0.14 (P = 0.0001) and slope to 0.32 (SE = 0.02, P = 0.0001).

Figure 1D. Trophic level normalized $\delta^{13}C$ *varied as a function of C/N as expected because of lipid isotope effects (*$r^2 = 0.60$*,* $P = 0.0001$*;* β *coefficient X,* $P = 0.0001$*,* β *coefficient* X^2*,* $P = 0.0001$*,* β *coefficient* X^3*,* $P = 0.0001$*).*

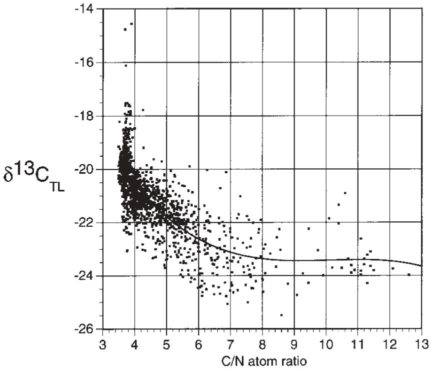


Figure 1E. Normalization for trophic level and C/N eliminated the relationship of $\delta^{13}C$ *with* $\delta^{15}N$ *(*$r^2 = 0.04$*,* $P = 0.0001$*; slope = 0.12, SE = 0.01,* $P = 0.0001$*; compare with Figure 1B).*

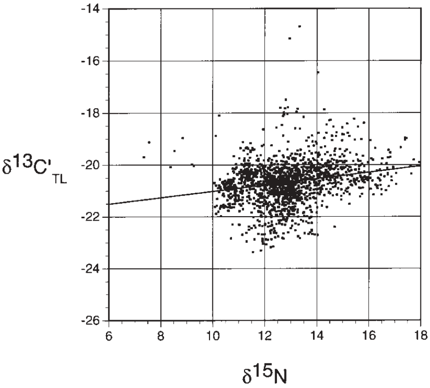


Figure 1F. Normalization for trophic level and C/N eliminated relationship of $\delta^{13}C$ *with C/N (*$r^2 = 0.07$*,* $P = 0.0001$*;* β *coefficient X,* $P = 0.0001$*,* β *coefficient* X^2*,* $P = 0.0072$*,* β *coefficient* X^3*,* $P = 0.072$*; compare with Figure 1D).*

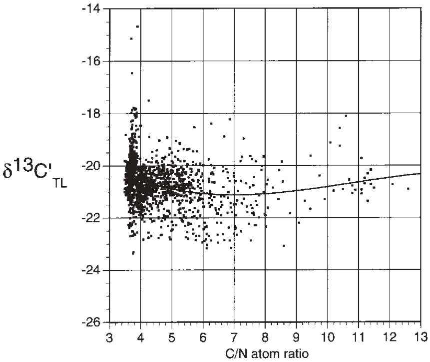


Figure 1G. Relationship of $\delta^{13}C'_{TL}$ with length suggesting carbon source variation throughout size range ($r^2 = 0.04$, $P = 0.0001$; slope $= 0.001$, $P = 0.0001$); SD of N. cristatus $\delta^{13}C'$ values from PWS and the GOA indicated by bars on right axis.

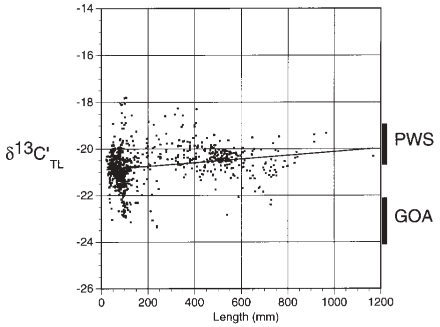
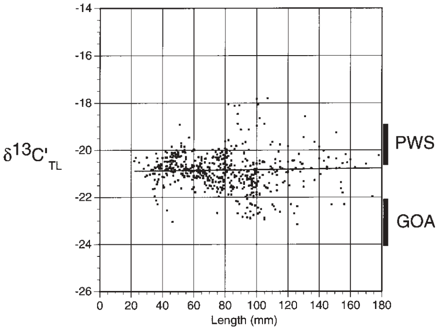


Figure 1H. Data from Figure 1G expanded to show only "foragefish," i.e., those nekton ≤180 mm.



