

The Southeast Bering Sea Ecosystem: Implications for Marine Resource Management

Final Report: Southeast Bering Sea Carrying Capacity
June 2004



US Department of Commerce
National Oceanic and Atmospheric Administration
National Ocean Service
Center for Sponsored Coastal Ocean Research
Coastal Ocean Program



DECISION ANALYSIS SERIES

The Decision Analysis Series has been established by NOAA's Coastal Ocean Program (COP) to present documents for coastal resource decision makers that contain analytical treatments of major issues or topics. The issues, topics, and principal investigators have been selected through an extensive peer review process. To learn more about the COP or the Decision Analysis Series, please write:

NOAA
Coastal Ocean Program
Room 9700
1315 East West Highway
Silver Spring, MD 20910

phone: 301-713-3338

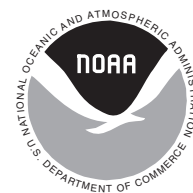
fax: 301-713-4044

web: <http://www.cop.noaa.gov>

Science for Solutions

NOAA COASTAL OCEAN PROGRAM

Decision Analysis Series No. 24



**The Southeast Bering Sea Ecosystem: Implications for
Marine Resource Management**

S. Allen Macklin¹ and George L. Hunt, Jr.² (Editors)

¹National Oceanic and Atmospheric Administration
Pacific Marine Environmental Laboratory
7600 Sand Point Way NE
Seattle, WA 98115

²University of California Irvine
Department of Ecology and Evolutionary Biology
Irvine, CA 92697

June 2004

U.S. DEPARTMENT OF COMMERCE

Donald L. Evans, Secretary

National Oceanic and Atmospheric Administration

Conrad C. Lautenbacher, Jr., Under Secretary for Oceans and Atmosphere

National Ocean Service

Richard Spinrad, Assistant Administrator

Center for Sponsored Coastal Ocean Research/Coastal Ocean Program

Robert Magnien, Director

This publication should be cited as:

Macklin, S.A., and G.L. Hunt, Jr. (Editors), 2004. The Southeast Bering Sea Ecosystem: Implications for Marine Resource Management (Final Report: Southeast Bering Sea Carrying Capacity). NOAA Coastal Ocean Program Decision Analysis Series No. 24, Silver Spring, MD 20910, 192 pp.

NOTICE

Mention of a commercial company or product does not constitute an endorsement by NOAA/ERL. Use of information from this publication concerning proprietary products or the tests of such products for publicity or advertising purposes is not authorized.

Contribution No. 2658 from NOAA/Pacific Marine Environmental Laboratory
Contribution S529 from Fisheries-Oceanography Coordinated Investigations

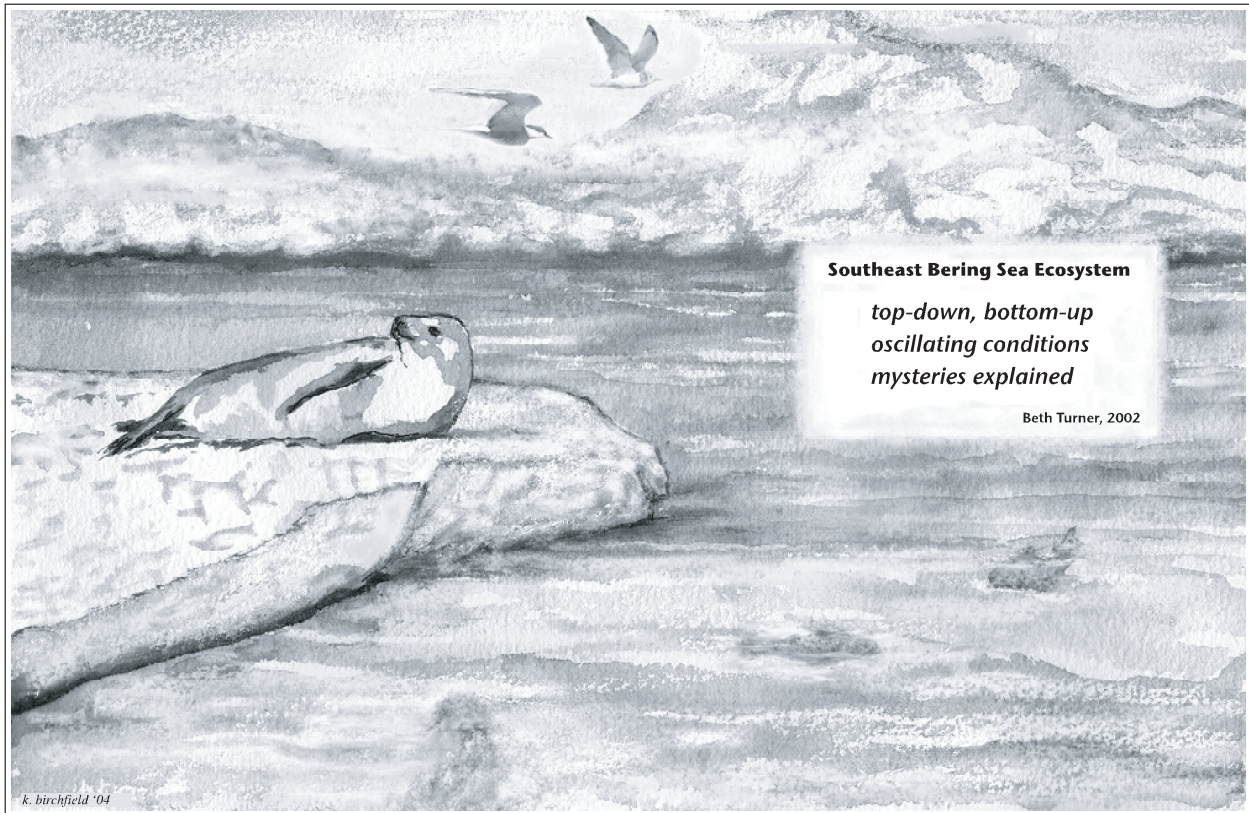
For sale by the National Technical Information Service, 5285 Port Royal Road
Springfield, VA 22161

Contents

Executive Summary	1
Part 1—Introduction	9
Part 2—Synthesis of Research: A Contemporary Understanding of the Southeast Bering Sea Ecosystem	11
2.1 Introduction	11
2.1.1 Brief history and goals of recent research programs	11
2.1.2 Structure of synthesis report	12
2.1.3 Brief description of the Southeastern Bering Sea	12
2.2 Climate and the Bering Sea Marine Ecosystem	15
2.2.1 Climate indices	15
2.2.2 Meteorological forcing	20
2.3 Physical Components of the Eastern Bering Sea Ecosystem	21
2.3.1 Sea Ice in the Eastern Bering Sea	21
2.3.2 Biological importance of the timing of ice retreat	26
2.3.3 Cold pool formation	28
2.3.4 Biological impacts of water temperature	29
2.3.5 On-shelf fluxes and nutrient replenishment	30
2.3.6 Stratification, mixing, and the vertical flux of nutrients	32
2.4 Biological Components of the Eastern Bering Sea Ecosystem	32
2.4.1 Primary production	32
2.4.2 Coccolithophore bloom	34
2.4.3 Zooplankton	38
2.4.4 Fish	44
2.4.5 Marine mammals and seabirds	51
2.5 What Controls Recruitment of Walleye Pollock?	62
2.6 Summary of Advances	68
2.6.1 Marine climate	68
2.6.2 Basin and slope waters	68
2.6.3 Shelf waters	68
2.6.4 Biological components of the ecosystem	69
2.7 Areas of Research Requiring More Attention	70
2.8 Acknowledgments	72
Part 3—Forecasting Abundance of Walleye Pollock: Indices for Juvenile Abundance	73
3.1 Introduction	73
3.2 Conceptual Framework for Development of Indices	76
3.2.1 A pollock-centric perspective of the southeastern Bering Sea ecosystem	76
3.2.2 A generic model of pathways of energy flow through the ecosystem	77
3.2.3 Other aspects of indices development	79
3.3 Development of Environmental Indices	80
3.3.1 Indices of stratification, potential supply of nutrients to the upper mixed layer, and turbulence experienced by larval pollock (Carol Ladd and Phyllis Stabeno)	80
3.3.2 An index related to wind turbulence and feeding success (Bern Megrey and Nick Bond)	83

3.3.3	Variations in net short wave radiation: Toward development of an index of when sufficient light exists for primary production (Jeff Napp and Nancy Kachel)	84
3.3.4	Indices related to sea ice (Sigrid Salo and Phyllis Stabeno)	86
3.3.5	Indices related to the cold pool and adjacent fronts (Peggy Sullivan)	89
3.3.6	Pribilof age-0 pollock as an index of pollock year-class strength (Jim Ianelli)	90
3.3.7	Model simulations	95
3.3.8	A matrix for cataloging indices (Allen Macklin)	100
3.4	Application of a Transport and Predation Index to Recruitment for Stock Assessment Purposes (Jim Ianelli)	103
3.4.1	Background	103
3.4.2	An application	105
3.4.3	Discussion	106
3.5	Changing Relationships between Climate and Biological Indices in the Eastern Bering Sea (Alan Springer)	112
3.5.1	Introduction	112
3.5.2	Observations	112
3.5.3	Physical-physical relationships	113
3.5.4	Physical-biological relationships	114
3.5.5	Biological-biological relationships	117
3.5.6	Discussion	120
3.6	Summary	125
3.6.1	Progress accomplished in the development of indices	125
3.6.2	Further development of indices	127
3.6.3	Concluding remarks	128
Part 4—Pribilof Islands: A Microcosm for the Southeast Bering Sea		
4.1	Overview of the Pribilof Island Ecosystem	129
4.2	Working Group Products	130
4.2.1	How large an area is the Pribilof region?	131
4.2.2	How much transport is there to this area from major pollock spawning regions?	132
4.2.3	How does the abundance of juvenile pollock near the Pribilof Islands compare with abundance along the Bering Sea Shelf?	133
4.2.4	How does the abundance of age-0 pollock near the Pribilof Islands relate to diet, survival, and energetics of higher predators?	142
4.2.5	How important is predation to pollock abundance near the Pribilof Islands?	146
4.3	Comparison of abundance of juvenile pollock and zooplankton between the Pribilof Islands and other shelf areas in the eastern Bering Sea based on acoustic surveys in 1997, 1998, and 1999 (Andreas Winter and Kenneth Coyle)	149
4.3.1	Methods	149
4.3.2	Results	154
4.3.3	Discussion	155
4.4	Summary and Conclusions	157
Part 5—SEBSCC Administration and Management		
5.1	Project Management Team	159
5.2	Technical Advisory Committee	161

5.3	Research Council	162
5.4	Project Coordination and Communication	162
5.5	Data Management	163
5.6	Research Structure and Methodology	164
5.7	Resources	165
5.8	Leverage and Collaboration	165
5.9	Research Components and Principal Investigators	165
5.10	Field Operations: SEBSCC Cruise Schedule	170
	Acknowledgments	172
	Part 6—References and SEBSCC Publications	173



Southeast Bering Sea Ecosystem

*top-down, bottom-up
oscillating conditions
mysteries explained*

Beth Turner, 2002

k. birchfield '04

The Southeast Bering Sea Ecosystem: Implications for Marine Resource Management (Final Report: Southeast Bering Sea Carrying Capacity)

S. Allen Macklin and George L. Hunt, Jr. (Editors)

Executive Summary

Background

Southeast Bering Sea Carrying Capacity (SEBSCC, 1996–2002) was a NOAA Coastal Ocean Program project that investigated the marine ecosystem of the southeastern Bering Sea. SEBSCC was co-managed by the University of Alaska Fairbanks, NOAA Alaska Fisheries Science Center, and NOAA Pacific Marine Environmental Laboratory. Project goals were to understand the changing physical environment and its relationship to the biota of the region, to relate that understanding to natural variations in year-class strength of walleye pollock (*Theragra chalcogramma*), and to improve the flow of ecosystem information to fishery managers.

In addition to SEBSCC, the Inner Front study (1997–2000), supported by the National Science Foundation (Prolonged Production and Trophic Transfer to Predators: Processes at the Inner Front of the S.E. Bering Sea), was active in the southeastern Bering Sea from 1997 to 1999. The SEBSCC and Inner Front studies were complementary. SEBSCC focused on the middle and outer shelf. Inner Front worked the middle and inner shelf. Collaboration between investigators in the two programs was strong, and the joint results yielded a substantially increased understanding of the regional ecosystem.

SEBSCC focused on four central scientific issues: (1) How does climate variability influence the marine ecosystem of the Bering Sea? (2) What determines the timing, amount, and fate of primary and secondary production? (3) How do oceanographic conditions on the shelf influence distributions of fish and other species? (4) What limits the growth of fish populations on the eastern Bering Sea shelf? Underlying these broad questions was a narrower focus on walleye pollock, particularly a desire to understand ecological factors that affect year-class strength and the ability to predict the potential of a year class at the earliest possible time. The Inner Front program focused on the role of the structural front between the well-mixed waters of the coastal domain and the two-layer system of the middle domain. Of special interest was the potential for prolonged post-spring-bloom production at the front and its role in supporting upper trophic level organisms such as juvenile pollock and seabirds. Of concern to both programs was the role of interannual and longer-term variability in marine climates and their effects on the function of sub-arctic marine ecosystems and their ability to support upper trophic level organisms.

The eastern Bering Sea contains an Oceanic Regime that occupies the basin and a Shelf Regime that occupies the eastern shelf. The Oceanic Regime of the eastern basin is influenced by Alaska Stream water that enters the Bering Sea through Amchitka and Amukta passes in the Aleutian Islands, and turns northeastward to form the Aleutian North Slope Current. This current is the major source of water for the Bering Slope Current that sometimes follows the depth contours of the eastern shelf northwestward with a regular flow, and sometimes degenerates into an ill-defined, variable flow characterized by numerous eddies and meanders. These eddies are potentially important as habitat for larval and juvenile pollock, and can carry these fish, as well as nutrient salts, from the Oceanic Domain into the Outer Shelf Domain.

The broad continental shelf (up to 500 km wide) of the southeastern Bering Sea is differentiated into three bathymetrically fixed domains: the Coastal Domain that extends from the shore to about the 50-m isobath, the Middle Shelf Domain, between the 50-m and 100-m isobaths, and the Outer Shelf Domain that ranges from 100 m to 200 m in depth. The domains are separated by fronts or transition zones, with the narrow (5 to 30 km) Inner Front or Structural Front between the Coastal Domain and the Middle Shelf Domain, the wide (>50 km) middle transition zone between the Middle Shelf Domain and the Outer Shelf Domain, and the Outer Front between the Outer Shelf Domain and the waters of the slope.

Results

Many of the important advances in our understanding of the coupling of regional atmospheric processes, physical processes in the Bering Sea, and biological responses to these forcing mechanisms have resulted from SEBSCC and Inner Front research. Among these advances in our knowledge are:

1. A new understanding of the importance of warm-season climate
2. An improved understanding of the functions of the Aleutian North Slope Current and the Bering Slope Current and their potential importance to fish
3. Documentation of eddies over the slope and along the outer shelf and their importance as habitats for fish and for the transport of small pollock onto the shelf
4. Development of a model that resolves eddies and suggests that the source of eddies in the southeastern Bering Sea basin is in the Bering Slope Current
5. Discovery of mean flows across the shelf, which, for short intervals in summer, can result in replenishment of salts and transport of oceanic zooplankton to the Inner Front
6. A clarification of the role of the timing of ice retreat for the timing and fate of the spring phytoplankton bloom

7. Understanding of the relative importance of winter and warm season conditions for determining the timing and strength of spring stratification and the potential for summer mixing across the pycnocline
8. An understanding of the temporal and spatial variability of the Inner Front and its role in nutrient fluxes from depth
9. A greater appreciation for the role of water temperature in the distribution of fish, especially pollock, the hatching time of pollock eggs, and the population dynamics of zooplankton
10. A greater appreciation for the role of episodic events in structuring the ecosystem
11. A new hypothesis concerning the role of wind-forced transport for the survival of juvenile walleye pollock
12. Evidence that the net annual primary production in the northern Bering Sea may be declining, whereas in the southeastern Bering Sea, increases in standing stocks of fish and non-crab benthic invertebrates do not suggest a decline in production
13. Commencement of research on the role of nanno- and microplankton, including coccolithophores, in the marine ecosystem of the southeastern Bering Sea
14. From re-examination of zooplankton time series, no evidence for a significant decline in zooplankton biomass within samples stratified by the domain in which they were collected
15. Immense increases in the biomass of large jellyfish and then a rapid decline to levels seen in the early 1980s
16. Observations of responses of crustacean zooplankton to variations in water temperature, including apparent shifts in the timing of breeding in shelf euphausiids, and the abundance of small shelf copepods
17. Determination that large cetaceans are now encountered more frequently in shelf waters than in the 1970s, and that substantial numbers are present over the shelf during summer
18. Progress in defining multiple hypotheses concerning the control of year-class strength in walleye pollock
19. Improved understanding of the foraging habits and diets of marine birds, northern fur seals, and Steller sea lions at the Pribilof Islands; the potential relationships between the abundance of adult pollock over the shelf and the reproductive success of black-legged kittiwakes at the Pribilof Islands
20. Evidence that sub-lethal food stress during the breeding season can lead to elevated levels of corticosteroids, and possibly elevated levels of post-breeding season mortality in seabirds

21. Development of a mechanistic explanation of how variations in climate could cause shifts in the mechanisms controlling walleye pollock populations (Oscillating Control Hypothesis)

Elements of these advances were used to develop indices for prediction of walleye pollock year-class strength. A conceptual switch model that relates survival of pollock from one developmental stage to the next is a function of environmental parameters, such as climate, sea ice, and timing of prey production. The Oscillating Control Hypothesis is an important climate element of the conceptual model. The following indices are some that were developed by SEBSCC as potentially useful for predicting pollock abundance based on elements of the conceptual model.

1. An index of wind turbulence versus larval feeding success
2. An index of variations in net short-wave radiation
3. A new index of sea ice that led to insight regarding changes in timing of spring in the region
4. Indices related to thermal conditions developed from the compilation of water temperature data taken during annual trawl surveys
5. An index developed from simulations by the Northeastern Pacific Regional Ocean Model System (NEPROMS) that combines early-life-history transport and predation by adult pollock
6. An index from autumn age-0 pollock abundance that may be an acceptable early predictor for pollock year-class strength

An examination of a large set of biological and physical indices showed that potential relationships could change sign with regime shifts, providing a clear warning that a simple model does not exist.

SEBSCC also addressed the importance of age-0 pollock in the Pribilof Island region as possible indicators of future eastern Bering Sea pollock recruitment, and discussed relationships of age-0 pollock to their prey and predators. To this end, the Pribilof Island region was considered to include an area extending along the shelf and shelf-break 100 nm from the center of the islands. This determination was based on ecological efficiency predicted by the energetic/trophic-web-based ECOPATH model. According to its prediction, the largest percentage of the energetic demands of regional biota was met by food sources within that boundary.

Age-0 pollock abundance near the Pribilof Islands was generally higher than in the surrounding area, and was about the same as abundance in the Inner Front region. Drogued buoy trajectories suggest that most pollock found near the Pribilofs during summer likely come from spawning areas near Unimak Pass. Some may be spawned near Bogoslof Island or even closer to the Pribilofs.

There may be an interaction among the spatial distribution of adult pollock (that appears to have two modes over the years: a northwest and

southeast mode), the relative importance of different pollock spawning areas and the summer wind patterns that can influence changes in the distribution of age-0 pollock over the summer. To wit, the abundance of age-0 pollock near the Pribilof Islands may change drastically throughout the summer.

It is difficult to establish a relationship between bird and mammal diets and abundance of age-0 pollock near the Pribilof Islands. No such relationships were found for murrelets or kittiwakes. Percent occurrence of age-0 pollock otoliths in fur seal scat was high throughout most summers, which suggests that large year classes cannot be distinguished from moderate-sized year classes by scat samples. However, small pollock year classes may be distinguishable using scat data.

The vast quantity of information collected during SEBSCC and Inner Front has led to new understanding and hypotheses of how the southeastern Bering Sea ecosystem functions. This information is providing input to the National Marine Fisheries Service's stock assessment of juvenile pollock. At present, the pathway to providing input is through a grass-roots approach; the integrative research method employed during SEBSCC included fisheries scientists at the Alaska Fisheries Science Center whose tasks are directed toward status of stocks. Some of these scientists were SEBSCC Principal Investigators and/or members of SEBSCC Working Groups. They were the ones who helped to develop indices of potential survival of early life histories of pollock and a formal technique to use such indices in stock assessment models. The quantitative use of annual metrics of the physical and biological environment is the next logical step in the progression toward improved forecasts of age-1 recruitment. As the management of fisheries matures toward an ecosystem-based approach, the integrated biophysical knowledge attained by fisheries scientists during SEBSCC and Inner Front will prove to be an invaluable foundation.

Future Research

Although a great deal of progress in understanding the forcing mechanisms and the ecosystem responses of the southeastern Bering Sea has been made since the early 1990s, there are still many unanswered questions that demand attention if we are to provide good stewardship for the resources of the Bering Sea shelf. Answers to these questions go beyond academic value; we need to understand the processes and mechanisms that determine how changes in global climate and the associated physical forcing affect the flow of energy to upper trophic level organisms including commercially valuable fish and shellfish, marine mammals, and seabirds. Below are listed a number of questions that require attention.

1. How do atmospheric forcing mechanisms influence the distribution and transport of salts, heat, nutrients, and organic matter in the eastern Bering Sea?
2. How is the timing and magnitude of cross-shelf flux controlled?

3. How do different patterns in the formation, thickness, extent, and melt-back of sea ice influence the ecosystems of the eastern Bering Sea shelf?
4. What controls the amount and fate of primary production?
5. What controls the biomass and productivity of upper trophic level organisms?
6. How can we translate information about Bering Sea ecosystems into products useful to those who are managing the fisheries of the eastern Bering Sea?

The following are logical next steps in the development and refinement of indices. The first steps deal with indices for estimating recruitment of age-1 pollock. The last is an index that may provide guidance regarding interpretation of the annual stock assessment from trawl results.

1. Continue comparisons with other model simulations and observations to provide verification of the Bering Sea model (NEPROMS).
2. Develop a wind index of nutrient supply to the shelf from Bering Canyon.
3. Develop a user interface and/or other techniques so the NEPROMS is more accessible as a tool.
4. Examine various indices versus occurrence of northwest and southeast centers of the adult pollock population.
5. Extract an index of zooplankton abundance from ECOSYM.
6. Develop a history of the time/space occurrence of the pollock-roe fishery to help define time/space limits for pollock eggs as initial points for trajectory simulations.
7. Develop a similar product for pollock spawning that occurs near Bogoslof Island.
8. Use temperature observations from annual trawl surveys to develop an index of the presence of the cold pool and the locations of the inner and middle fronts (i.e., the boundaries of the middle shelf domain) in given years.
9. Use temperature observations to create annual distributions of temperature that, in turn, can be used to simulate zooplankton production.
10. Examine the influence of changes in the physical environment (e.g., water temperature, location of fronts) on preferred habitat for pollock, and how variations in these features affect estimates from trawl results.

With the results of SEBSCC and the Inner Front Study, the stage is set for future research programs to increase understanding of regional processes, their coupling to larger-scale phenomena, and the impacts that changes to this ecosystem will have on our society, and vice versa. Several programs and projects on the immediate horizon will be the first to contribute. Programs such as the Bering Sea Ecosystem Study (BEST) (<http://www.arcus.org/bering/>) and the Study of Environmental Arctic Change (SEARCH) (<http://psc.apl.washington.edu/search/>) are developing research plans for the Bering Sea and the waters to the north, and they will be supported by ongoing efforts from the North Pacific Research Board, Fisheries-Oceanography Coordinated Investigations (FOCI), the National Marine Fisheries Service, Alaska Ocean Observing System, North Pacific Anadromous Fish Commission, and others.

Part 1—Introduction

As a society, we recognize that the bounty of our planet is not endless. Accordingly, we develop and apply techniques that enable us to better manage resources. With the establishment of the exclusive economic zone (EEZ) of U.S. coastal waters in 1976, our society realized that many valuable resources are maritime in nature. Legislation was adopted to provide for their protection, and the ensuing decades brought into existence systematic research and managerial programs to optimize the balance between resource utilization and conservation. The principles to effect such balance are called stewardship. Some coastal stewardship programs have been less than effective, however, as demonstrated by the collapse of the Georges Bank fishery off New England. Although it is difficult to discern who or what is to blame for fishery collapses, i.e., whether they are the result of natural processes, anthropological influence, or a mixture of both, the outcome is certain. The penalties for failure to maintain rich, viable fisheries are billions of dollars of lost revenue and loss of livelihood to all dependent on the industry for an unknown period of time.

Of all U.S. coastal waters, the Gulf of Alaska and Bering Sea ecosystems are among the most productive, supporting vast populations of fishes, birds, and marine mammals. The Alaskan EEZ is crucial to the U.S. economy. Fish and shellfish from these waters constitute nearly 50% of the U.S. and 5% of the world harvest. Alaskan pollock, salmon, halibut, and crab generate over \$2 billion in revenue each year and provide an important source of high protein food. Pollock also provide food for numerous fish, marine birds and mammals and as such are a keystone or node of Alaskan ecosystems. Until recently, these most productive waters haven't seen the same commercial pressure as other U.S. fisheries, and the opportunity to manage them successfully is still with us.

Southeast Bering Sea Carrying Capacity (SEBSCC) was a NOAA Coastal Ocean Program project designed to conduct basic research on the Bering Sea ecosystem and transfer information to applied management of fish stocks. SEBSCC began in the final months of fiscal year 1996 and closed at the end of fiscal year 2002. The project contributed to resource management by examining ecosystem dynamics and survival of walleye pollock in the southeastern Bering Sea. The goals of SEBSCC were to understand the overall workings of the ecosystem (the changing physical environment and its relationship to the biota of the region), to relate that understanding to natural variations in year-class strength of walleye pollock (*Theragra chalcogramma*), and transfer this information to fishery managers. Incorporating scientific understanding of survival processes represents an advance from the classical fishery management technique of survey and projection.

The model for SEBSCC's information transfer came from the Fisheries-Oceanography Coordinated Investigations (FOCI) in the Gulf of Alaska. FOCI provides information from research directly to NOAA's National Marine Fisheries Service advisory team whose mission is to advise the North Pacific Fisheries Management Council on the status of pollock stocks in the Gulf of Alaska and Bering Sea. In this way, researchers play a unique role

of directly transferring results to applied management. Moreover, the investment in research is a small fraction (less than 0.04%) of the commercial value of the Alaskan stocks. Beginning in 1992, FOCI scientists have analyzed biological and physical time series to estimate survival qualitatively. This scientific application significantly simplifies the stock projection analysis used by NMFS to recommend fishing quotas to the management council. As our understanding of how ecosystem processes interact to limit or encourage survival of young pollock, our ability to provide more accurate and quantitative forecasts will increase. With SEBSCC, research has begun to address the more complex questions of survival in the Bering Sea. SEBSCC scientists coordinated their research efforts with several international scientific organizations to address the effect of climate fluctuations on the Bering Sea ecosystem. As we understand how these systems function, we will become more able to forecast changes. These include not only large changes in abundance of pollock, but also changes in the ecosystem that favor other species. Such knowledge will permit commercial interests to reallocate and focus their efforts. With time, this ongoing fisheries oceanographic research will provide expanded social and economic benefits. As our knowledge of natural variations in the population of commercially valuable stocks increases, the application of scientific techniques will occupy a growing niche in the management process. Our ability to understand ecosystem interactions will amplify our ability to maintain and allocate coastal resources effectively.

Part 2—Synthesis of Research: A Contemporary Understanding of the Southeast Bering Sea Ecosystem

RESULTS FROM THE SYNTHESIS WORKING GROUP ON THE SOUTHEASTERN BERING SEA: RECENT ADVANCES IN KNOWLEDGE FROM BERING SEA FOCI, SOUTHEAST BERING SEA CARRYING CAPACITY AND THE INNER FRONT PROGRAM

Principal Author: George L. Hunt, Jr.