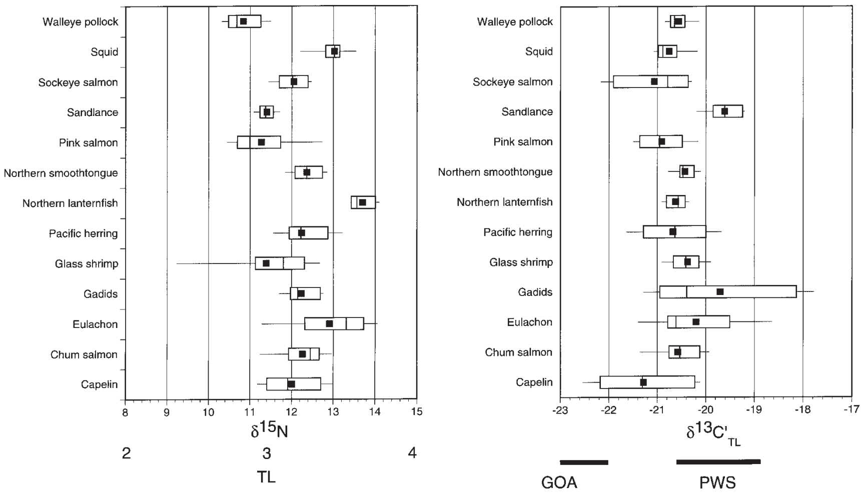


Figure 2. Isotopic analysis of Prince William Sound forage-class nekton by species. A (left). "Forage-fish" $\delta^{15}N$ box and whisker plots (10, 25, 50, 75, and 90th percentiles and means are indicated) and interpreted TLs suggesting species-level differences in realized trophic level. B (right). "Forage-fish" (box and whisker plots as in Figure 2A) and Neocalanus cristatus (SD range of samples from the GOA and PWS) $\delta^{13}C'_{TL}$ suggesting species-level differences in dependency on carbon source.

tently lower in TL. Glass shrimp had the greatest range in $\delta^{15}N$ consistent with facultative herbivory although principally carnivorous.

Box and whisker plots of $\delta^{13}C'_{TL}$ data of nekton ≤180 mm (Figure 2B) suggest some variance in carbon source dependencies. There was spatial variability in the degree to which GOA-derived carbon is found in young-of-the-year herring which was concordant with energetic content (Kline and Paul In press). Those fishes with higher GOA content (i.e., more negative $\delta^{13}C'_{TL}$ values), such as capelin and pink salmon fry, are more likely to have been affected by variance in flux of zooplankton from the GOA to PWS. Conversely, those species with high $\delta^{13}C'_{TL}$, such as juvenile gadids and sand lance, are likely not to be directly affected by zooplankton inputs. These results thus provide evidence of bottom-up effects with an inherent source of environmental variability. Particularly noteworthy are potential species-level differential effects that could result in the advantage of one species over another as a function of oceanographic conditions that moderate zooplankton flux from the GOA to PWS.

Summary

In summary: (1) $\delta^{15}N$ relates to trophic level and can be used to delineate forage-class species; (2) $\delta^{13}C'_{TL}$ can be related to carbon source which can be related to oceanographic processes affecting nekton production; and (3) species-level differences in dependencies on GOA carbon exist within the forage fish class nekton, suggesting bottom-up effects in community structure.

Acknowledgments

The research described in this paper was part of the Sound Ecosystem Assessment (SEA) project funded by the *Exxon Valdez* Oil Spill Trustee Council. However, the findings and conclusions presented by the author are his own and do not necessarily reflect the views or position of the council. The author acknowledges Captain Mike Geagel, the crew of the R/V *Bering Explorer*, E. Stockmar, and B. Barnett for field and laboratory assistance in zooplankton sampling. The author acknowledges the captains and crews of the F/V *Alaska Beauty* and other fishing vessels used in this study. M. Powell, K. Antonucci, and D. Salmon collected the majority of the nekton samples. E. Brown and M. Willette coordinated the nekton sampling. Preparation of samples for mass spectrometry was done by R. Sundown, K. Antonucci, and B. Barnett. B. Barnett was responsible for the mass spectrometry. Discussions with D. Schell and R. Spies on isotope gradients, with T. Cooney and L. Tuttle on *Neocalanus* life histories, and with D. Salmon and S. Vaughan on regional physical oceanography provided the author with much insight.

References

Cabana, G., and J. B. Rasmussen. 1994. Modeling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. Nature 372:255-257.

Conway, N.M., M.C. Kennicut II, and C.L. Van Dover. 1994. Stable isotopes in the study of marine chemosynthetic-based ecosystems. In: K. Lajtha and R.H. Michener (eds.), Stable isotopes in ecology and environmental science. Blackwell, Oxford, England, pp. 158-186.

Cooney, R.T. 1986. The seasonal occurrence of *Neocalanus cristatus*, *Neocalanus plumchrus*, and *Eucalanus bungii* over the shelf of the northern Gulf of Alaska. Contintental Shelf Res. 5:541-553.

Craig, H. 1957. Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. Geochim. Cosmochim. Acta 12:133-149.