With participation and contributions from:

Chris Baier, Nick Bond, Ric Brodeur, Troy Buckley, Lorenzo Ciannelli, Liz Connors, Chuck Fowler, Susan Henrichs, Jerry Hoff, Anne Hollowed, George Hunt, Jim Ianelli, Nancy Kachel, Carol Ladd, Allen Macklin, Lyn McNutt, Jeff Napp, Jim Overland, Sigrid Salo, Robert Schabetsberger, Jim Schumacher, Beth Sinclair, Alan Springer, Phyllis Stabeno, Al Tyler, Lucy Vlietstra, Muyin Wang, and Terry Whitledge

2.1 Introduction

2.1.1 *Brief history and goals of recent research programs*

The Bering Sea is a semi-enclosed sea that connects the North Pacific and Arctic Oceans. The 500-km-wide eastern continental shelf encompasses about one-half of its area and supports extraordinarily rich marine resources. These are of vital importance to the economic survival, subsistence, and cultural foundations of the many indigenous people of western Alaska (IARPC, 2001). Marine resources of the Bering Sea include fisheries equal to about one half of the United States' fishery production, about 80% of the seabirds found in the nation's waters, and substantial populations of marine mammals (NRC, 1996; IARPC, 2001). Its fishery landings include walleye pollock (*Theragra chalcogramma*, a nodal species in the shelf ecosystem), salmon, halibut and crab, and generate over \$2 billion in revenue each year (IARPC, 2001). It is thus vital to the economic and social well being of the region that we understand the factors that determine the productivity of the Bering Sea. Such information will facilitate the wise exploitation and stewardship of this most important marine ecosystem.

Since the mid 1990s, two coordinated research programs, the Southeast Bering Sea Carrying Capacity (SEBSCC) project (1996–2002), supported by the Coastal Ocean Program of NOAA, and the Inner Front study (1997–2000), supported by the National Science Foundation (Prolonged Production and Trophic Transfer to Predators: Processes at the Inner Front of the S.E. Bering Sea), were active in the southeastern Bering Sea (Macklin *et al.*, 2002). These two studies were complementary, with one focused on the middle and outer shelf (SEBSCC) and the other (Inner Front) on the inner shelf. Collaboration between investigators in the two programs was strong. In addition, the Bering Sea FOCI (Fisheries-Oceanography Coordinated Investigations) program, funded by NOAA's Coastal Ocean Program,

was active from 1991 through 1997, and many of the FOCI investigators were also participants in the Inner Front and SEBSCC programs.

The goals of the Bering Sea FOCI program were to understand the factors that control the abundance of fish populations, and, in particular, the abundance and stock structure of walleye pollock in the Bering Sea (Macklin, 1999). A specific objective was to reduce uncertainty in managing these fish. The goals of the SEBSCC program were to increase understanding of the southeastern Bering Sea ecosystem, to document the ecological role of juvenile walleye pollock and factors that affect their survival, and to develop and test annual indices of pre-recruit (age-1) pollock abundance (Macklin *et al.*, 2002). SEBSCC focused on four central scientific issues: (1) How does climate variability influence the marine ecosystem of the Bering Sea? (2) What limits the growth of fish populations on the eastern Bering Sea shelf? (3) How do oceanographic conditions on the shelf influence distributions of fish and other species? (4) What determines the timing, amount, and fate of primary and secondary production? Underlying these broad goals was a narrower focus on walleye pollock. Of particular concern was the understanding of ecological factors that affect year-class strength and the ability to predict the potential of a year-class at the earliest possible time. The Inner Front program focused on the role of the structural front between the well-mixed waters of the coastal domain and the two-layer system of the middle domain. Of particular interest was the potential for prolonged post-spring-bloom production at the front and its role in supporting upper trophic level organisms such as juvenile pollock and seabirds. Of concern to both programs was the role of interannual and longer-term variability in marine climates and their effects on the function of sub-arctic marine ecosystems and their ability to support upper trophic level organisms (see also Francis *et al.*, 1998).

2.1.2 Structure of synthesis report

In this section of the final report, we provide an overview of the contributions of the SEBSCC and Inner Front programs to our understanding of processes in the southeastern Bering Sea. We begin with a brief description of the physical environment and marine climate of the eastern Bering Sea. We follow with an examination of changes and mechanisms of change for the physical and biological components of the eastern Bering Sea ecosystem. We then discuss several conceptual hypotheses that provide possible avenues toward understanding changes in the amount and fate of production in the southeastern Bering Sea, and how climate change may affect the function of this ecosystem. Finally, we identify a series of questions that recent work suggests will be important to answer in our quest for a fuller understanding of the function of the eastern Bering Sea in a changing climate.

2.1.3 Brief description of the Southeastern Bering Sea

The Bering Sea consists of a deep central basin, a northwestern shelf in the Gulf of Anadyr that reaches south along the Kamchatka Peninsula, and a broad eastern shelf that stretches from the Alaska Peninsula to Russia and

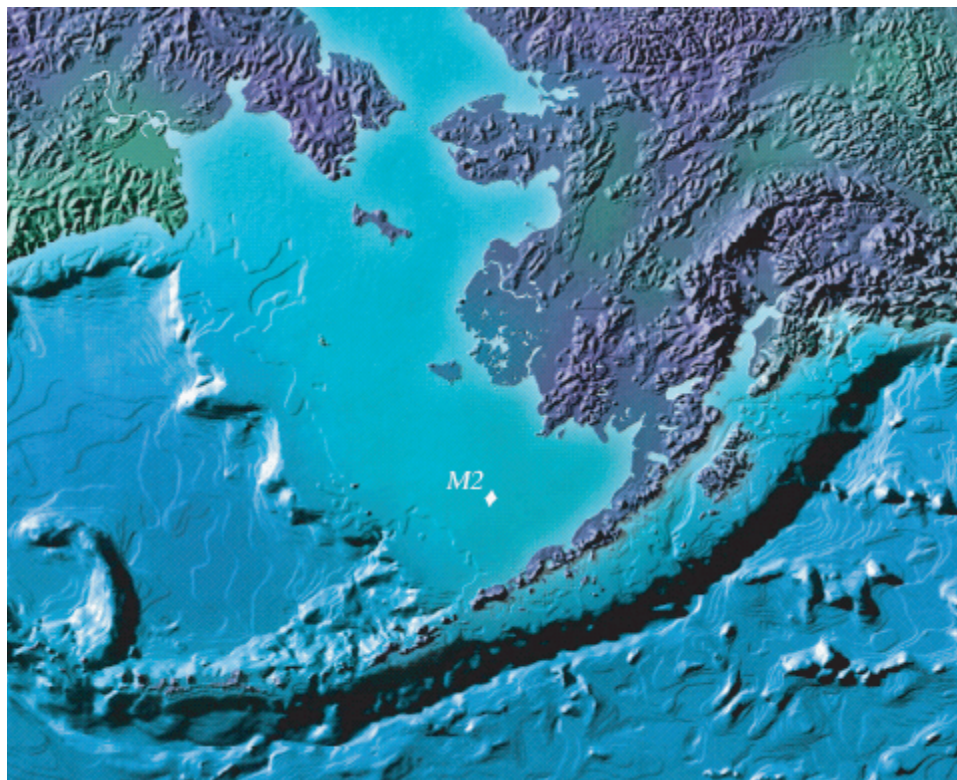


Figure 2.1: Three-dimensional view of the eastern Bering Sea, with location of the biophysical mooring M2 shown. Map courtesy of K. Birchfield.

the Bering Strait (Fig. 2.1). For the purposes of this report, the waters of the eastern Bering Sea can be divided into an Oceanic Regime that occupies the basin and a Shelf Regime that occupies the eastern shelf. The eastern shelf can be further sub-divided into the southeastern shelf and a northeastern shelf, with the dividing line running east-west just south of St. Matthew Island from the coast to the shelf edge.

The following overview of the Oceanic Regime is based on the description of Schumacher *et al.* (2003). The Oceanic Regime of the eastern basin is influenced by Alaska Stream water that enters the Bering Sea through Amchitka and Amukta passes in the Aleutian Islands, and turns right to form the Aleutian North Slope Current (ANSC; Reed and Stabeno, 1999) (Fig. 2.2). This current in turn provides the major source of water for the Bering Slope Current (BSC) that varies between following the depth contours of the eastern shelf northwestward with a regular flow, and becoming an ill-defined, variable flow characterized by numerous eddies and meanders (Stabeno *et al.*, 1999a). The eddies occur not only in water seaward of the eastern shelf (Schumacher and Reed, 1992), but also in waters as shallow as 100–122 m deep (Reed, 1998). These eddies are potentially important as habitat for larval and juvenile pollock, and can carry these fish, as well as nutrient salts, from the Oceanic Domain into the Outer Shelf Domain (Schumacher and Stabeno, 1994; Stabeno *et al.*, 1999a).

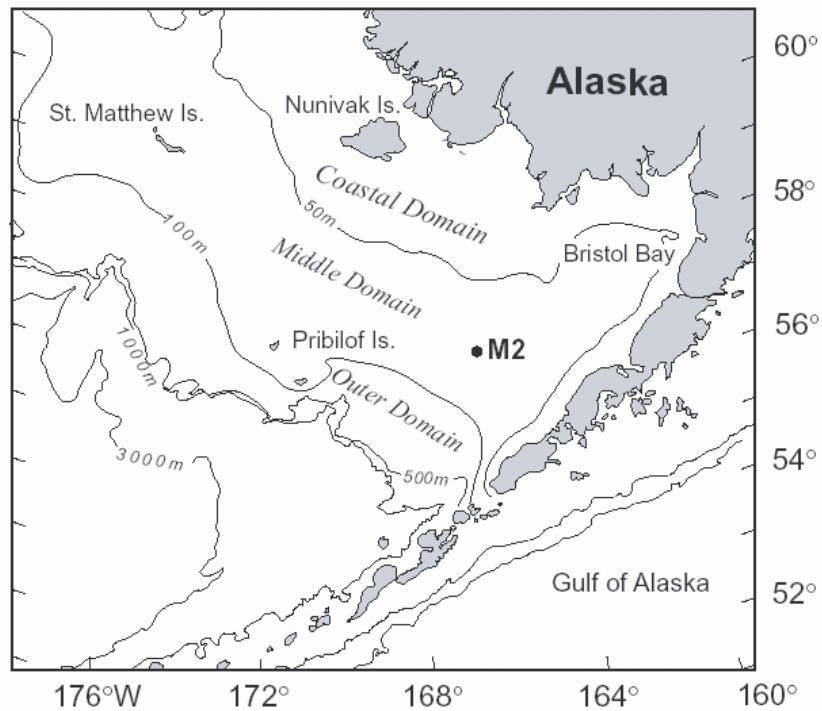


Figure 2.2: Southeastern Bering Sea showing isobaths and domains. Map courtesy of N. Kachel.

The broad continental shelf (up to 500 km wide) of the southeastern Bering Sea is differentiated into three bathymetrically fixed domains, which include the Coastal Domain that extends from the shore to about the 50-m isobath, the Middle Shelf Domain, between the 50-m and 100-m isobaths, and the Outer Shelf Domain that ranges from 100 m to 200 m in depth (Fig. 2.3) (Iverson *et al.*, 1979b; Coachman, 1986; Schumacher and Stabeno, 1998; Stabeno *et al.*, 2001). The domains are separated by fronts or transition zones, with the narrow (5 to 30 km) Inner Front or Structural Front between the Coastal Domain and the Middle Shelf Domain, the wide (>50 km) middle transition zone between the Middle Shelf Domain and the Outer Shelf Domain, and the Outer Front between the Outer Shelf Domain and the waters of the slope. In summer, the Coastal Domain is well mixed to weakly stratified, the Middle Shelf Domain is strongly stratified, and the Outer Shelf Domain has well mixed upper and lower layers with a zone of gradually increasing density between (Schumacher *et al.*, 2003). During summer in the Middle Shelf Domain, the temperature difference between the upper and lower layers can be greater than 8°C, and changes in density are dominated by temperature rather than salinity (Hunt *et al.*, 2002a). In the northeastern Bering Sea, changes in tidal energy and freshwater discharge from the Yukon River affect the location of the fronts, with the Inner Front occurring in water 30 m or less (Schumacher and Stabeno, 1998). During summer in

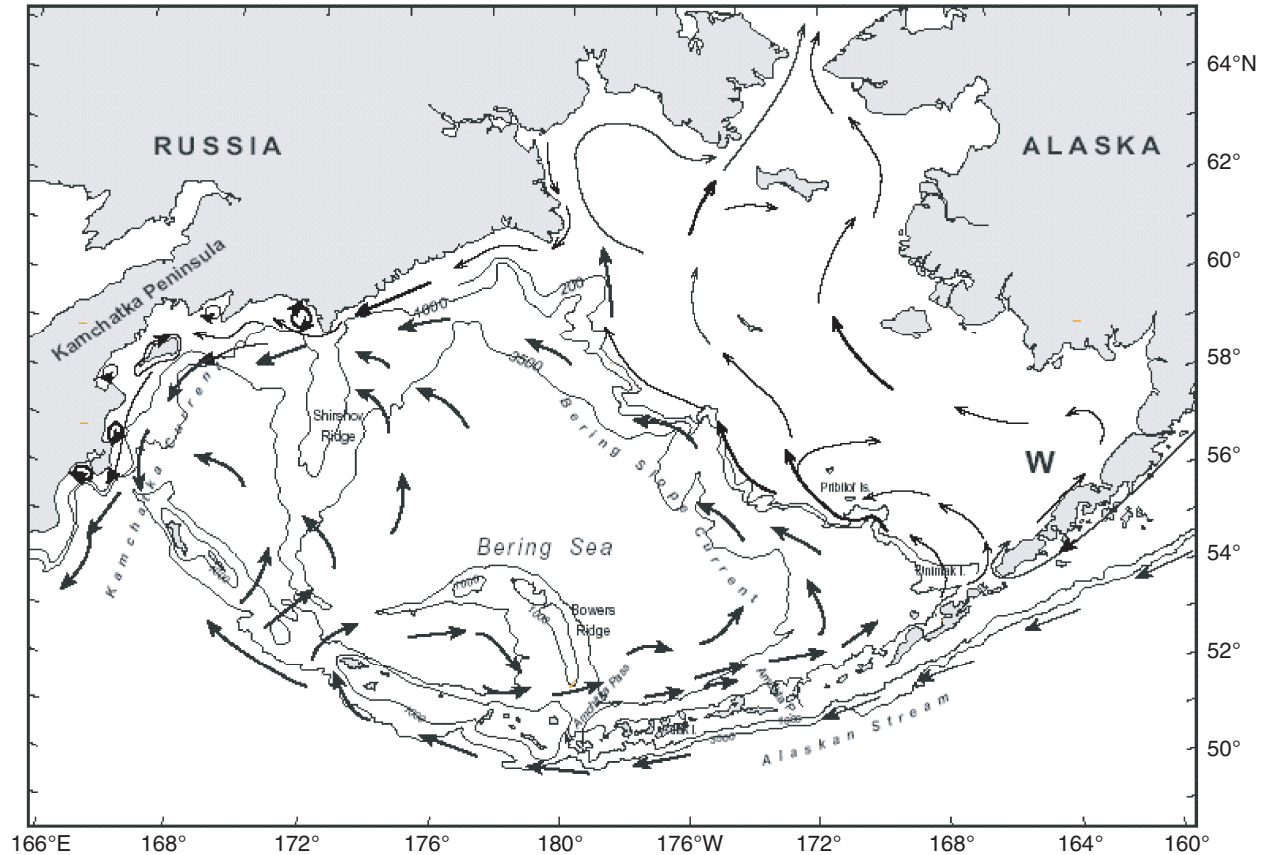


Figure 2.3: Schematic of major currents in the Bering Sea. From Stabeno *et al.* (1999a).

Norton Sound, a two-layered system can occur in water as shallow as 20 m. In winter, the water column there is well mixed.

2.2 Climate and the Bering Sea Marine Ecosystem

An important development in fisheries oceanography during the last decades of the twentieth century was the realization that climate variability, at the scale of decades, could have profound impacts on the function of marine ecosystems. Of particular importance was the realization that seemingly small shifts in the mean values of atmospheric variables, at least when compared to their interannual variability, could result in major changes in the productivity or standing stocks of fish populations. Recent work has suggested that climate variations may affect the mechanisms (e.g., bottom-up or top-down) that control populations, such that the impact on fish stocks of a given rate of harvest may be quite different in different climate patterns.

2.2.1 Climate indices

For the North Pacific Ocean, among many potential indices of climate variability, there are three well-studied indices of climate patterns that de-

pend on variability in winter, the Pacific Decadal Oscillation (PDO), the El Niño/Southern Oscillation (ENSO), and the Arctic Oscillation (AO). The PDO is defined as the leading mode of sea surface temperature variability in the North Pacific (north of 20°N), and has time scales of 20–30 years (Ladd *et al.*, unpublished manuscript; Mantua and Hare, 2002) (Fig. 2.4). The PDO is a major mode of variability (Wallace *et al.*, 1992), yet it explains only 21% of the variance of the monthly SST and is primarily centered on the central North Pacific rather than the Gulf of Alaska and Bering Sea. The ENSO has widespread influence on global climate variability at time scales of 2–7 years, and has its greatest influence in the tropics. Recently, ENSO has been shown to have a small but significant influence on the marine climate of the Bering Sea via atmospheric teleconnections (Niebauer, 1998; Hollowed *et al.*, 2001; Martin *et al.*, 2001; Overland *et al.*, 2001). The AO is defined as the leading mode of sea level pressure variability north of 20°N, and consists of a pattern of zonally symmetric variability in the strength of the polar vortex (Thompson and Wallace, 1998; Ladd *et al.*, unpublished manuscript). The AO has its largest variance in winter (January–March). The strongest mode of variability in the AO is interannual, but it also varies at decadal scales, having changed sign in 1976 and again in 1989 (Thompson and Wallace, 1998; Overland *et al.*, 1999) (Fig. 2.4). The AO has an influence on the Bering Sea through its affect on the Aleutian Low, which is the monthly or seasonal mean location of the center of low sea level pressure over the North Pacific (Overland *et al.*, 1999). The value and position of the Aleutian Low reflects the strength and distribution of storm tracks in the southern Bering Sea and sub-arctic Pacific Ocean. These storms have great influence on the marine climate of the Bering Sea in winter.

A fourth index of atmospheric pressure, the North Pacific (NP) pattern, represents the leading mode in spring of the 700 hPa height and is most prominent from March through July (Barnston and Livezey, 1987; Ladd *et al.*, unpublished manuscript). The NP consists of a north-south pressure dipole, and its strong variance in spring relates to storminess in the Bering Sea (Overland *et al.*, 2002).

In the North Pacific region, the wintertime indices, in conjunction with indices of biological responses in marine ecosystems, have been used to identify abrupt shifts in climatic forcing and ecosystem response at decadal time scales (e.g., Trenberth and Hurrell, 1995; Mantua *et al.*, 1997; Francis *et al.*, 1998; Hare and Mantua, 2000; McFarlane *et al.*, 2000; Hollowed *et al.*, 2001). Two of these regime shifts have been identified in the past thirty years. One followed the winter of 1976–1977, in which the PDO and the AO both shifted (Fig. 2.4). A second shift, of just the AO, occurred after the winter of 1988–1989 (Ebbesmeyer *et al.*, 1991; Hare and Francis, 1995; Sugimoto and Tadokoro, 1998; Beamish *et al.*, 1999b; Brodeur *et al.*, 1999a; Hare and Mantua, 2000). There is some evidence of a third shift in the winter of 1998–1999 (Schwing and Moore, 2000; Peterson *et al.*, 2002). Although the ENSO appears to alternate between two states that are repeatedly visited, that does not appear to be the case for regime shifts in the southeastern Bering Sea, where the few regimes documented so far have each had unique characteristics.

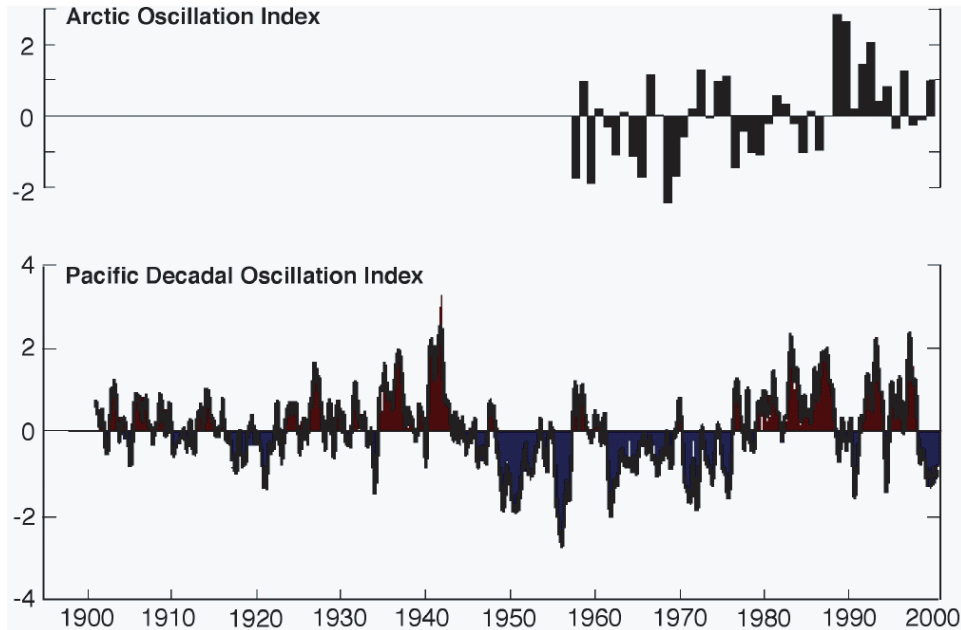


Figure 2.4: Time series of the Arctic Oscillation (AO) and the Pacific Decadal Oscillation (PDO). Note the change from negative to positive in the PDO as of 1977 and from positive to negative in 1998. The AO showed a shift from negative to positive about 1989. Updated from Overland *et al.* (1999).

The main climate feature influencing the southeastern Bering Sea is the Aleutian Low (Fig. 2.5). The Bering Sea lies between the cold Arctic air mass to the north and warmer maritime air mass of the North Pacific. Over the Bering Sea, there is a region of strong gradients in sea-level pressure (SLP) between the Aleutian Low and the high pressure over the Arctic. Considerable interest has developed around low frequency (multi-decadal) variability in the North Pacific in both the physical and biological portions of the North Pacific ecosystem (Minobe, 1999). Hare and Mantua (2000) found evidence in 100 time series for regime-like jumps in these records near 1977 and 1989. The evidence was clearer in the biological data than in the physical data. Their second mode showed strong covariability between physical and biological variations in the Bering Sea over the past 40 years.

To investigate this variability, the strength of the Aleutian Low is plotted in Fig. 2.6 for 1900 through 2000. Visually, there are some indications of a lowering of SLP after 1927, higher pressures from 1947–1977, and an event near 1990. However, the main feature of this plot is the large change from year to year. In fact, almost two-thirds of the variance in this record is at time scales shorter than 5 years (Overland *et al.*, 1999). When one looks at the time series after 1977, almost half the years have SLP values near or slightly above the mean (horizontal line) that occur between years of record low SLP. Using a 5-year running mean is not particularly representative of individual years, either for periods when the values were near average or for

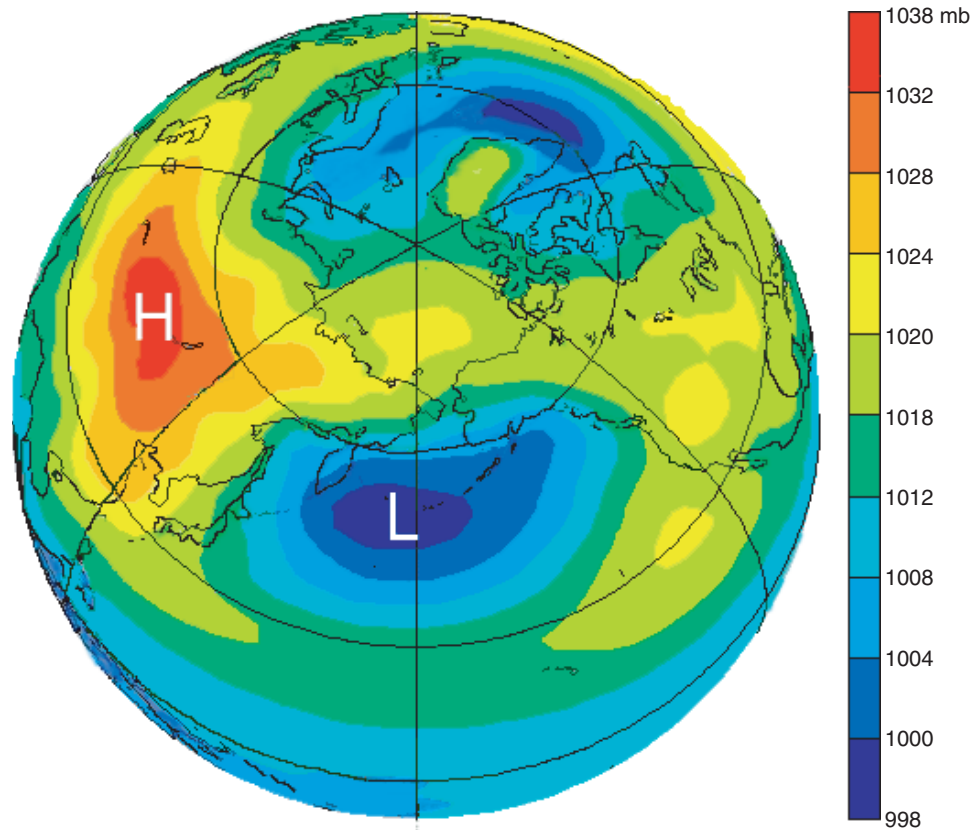


Figure 2.5: The location of the Aleutian Low, the statistical mean location of winter low pressure cells in the northern North Pacific. Figure courtesy of J.E. Overland.

those periods with large negative anomalies, as the averaged data remove the signal from the extreme years that may force the system.

One approach to modeling the variability of the Aleutian low time series is to fit its auto-correlation function, the correlation of the time series with itself as a function of lag between the series. Fig. 2.7 shows the auto-correlation function (the vertical stick plots) repeated in all three plots as a function of lag in years. The values are all small, generally less than 0.3; however, the values are mostly positive, suggesting a broad contribution of frequencies to the original time series, rather than a Gaussian distribution of random errors. The solid heavy lines represent three models of the time series (Percival *et al.*, 2001). The left plot is an Auto-Regressive (AR) red noise model that rapidly decays to zero. The middle plot is a long memory (LM) model that rapidly decays in the first years but then has a broad contribution from longer lags. The third model (right) is a 50-year oscillation plus white noise. All three models are fit with two free parameters and all are candidates to represent the Aleutian Low, because a 100-year record is too short an interval to say one model is superior based on classical statistical grounds.

We have additional information that favors the long memory model. The

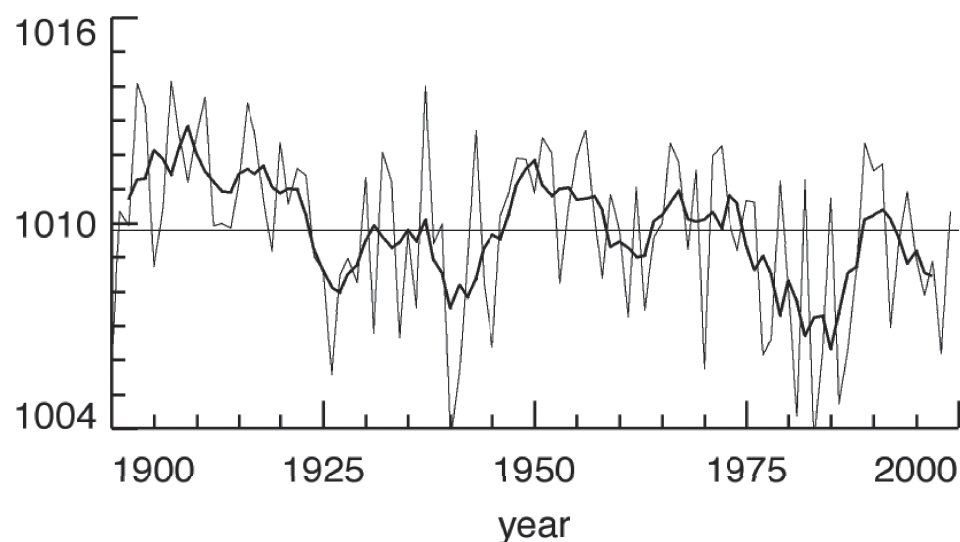


Figure 2.6: The strength of the Aleutian Low with respect to the long-term mean, annual signal, and 5-year running mean. Note that the signal is dominated by extremely strong interannual variability. From Percival *et al.* (2001).