DeNiro, M.J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochim. Cosmochim. Acta 42:495-506.

Fry, B. 1988. Food web structure on the Georges Bank from stable C, N, and S isotopic compositions. Limnol. Oceanogr. 33:1182-1190.

Fry, B., and E.B. Sherr. 1984. $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. Contrib. Mar. Sci. 27:13-47.

Gifford, D.J. 1993. Protozoa in the diets of *Neocalanus* spp. in the oceanic subarctic Pacific. Prog. Oceanogr. 32:223-237.

Hobson, K.A., and H.E. Welch. 1992. Determination of trophic relationships within a High Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar. Ecol. Prog. Ser. 84:9-18.

Kiriluk, R.M., M.R. Servos, D.M. Whittle, G. Cabana, and J. Rasmussen. 1995. Using ratios of stable nitrogen and carbon isotopes to characterize the biomagnification of DDE, mirex, and PCB in a Lake Ontario pelagic food web. Can. J. Fish. Aquat. Sci. 52:2660-2674.

Kline, T.C. 1996. Recruitment of *Neocalanus cristatus* into Prince William Sound (Alaska, USA) evidenced by natural stable isotope abundance. EOS, Transactions A.G.U. 76(3):OS43.

Kline, T.C., and A.J. Paul. In press. Fall isotopic and somatic energy signatures of young of the year Pacific herring at two sites in Prince William Sound, Alaska: Implications for trophic studies.

Kling, G.W., B. Fry, and W.J. O'Brien. 1992. Stable isotopes and plankton trophic structure in arctic lakes. Ecology 73:561-566.

Macko, S.A., and N.E. Ostrom. 1994. Pollution studies using stable isotopes. In: K. Lajtha and R.H. Michener (eds.), Stable isotopes in ecology and environmental science. Blackwell, Oxford, England, pp. 45-62.

McConnaughey, T., and C.P. McRoy. 1979. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. Mar. Biol. 53:257-262.

Michener, R.H., and D.M. Schell. 1994. Stable isotope ratios as tracers in marine aquatic food webs. In: K. Lajtha and R.H. Michener (eds.), Stable isotopes in ecology and environmental science. Blackwell, Oxford, England, pp. 138-157.

Miller, C.B. 1993. Development of large copepods during spring in the Gulf of Alaska. Prog. Oceanogr. 32:295-317.

Miller, C.B., B.W. Frost, H.P. Batchelder, M.J. Clemons, and R.E. Conway. 1984. Life histories of large, grazing copepods in a subarctic ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in the northeast Pacific. Prog. Oceanogr. 13:201-243.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}N$ and animal age. Geochim. Cosmochim. Acta 48:1135-1140.

Nadelhoffer, K.J., and B. Fry. 1994. Nitrogen isotopes studies in forest ecosystems. In: K. Lajtha and R.H. Michener (eds.), Stable isotopes in ecology and environmental science. Blackwell, Oxford, England, pp. 22-44.

Niebauer, H.J., T.C. Royer, and T.J. Weingartner. 1994. Circulation of Prince William Sound, Alaska. J. Geophys. Res. 99:113-126.

Owens, N.J.P. 1987. Natural variations in ^{15}N in the marine environment. Adv. Mar. Biol. 24:389-451.

Parsons, T.R. 1987. Ecological relations. In: D.W. Hood and S.T. Zimmerman (eds.), The Gulf of Alaska: Physical environment and biological resources. U.S. Government Printing Office, Washington, DC, pp. 561-574.

Rau, G.H., T. Takahashi, D.J. Des Marais, and C.W. Sullivan. 1991. Particulate organic matter δ^{13}C variations across the Drake Passage. J. Geophys. Res. 96:15131-15235.

Rau, G.H., D.G. Ainley, J.L. Bengtson, J.J. Torres, and T.L. Hopkins. 1992. ^{15}N/^{14}N and ^{13}C/^{12}C in Weddell Sea birds, seals, and fish: Implications for diet and trophic structure. Mar. Ecol. Prog. Ser. 84:1-8.

Rau, G.H., A.J. Mearns, D.R. Young, R.J. Olson, H.A. Schaffer, and I.R. Kaplan. 1983. Animal ^{13}C/^{12}C correlates with trophic level in pelagic food webs. Ecology 64:1314-1318.

Schell, D.M. 1996. Testing conceptual models of marine mammal trophic dynamics using carbon and nitrogen stable isotope ratios. OCS Study MMS 95-0057, U.S. Dep. Interior, pp. 86-96.

Wada, E., H. Mizutani, and M. Minagawa. 1991. The use of stable isotopes for food web analysis. Crit. Rev. Food Sci. Nutr. 30:361-371.