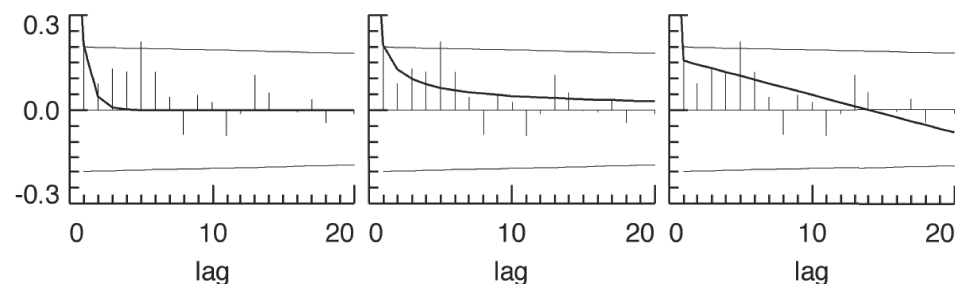


Figure 2.7: Auto-correlation functions (stick plots) of the Aleutian Low time series, with three models of the time series: **Left:** Auto-Regressive, **Middle:** Long memory, and **Right:** 50-year oscillation plus white noise. (From Percival *et al.*, 2001.)

LM model assumes contributions from many processes with different time lags, while the AR model represents a single time scale. It is more reasonable to expect that many processes, such as North Pacific SST, Arctic air masses, ENSO, and Siberian storm systems, influence atmospheric variability over the Bering Sea. We also know from the work of Hare and Mantua (2000) that regime-like behavior favors the LM and oscillator models, as the LM model is about 5 times more likely to have a 20-year run of all positive or negative values than the AR model.

What does this mean for the biology of the Bering Sea? Instead of a pure regime shift model of the physical system with changes spread over 20+ years, we have a physical system that has a strong response in 1 or 2

years. The low frequencies contribute to the timing of these strong events. In this conceptual model, the impact of the change in the physical system is large enough to promote the reorganization of the ecosystem. The massive increase in pollock after 1978 and 1989 (Wespestad *et al.*, 2000) and the 1997 coccolithophore event (Sukhanova and Flint, 1998; Vance *et al.*, 1998; Overland *et al.*, 2001) follow these patterns. Thus, the regimes seen in the biological data of Hare and Mantua (2000) may be the result of a continuing decadal ecosystem reorganization following a major meteorological extreme.

2.2.2 Meteorological forcing

Variability in SST warming is expected to be a dominant factor on the Bering Sea shelf during the warm season. Figure 2.8 summarizes the 40-year record of the rate of warming in early summer and 1 August SST (top panel); two crucial components of the surface heating, the downward shortwave (solar) radiation and latent heat fluxes (middle panel); and two aspects of the wind, the rate of wind mixing (u_x^3) (Fig. 2.8, bottom panel), and along-shelfbreak wind stress (Fig. 2.9, bottom panel). These time series reveal that recent August SSTs are roughly 1°C warmer than those typifying the 1960s. Much of the trend in this heating can be attributed to a long-term tendency toward more solar heating and decreasing surface latent heat fluxes, or evaporative cooling, over the 40-year record. Interannual variability in the summertime warming appears to be due to a combination of variations in solar heating and wind mixing.

The physical state of the ocean over the shelf during spring and summer has been well documented only since 1995, which compromises interpretation of decadal-scale changes in the marine ecosystem. Recent work has indicated that there exists a viable approach for addressing this lack of direct oceanographic observations for retrospective analyses. Specifically, it appears that reasonably accurate hindcasts of the evolution of thermal profiles over the shelf can be made using a 1-D ocean model (the Price-Weller-Pinkel or PWP model) forced by surface winds and heat fluxes generated from reanalysis of historical records (Ladd *et al.*, unpublished manuscript). These hindcasts can be used to estimate not just temperatures (an important factor for zooplankton growth rates) but also the supply of nutrients to the euphotic zone, with implications for summertime primary production.

Progress has been made in understanding the impact of climate variations on the Bering Sea shelf, but there remain a host of important but unanswered questions. For example, while the mean flow on the shelf is sluggish, it is likely at times to be significant. It remains unclear which aspects of atmospheric forcing are important to cross-shelf flow, and what time scales are of primary importance to these events. In general, the sources and potential predictability of climate variations for the Bering Sea in spring through fall are poorly understood. In particular, little attention has been devoted to air-sea interactions during fall and the possible ramifications of their variability for the ecosystem. Thus, while there is a growing appreciation that relatively short-lived but intense events can account for a disproportionate share of the seasonally integrated forcing, it remains unknown how the fre-

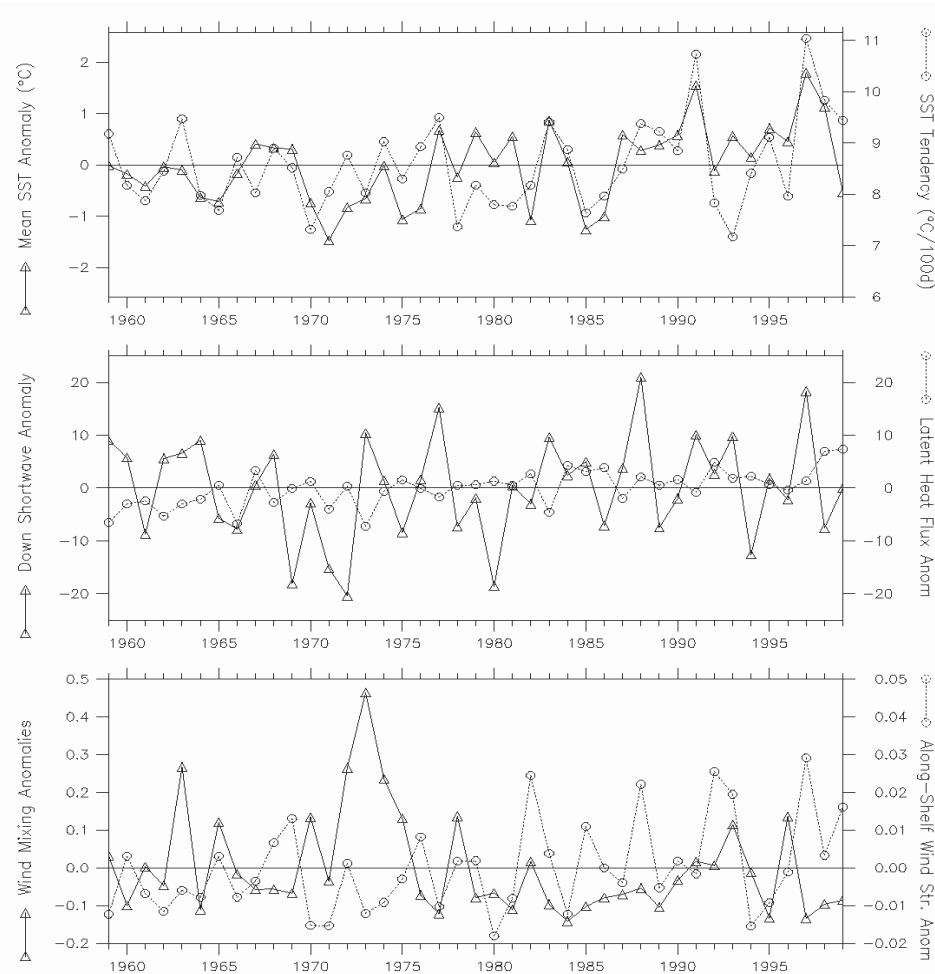


Figure 2.8: Summer season averages for 1959–1999. **Top:** SST tendency (solid line, $^{\circ}\text{C } 100 \text{ d}^{-1}$) and SST anomaly on 1 August (dotted line, $^{\circ}\text{C}$), both at 57°N , 164°W . The zero anomaly line for SST also represents the value of the mean SST tendency. **Middle:** Downward shortwave radiative heat flux anomaly (solid line, W m^{-2}) and surface latent heat flux (dotted line, W m^{-2}), both at 57°N , 167°W . **Bottom:** Wind mixing anomaly at 57°N , 164°W (solid line, $\text{m}^3 \text{ s}^{-3} \times 100$) and along-shelf wind stress anomaly at 56°N , 169°W (dotted line, N m^{-2}). From Bond and Adams (2002).

quency and timing of these events relate to the longer-term variations in climate.

2.3 Physical Components of the Eastern Bering Sea Ecosystem

2.3.1 Sea Ice in the Eastern Bering Sea

Sea ice extent is a crucial aspect of the physical environment of the eastern Bering Sea shelf. The Bering Sea is a marginal ice zone, which is typically ice free from June through October. Beginning in November, cold winds from the Arctic cool the water and begin the formation of ice in the polynyas

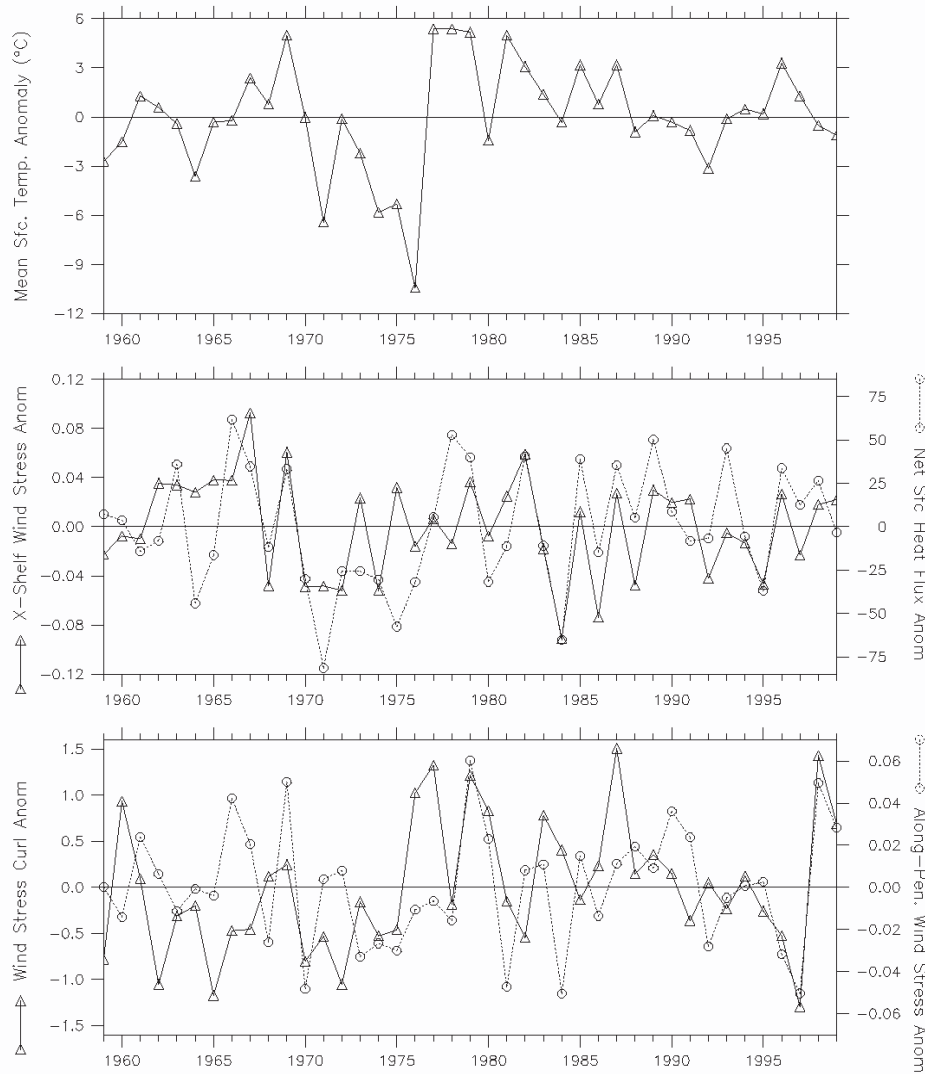


Figure 2.9: Winter season average anomalies for 1959–1999. **Top:** Surface temperature at 57°N , 164°W (solid line, $^{\circ}\text{C}$). **Middle:** Cross-shelf wind stress at 57°N , 164°W (solid line, N m^{-2}), and net surface-heat flux at 56°N , 172°W (dotted line, W m^{-2}). **Bottom:** Wind stress curl at 55°N , 173°W (solid line, $\text{N m}^{-3} \times 10^7$) and along-peninsula wind stress at 53°N , 173°W (dotted line, N m^{-2}). From Bond and Adams (2002).

that form on the lee sides of islands and coasts. Throughout winter, the prevailing winds advect the ice southward into warmer water where the ice melts at its southern edge, cooling and freshening the seawater (Pease, 1980; Niebauer *et al.*, 1999). Recently, Niebauer (1998) has found that the position and depth (strength) of the Aleutian Low has a significant effect on the sea ice cover of the Bering Sea, and that the effect of the Aleutian Low is linked to ENSO events. The maximum southerly extent of the ice and the amount of ice melt affect fluxes of heat and salt, thereby influencing both baroclinic flow and the temperature at the bottom (the cold pool)

in the Middle Shelf Domain (Ohtani and Azumaya, 1995; Schumacher and Stabeno, 1998; Wyllie-Echeverria and Wooster, 1998).

One of the more readily observed impacts of climate change on the eastern Bering Sea ecosystem is the extent and duration of sea ice over the Bering Sea shelf (Niebauer, 1998; Stabeno *et al.*, 2001; Hunt *et al.*, 2002a). The seasonal variation in the position of the ice edge is about 1700 km, the most extensive of any Arctic or sub-arctic region (Niebauer, 1998). In an average winter, about 75% of the eastern shelf is ice covered, but the amount and duration of ice cover can vary interannually by up to 25% of the seasonal range, depending on the wind field (Niebauer, 1983, 1998; Schumacher and Stabeno, 1998). During the last two decades, the maximum ice extent over the eastern shelf occurred, on average, in March, but maximum ice extents have been as early as January (in 2000), and as late as the end of April (in 1976) (Stabeno and Hunt, 2002). During the early and mid 1970s, ice arrived early over the southeastern shelf and persisted into spring. Following this cold period, there was a warmer period when sea ice was less common. Finally, in 1989 there appeared to be a shift to cooler conditions although not as cold as those observed in 1972–1976 (Stabeno *et al.*, 2001).

During cold winters, ice can cover most of the eastern shelf (Stabeno *et al.*, 2001). Alternately, during warmer winters, ice does not extend much farther south than St. Matthew Island. Analysis of ice charts (Fig. 2.10) shows that decadal patterns of variability are evident (Niebauer, 1998; Hunt *et al.*, 2002a). In the period from 1977 to 1996, there was a 5% reduction of ice cover as compared to 1947–1977 (Niebauer, 1998). Interannual and decadal-scale variability in sea-ice coverage was greater at the southernmost edge of the ice field than farther north (Fig. 2.10). Between 57 and 58°N, there was an apparent decrease in days with ice after 1 January between 1972–1976 (mean number of days with ice 130 ± 18 SD) as compared with 1977–1989 (67 ± 26 SD, $t = 1.767$, $p = 0.096$) and 1990–2000 (76 ± 23.3 SD, $t = 2.036$, $p = 0.061$). The average pattern of ice coverage has also changed since the early 1970s (Fig. 2.11), when the maximum extent of the zone in which $\geq 10\%$ ice cover was present annually for >2 weeks extended farther south and west than it did in the 1980s or the 1990s (Stabeno *et al.*, 2001). Additionally, in the 1980s and 1990s, the zone where ice lasted for at least 2 weeks withdrew northeastward along the Alaska Peninsula. Most of the north side of the Peninsula has been ice free since 1990. The 1989 regime shift did not result in a return to the extensive ice conditions present before 1977.

In the eastern Bering Sea, a proxy for sea ice extent is the mean winter (Jan–Apr) surface temperature (Bond and Adams, 2002). The 40-year record for the site of Mooring 2 (top panel of Fig. 2.9) shows a notably cold period in the early to middle 1970s, and a warm period in the late 1970s into early 1980s, but conditions during the 1990s are similar to those in the 1960s. The time series of atmospheric parameters directly related to sea ice (middle panel of Fig. 2.9) indicate that the presence of sea ice is a function of not just the cross-shelf component of the wind, but is also strongly related to the net surface heat fluxes, which are determined by air and water temperatures and wind speed. Niebauer (1998) found that before the regime

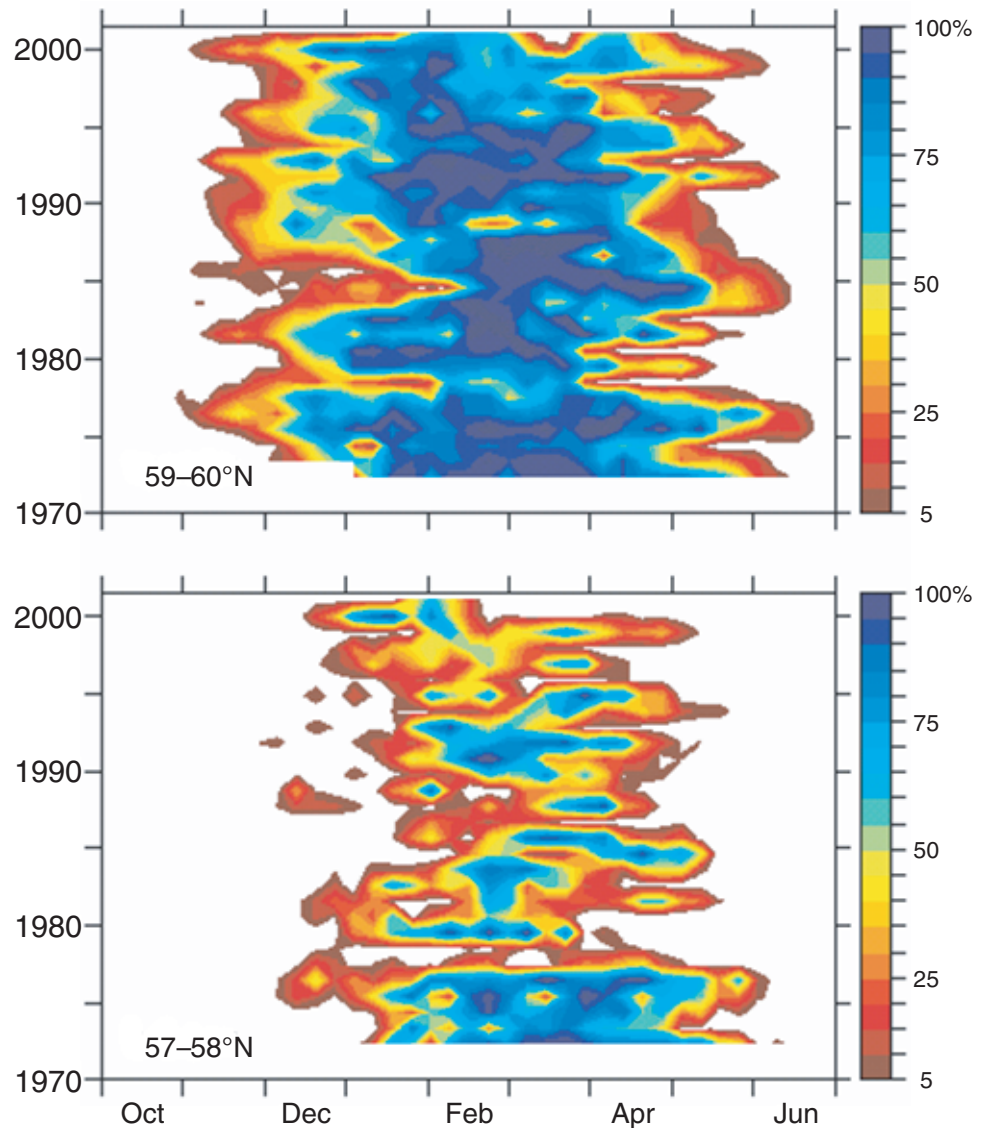


Figure 2.10: Percent ice cover for two latitudinal bands in the eastern Bering Sea. Note the decrease in ice cover in the southern region as of about 1977, whereas there is little evidence for a change in ice cover at this time in the more northerly region. From Hunt *et al.* (2002a).

shift of 1976–1977, below-normal ice cover in the eastern Bering Sea was associated with El Niño conditions, during which the center of the Aleutian Low shifted eastward, and resulted in warm air from the Pacific flowing over the southeastern Bering Sea. After the regime shift, the Aleutian Low was located even farther eastward during El Niño periods, and under these circumstances the southeastern shelf was subjected to north and east winds from the interior of Alaska, which resulted in increased ice cover.

An examination of the timing of the ice retreat and air temperature at 500 hPa (~ 5 km altitude) reveals that during the last decade there has been

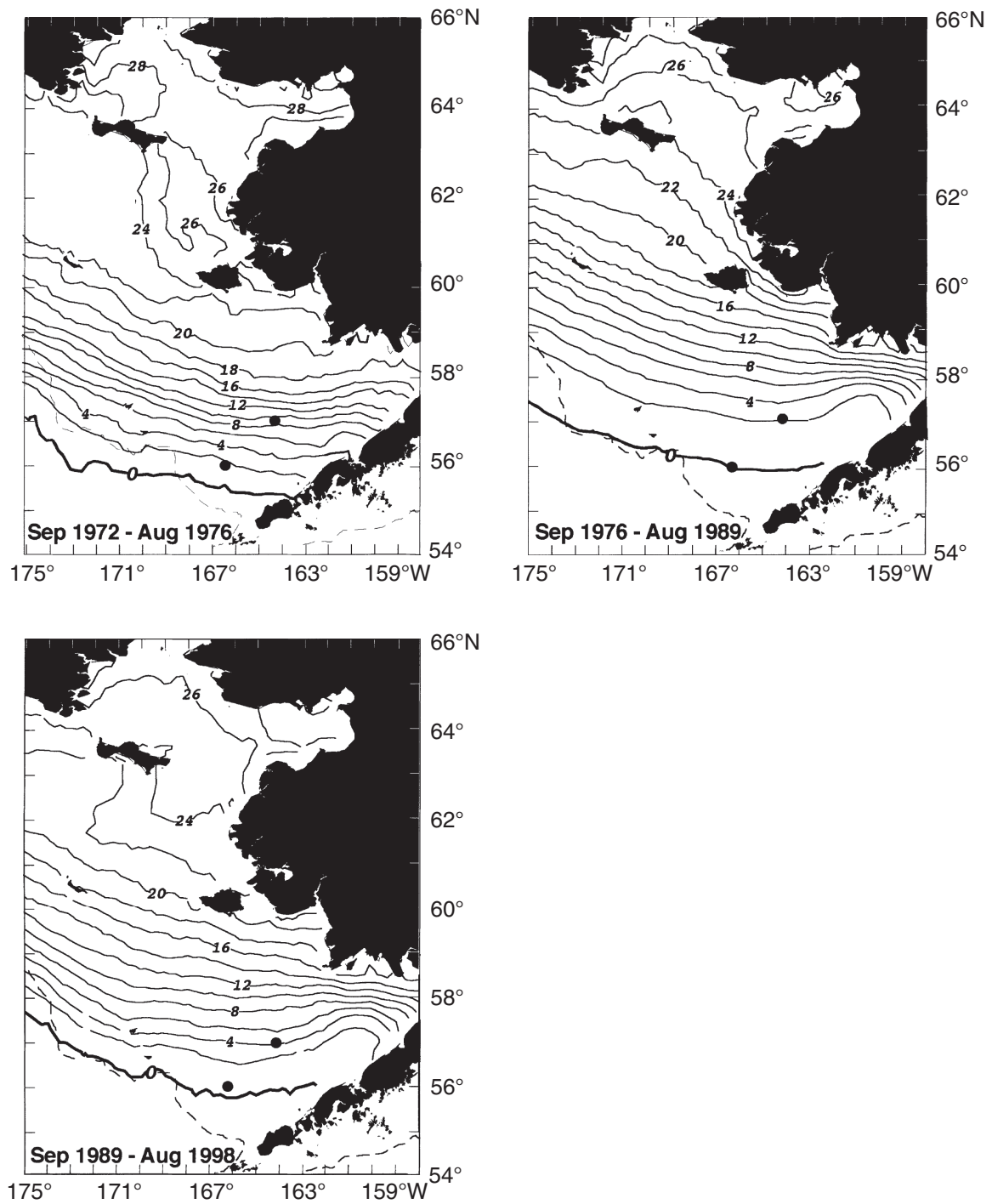


Figure 2.11: Contours of the number of weeks that $>10\%$ sea-ice cover was present over the eastern Bering Sea shelf. After Stabeno *et al.* (2001).

Table 2.1: Relationship between the timing of ice retreat and the type of spring bloom (from Hunt and Stabeno, 2002).

	Bloom Occurs at Ice Edge	Bloom in Open Water
Ice gone by mid March	0	7
Ice remains after late March	6	0

a marked change in the timing of spring transitions (Stabeno and Overland, 2001). While sea ice has extended farther south in the last decade, it has retreated more quickly, resulting in the northern Bering Sea being ice free earlier than in previous decades. In addition, atmospheric temperature during May has increased by 3°C in the 1990s compared to the 1980s.

2.3.2 *Biological importance of the timing of ice retreat*

In the southeastern Bering Sea, the timing of spring primary production is determined by a combination of the date of ice retreat, stabilization of the water column by solar heating, and the cessation of strong storm activity (Sambrotto *et al.*, 1986; Stabeno *et al.*, 1998, 2001; Eslinger and Iverson, 2001). The timing of the spring bloom is important because it determines the ambient water temperatures in which grazers of the bloom must forage. Data illustrative of the conditions that determine the timing of the spring bloom were obtained from Mooring 2, located in ~72 m of water in the middle domain (Figs. 2.1, 2.12). If ice retreat comes before mid-March, there is insufficient light to support net production in the well-mixed water column (e.g., Fig. 2.12: 1996, 1998, 2000). Without ice remaining after mid March, the spring bloom is delayed until May or June, after winter winds have ceased and thermal stratification stabilizes the water column (Fig. 2.12) (Stabeno *et al.*, 1998, 2001; Eslinger and Iverson, 2001). If ice melt occurs in April or May, there is an early, ice-associated bloom (e.g., Fig. 2.12: 1995, 1997, 1999). The pattern of late ice retreats with early ice-related blooms and early ice retreats with late blooms has held since the 1970s (Table 2.1). Although wind mixing of the water plays a role in determining when the bloom will occur, it is apparent in Fig. 2.13 that the timing of the last winter storm is less important than the date of ice retreat in determining the timing of the bloom. Thus, early blooms occur in cold water and are related to ice-edge blooms, whereas late blooms occur in relatively warm water and are not related to the ice edge (Figs. 2.12, 2.14).

We also often see evidence of chlorophyll in the water under the ice during ice melt. This may be evidence of the release of ice algae or seeding of the bloom by ice algae. However, we do not know the origin of this signal, or if its species composition is the same as that of the open water bloom. This requires further investigation.

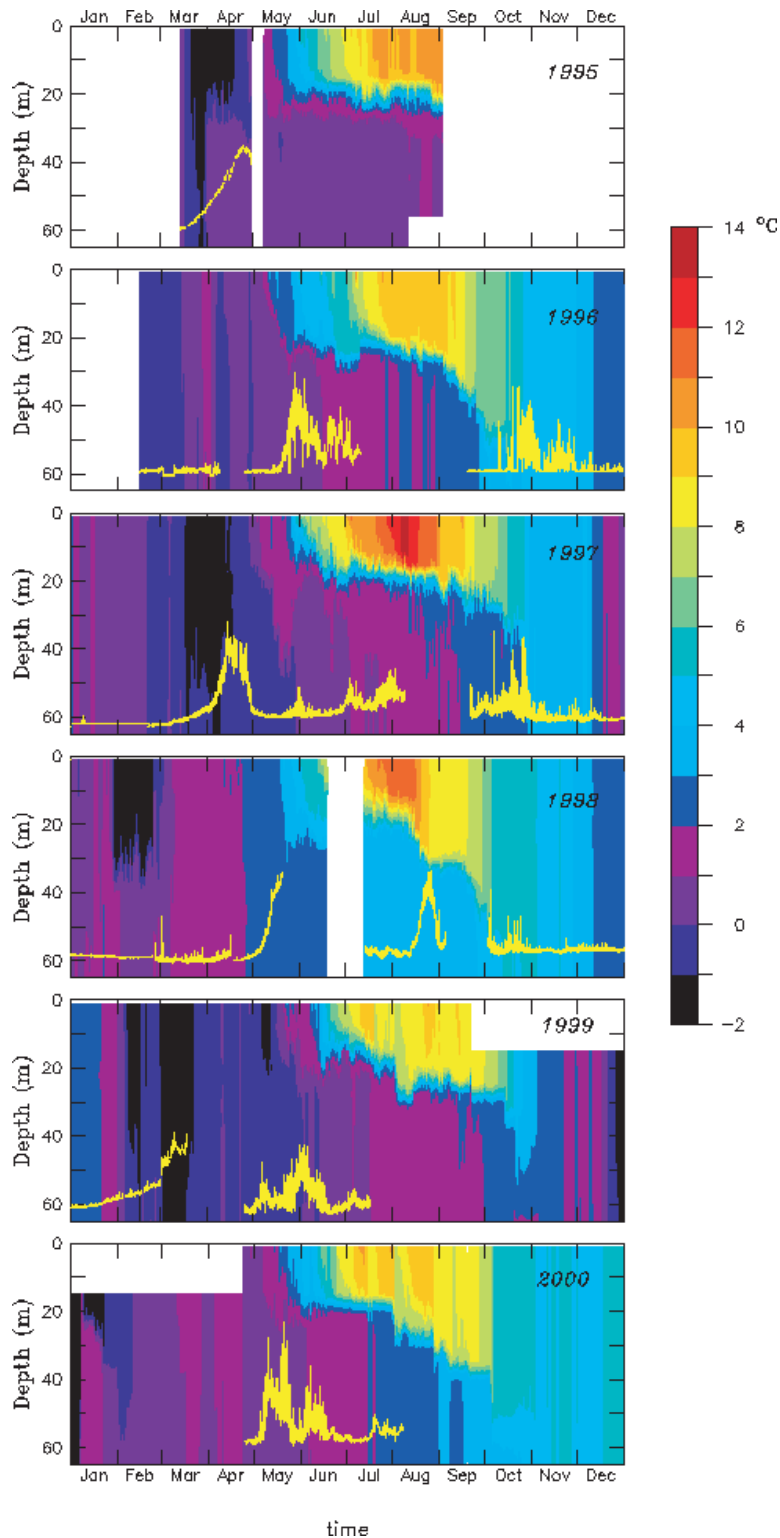


Figure 2.12: Time series of ocean temperatures and fluorescence from Mooring 2. The thin yellow line at the bottom of each panel is fluorescence scaled to the maximum each year. Temperature of $<-1^{\circ}\text{C}$ indicates the presence of melting ice. From Hunt *et al.* (2002a).

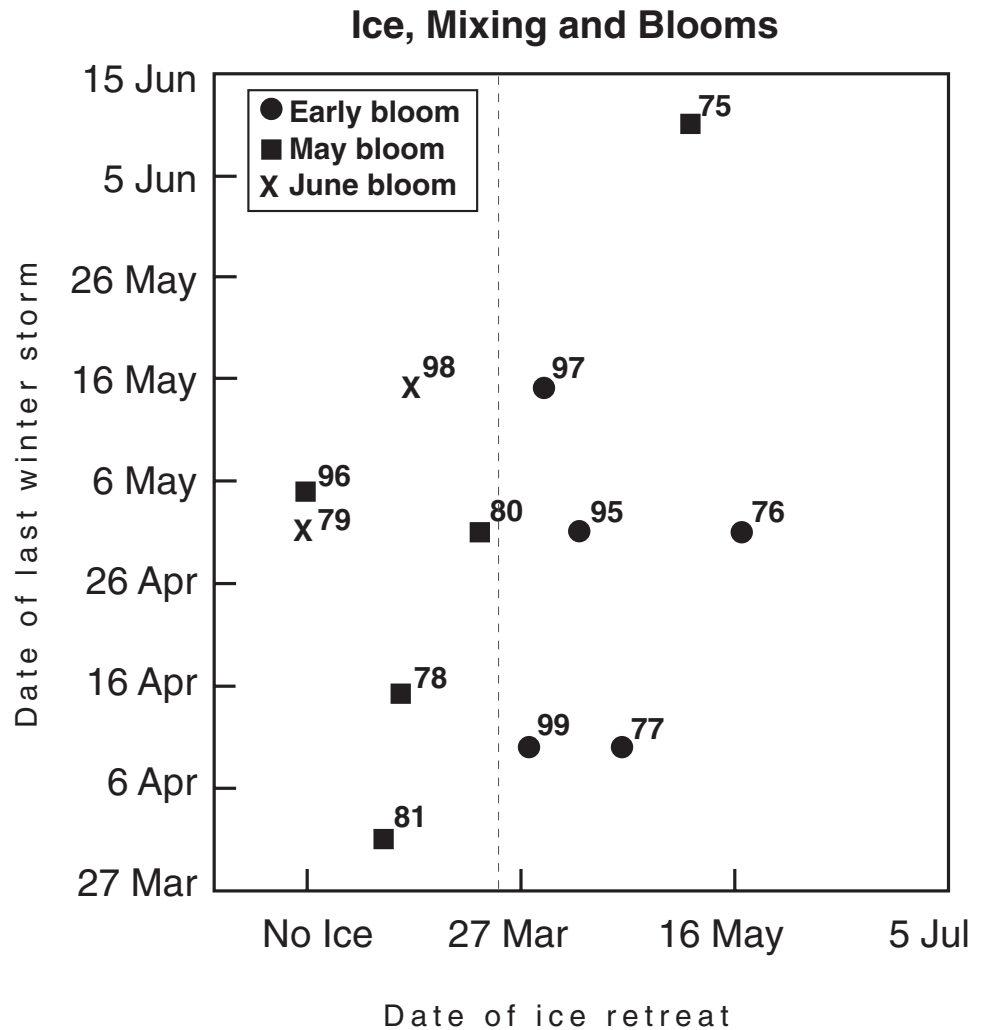


Figure 2.13: The relationship between the timing of the last winter storm, ice retreat, and the relationship of the bloom to sea ice. Note that blooms that occur to the right of the dotted gray line are associated with the ice edge. From Hunt *et al.* (2002a).

2.3.3 Cold pool formation

The bottom waters over the eastern Bering Sea shelf show considerable inter-annual variation in temperature. Over the northern parts of the shelf, cold, salty brine is rejected as sea ice forms in polynyas, and this dense water sinks to the bottom. Density flows to the north carry much of this salty bottom water through Bering Strait to the Arctic Ocean where it contributes to the halocline (Cavaliere and Martin, 1994; Schumacher and Stabeno, 1998).

Over the central and southeastern Bering Sea shelf, cold bottom waters are formed when sea ice melts, and the cold, fresh meltwater is mixed throughout the water column by storms (Stabeno *et al.*, 1998). These meltwaters can chill the entire water column to about -1.7°C . When the surface

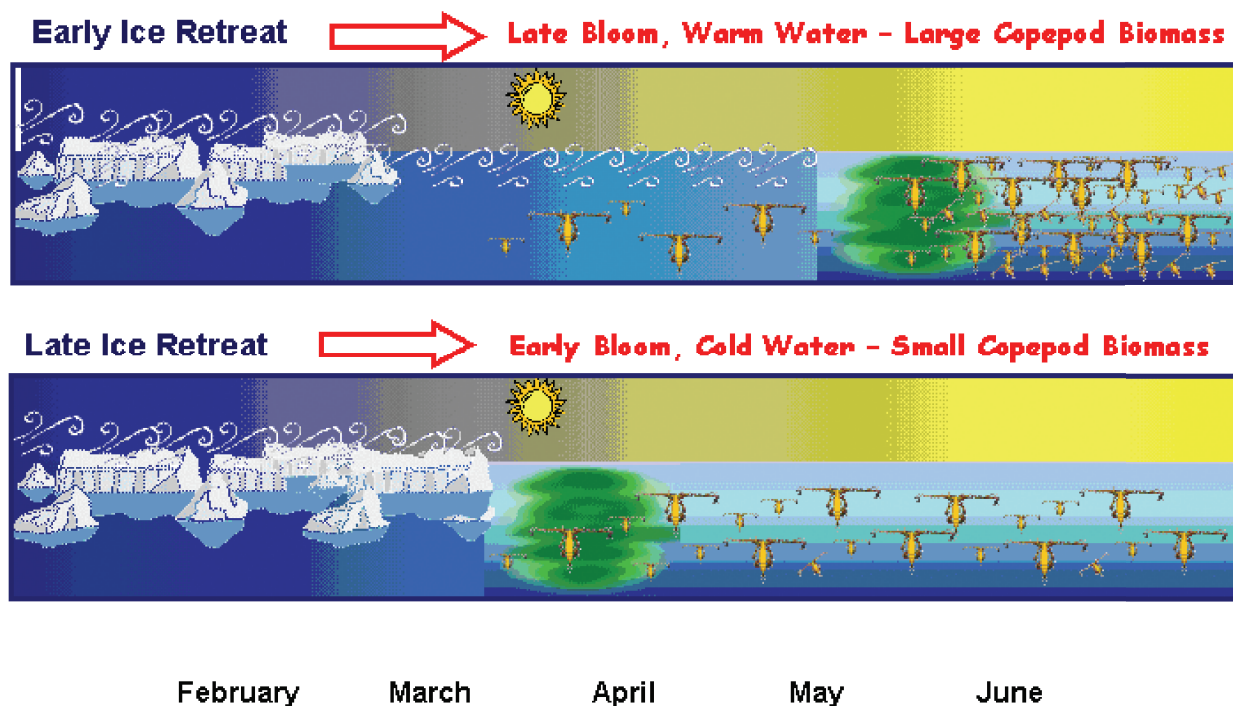


Figure 2.14: Relationship between timing of ice retreat, whether the bloom will occur in association with ice in cold water or in open, warmer water, and the potential effect of a warm water bloom on copepod production. After Hunt *et al.* (2002a).

waters are warmed by solar radiation in spring, a thermocline forms, and the cold bottom waters are largely insulated from further heating (Coachman *et al.*, 1980; Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1995). Bottom temperatures in this “cold pool” warm slightly over the summer, but may remain below 2°C until storm-induced mixing occurs in fall (Ladd *et al.*, unpublished manuscript). The extent and temperature of the southern cold pool is dependent on the amount of ice melt that occurs, and since ice is constantly melting as it is advected south, the amount of meltwater generated is a function of the duration of time that ice is present (Pease, 1980; Overland and Pease, 1982). The southern extent of the cold pool may also be influenced by the cross-shelf advection of warm water in winter (see 2.3.5, below), but the importance of advection of the warm water for cold pool limitation has not been investigated.

2.3.4 Biological impacts of water temperature

The temperature of the water column beneath the surface is important for determining the rates of the physiological processes of organisms residing there. Physiological processes vary as a power function of temperature, and phytoplankton growth is less sensitive to water temperature than is zooplankton growth (see also Vidal, 1980; Vidal and Smith, 1986; Townsend *et al.*, 1994). Water temperature exerts a strong influence on the growth

rates of zooplankton, and is often thought of as more important than food availability for limiting the growth rates of small-bodied copepods (McLaren, 1963; Corkett and McLaren, 1978; Vidal, 1980; Dagg *et al.*, 1984; Huntley and Lopez, 1992). Thus, in years with warm water, Walsh and McRoy (1986) hypothesized that zooplankton would capture more of the primary production than in cold years, and the greater production of zooplankton in warm years would support the pelagic community, e.g., fish such as pollock. Thus, in the middle domain where interannual environmental variability is greatest, water temperature is likely to play a major role in interannual variation in copepod biomass (Smith and Vidal, 1984, 1986; Napp *et al.*, 2000) (See section 2.4.3 Zooplankton).

Water temperature also affects the timing of hatching and survival of pollock eggs (Blood, 2002). Modeling of hatching times based on laboratory experiments and temperatures found in the Bering Sea predicted that the hatching periods for pollock eggs could vary as much as 13 days between the warmest and coldest years encountered between 1995 and 1998. A longer incubation period means that the eggs are exposed to predation for a greater period and that there is increased risk of exposure to extreme low temperatures as the eggs in the upper water column can be subjected to temperature variations driven by short-term weather fluctuations. Malformation of pollock embryos has been reported for eggs incubated at -1°C (Nakatani and Maeda, 1984), a temperature not infrequently encountered in the shelf waters of the Bering Sea shelf in late winter and early spring (Hunt *et al.*, 2002a).

The cold pool has important effects on the distribution and survival of fish. For example, juvenile walleye pollock prefer to avoid waters $<2^{\circ}\text{C}$ (Wyllie-Echeverria, 1996). When the southern cold pool is of reduced size, these fish spread out over much of the middle domain in shelf waters not frequented by adult pollock. When the southern cold pool is extensive, the juvenile pollock move toward the warmer waters of the outer domain and shelf edge, where they are subject to increased levels of cannibalism by adult pollock that reside in these outer shelf waters (Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1995, 1996; Wyllie-Echeverria and Wooster, 1998).

2.3.5 On-shelf fluxes and nutrient replenishment

On-shelf fluxes of nutrient salts from the basin are critical for the long-term productivity of the eastern Bering Sea shelf, but the mechanisms responsible for forcing these fluxes are still not well understood. In the northern Bering Sea, it has been suggested that water from the basin and slope crosses the shelf to flow northward through Anadyr Strait and Bering Strait (Fig. 2.3) (Shuert and Walsh, 1993). Nutrients in this water would then be available to support the extraordinarily high rates of summertime production found in the Chirikov Basin and northward through Bering Strait (Springer *et al.*, 1996). This process would also provide a mechanism for the transport of large oceanic copepods onto the northern shelf, where they support immense populations of planktivorous seabirds (Springer and Roseneau, 1985; Springer *et al.*, 1987, 1989; Hunt and Harrison, 1990; Hunt *et al.*, 1990; Rus-

sell *et al.*, 1999). However, the exact connections to the Bering Sea basin remain unclear, as observations by Stabeno and Reed (1994) and model results (Overland *et al.*, 1994) suggest that the Bering Slope Current, the presumed source of water carrying nutrients and copepods to the Chirikov Basin, may turn westward south of 59°N. Rather, the source of the slope water passing through Anadyr Strait may be water that has advected onto the outer shelf episodically or through the canyons of the shelf edge as far south as Bering Canyon; these then flow along the outer shelf with increasing intensity to the north and west, and thence through Anadyr Strait (Stabeno *et al.*, 1999a).

Over the southeastern Bering Sea shelf, nutrient replenishment was initially thought to result from tidally driven diffusion (Coachman, 1986). However, more recent work shows that the coefficients required for tidally driven diffusion are larger than those present on the shelf (Stabeno *et al.*, 2001). Although mean annual current velocities over the middle shelf at Mooring 2 are weak, currents averaged over shorter periods (e.g., daily) can exceed 25 cm s⁻¹. Currents are strongest in near-surface waters (34-month mean, 1.2 cm s⁻¹ at 15 m), and much weaker at the bottom (0.2 cm s⁻¹ at 60 m) (Stabeno *et al.*, 2001). Currents are strongest in winter and weakest in summer. In 1998, these currents were sufficiently strong to advect organisms typical of the oceanic regime into Middle Domain waters adjacent to the Inner Front near Cape Newenham and Nunivak Island (Hunt *et al.*, 1999; Coyle and Pinchuk, 2002b). It is also hypothesized that the generally seaward movement of sea ice in winter may result in an onshore flow at depth that could contribute to replenishment of nutrients over the southeastern shelf, but this hypothesis has yet to be investigated (Schumacher and Alexander, 1999).

Mechanisms for on-shelf transport of nutrients include eddies that bring slope waters onto the shelf at least as far as the 150-m isobath (Stabeno *et al.*, 1999a; Stabeno and Van Meurs, 1999; Okkonen, 2001; Johnson *et al.*, 2004), and Reed (1998) has observed them in waters between 100 and 120 m about 20% of the time (Fig. 2.3). However, eddies are rare in water <100 m deep, and other mechanisms are required to replenish nutrients in the Middle and Inner Domains. Two regions of preferential on-shelf flow are Bering Canyon, which is just north of the Aleutian Islands near Unimak Pass, and the area west of the Pribilof Islands, where the shelf break narrows (Stabeno *et al.*, 1999a). There, acceleration of flow over the outer shelf (Coachman, 1986; Schumacher and Stabeno, 1998) results in entrainment of slope water (Stabeno *et al.*, 1999b). On-shelf flow west of the Pribilof Islands can move into the Middle Domain where it is marked by a front to the northeast of St. Paul Island (Flint *et al.*, 2002), or it may be entrained around the islands in tidal currents (Stabeno *et al.*, 1999b). Two measures of the atmospheric forcing of the ocean circulation, the wind stress curl and the wind stress along the Alaskan Peninsula/Aleutian Island chain, also exhibit substantial variability (bottom panel of Fig. 2.9), but it remains an open question whether the flow over the shelf is sensitive to these effects.

2.3.6 Stratification, mixing, and the vertical flux of nutrients

Shelf waters of the southeastern Bering Sea, although well mixed during winter by storms, stratify in late spring from solar heating (Eslinger and Iverson, 2001; Ladd *et al.*, unpublished manuscript). This stratification inhibits vertical flux of nutrients, and once the spring bloom has exhausted them from the upper mixed layer, the lack of nutrients limits new production. These nutrients can be replenished when processes break down the stratification. Sambrotto *et al.* (1986) identified the importance of summer storms as a mechanism for deepening the pycnocline and stirring nutrients into the upper mixed layer where they could be taken up by plant cells in the presence of light. Analysis of wind speed cubed, a measure of the ability of winds to mix the upper water column, shows that summer winds have declined since the early 1980s (Fig. 2.15). Ladd *et al.* identified the importance of winter conditions for determining the strength of the pycnocline, and hence the ease with which it could be eroded by storms. A second pathway for the movement of nutrients from depth to the surface layers is upward mixing in the vicinity of fronts (Iverson *et al.*, 1979a; Sambrotto *et al.*, 1986; Kachel *et al.*, 2002). For example, this upward mixing can result in regions of high productivity on the stratified side of the inner front (Hunt *et al.*, 1996a; Kachel *et al.*, 2002). These mechanisms require the availability of a pool of nutrients at depth in the vicinity of the front. In 1997, after the completion of the spring bloom, a severe storm in late May mixed the water column to depths of 65 m or more and resulted in renewed production. The result was a depletion of nutrients to 60 m or more, and a lack of availability of nutrients at the base of the inner front and at the pycnocline for mixing into the upper mixed layer (Stockwell *et al.*, 2001). This observation pointed to the importance of episodic events in structuring the ecology of shelf waters.

2.4 Biological Components of the Eastern Bering Sea Ecosystem

2.4.1 Primary production

During the past decade, we have made considerable advances in our understanding of factors influencing the timing of the spring bloom (see above, Stabeno *et al.*, 2001; Hunt *et al.*, 2002a; Hunt and Stabeno, 2002). However, we know less about the magnitude of the bloom, and whether the amount of production varies between ice-associated and open-water blooms. Alexander and Niebauer (1981) and Niebauer *et al.* (1981, 1990, 1995) suggest that in the early 1980s the ice edge-bloom used to be as great or greater than the open-water bloom. In 1997, which had an ice-associated bloom followed by a second, open-water bloom subsequent to a mixing event in May, primary production, based on nutrient drawdown, was greater than in the early 1980s (Stockwell *et al.*, 2001).

The question of whether there has been a change in the amount of net annual new production is important. Schell (2000), using stable isotope ratios from carbon sequestered in the baleen of bowhead whales during periods of feeding in the northern Bering Sea, estimated that primary production

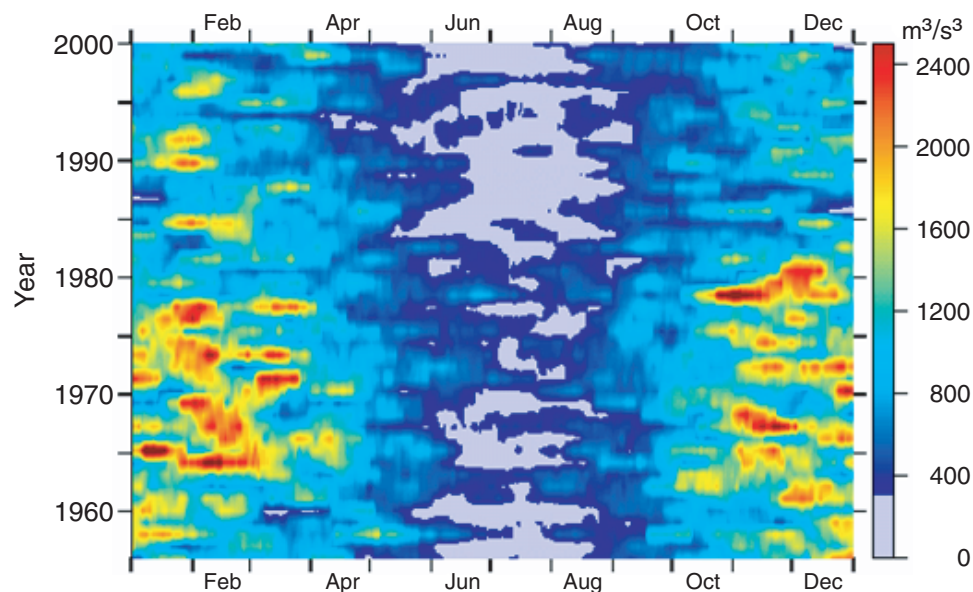


Figure 2.15: Wind speed cubed at St. Paul Island. Note that since the late 1970s, winter winds have been less strong, and in summer, there have been more periods of wind below the long-term average (those areas in light gray). From Hunt *et al.* (2002a).

in the Bering Sea had decreased by as much as 30 to 40% since 1967, with almost all of the decrease coming since 1976. Cullen *et al.* (2001) questioned whether some of this effect was the result of anthropogenic CO₂ or changes in the species composition of the phytoplankton. However, Schell (2001) provided additional information, including data from stable isotopes of nitrogen, which corroborates the earlier findings. Grebmeier and Cooper (1994, 2002), Grebmeier and Dunton (2000), and Grebmeier (1992) have found evidence for declines in sediment oxygen respiration of as high as 73% over the period 1987 to 2002, with declines in benthic biomass of 89% over a longer period. In addition, they have documented changes in the species composition of benthic bivalves and other fauna. Taken together, these studies point to a decline in production levels for the northern Bering Sea, including in the Saint Lawrence Island polynya region south of the island. These reductions in production may be related to reduced northward flow through Bering Strait (Roach *et al.*, 1995) and a consequent diminution of nutrient advection from the Bering Sea basin onto the northern shelf.

In the southeastern Bering Sea, there appears to be no clear indication of a decrease in production, though Hiron *et al.* (2001) have attempted to extend the results of Schell (2000) to the remainder of the eastern Bering Sea and Gulf of Alaska by examining stable isotope ratios in the teeth of harbor seals (*Phoca vitulina*), northern fur seals (*Callorhinus ursinus*) and Steller sea lions (*Eumetopias jubatus*). For these species, when data from teeth from both the Gulf of Alaska and the Bering Sea were combined, they found a significant decline in the $\delta^{13}\text{C}$ in sea lions and similar, though non-significant,

trends in harbor seals and fur seals. However, from their published data, it is difficult to tell whether these trends depend upon the combination of data from the Bering Sea and the Gulf of Alaska, or whether the trends would hold up within regions as well.

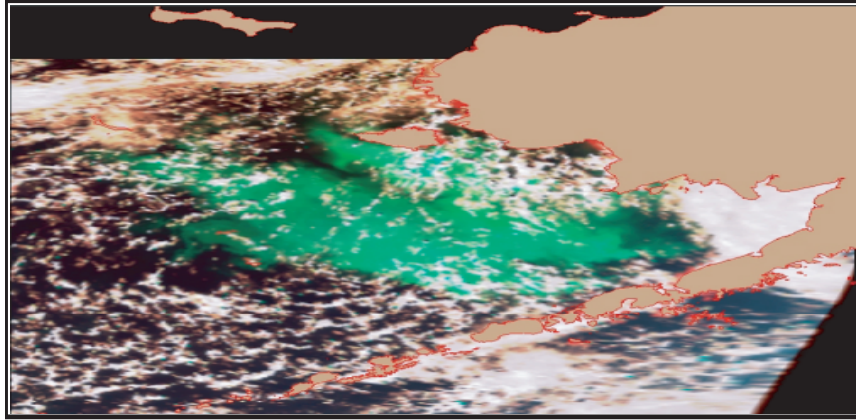
In contrast, in 1997, estimates of primary production in the southeastern Bering Sea, based on the reduction of nitrate over the middle and inner shelf, suggested that new production might have been between 10 and 30% greater in 1997 than in the early 1980s (Stockwell *et al.*, 2001). Estimates for production levels in 1998 and 1999, however, do not appear to differ from those of the early 1980s (Whitledge, University of Alaska Fairbanks, personal communication). In contradiction to these estimates of productivity in 1997, 1998, and 1999, sediment trap data supported the notion that productivity was higher in 1998 than 1997 (Smith *et al.*, 2002), as did data from the uptake of ammonium (Rho, 2000). However, $\delta^{13}\text{C}$ values from copepods in the 1997–1999 period were lower than found by Schell *et al.* (1998). Smith *et al.* hypothesized that this decline in $\delta^{13}\text{C}$ could be the result of diminished production, similar to that found by Schell (2000), or it could be the result of other factors. Interestingly, in the period 1997–1999, Smith *et al.* did not find a decrease in $\delta^{13}\text{C}$ in euphausiids and chaetognaths, as would have been expected if the decline in copepod $\delta^{13}\text{C}$ was the result of changes in primary productivity. Based on the sum of the above results and the high stable or increasing biomass of fish and invertebrates over the southeastern shelf (see below), it seems most unlikely that there has been a marked reduction in primary production there since the 1970s (Hunt *et al.*, 2002a).

2.4.2 *Coccolithophore bloom*

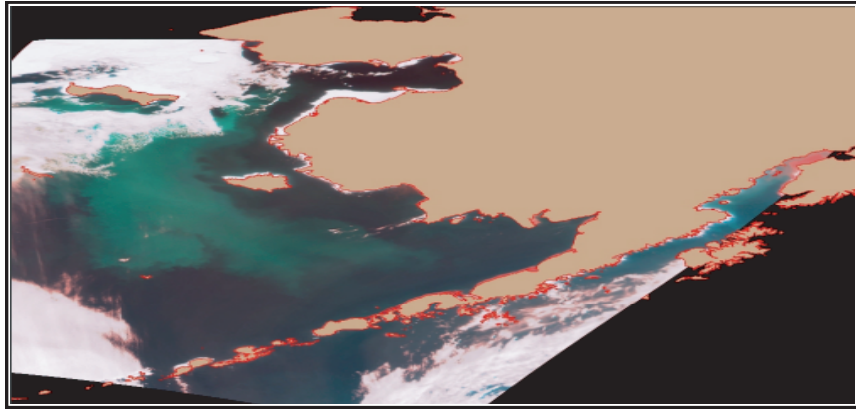
In the 1990s, there were marked anomalies in the species composition of phytoplankton in the eastern Bering Sea. Although diatoms typically dominate phytoplankton biomass in the eastern Bering Sea (Sukhanova *et al.*, 1999), in the late 1990s, coccolithophore blooms dominated summer phytoplankton assemblages over much of the shelf (Figs. 2.16, 2.17) (Sukhanova and Flint, 1998; Vance *et al.*, 1998; Napp and Hunt, 2001; Stockwell *et al.*, 2001). Coccolithophores are small (5–20 μm) phytoplankton surrounded by calcium carbonate plates. Coccolithophore blooms are common in the North Sea, Gulf of Maine, and coastal eastern North Pacific, and characteristically occur in nutrient depleted waters with warm, shallow mixed layers (Holligan *et al.*, 1983; Mitchell-Innes and Winter, 1987; Balch *et al.*, 1992; Townsend *et al.*, 1994). High densities of coccoliths result in a whitening of the water detectable by satellite imagery (Holligan *et al.*, 1983; Balch *et al.*, 1991; Brown and Yoder, 1993; Gower, 1997). Although coccolithophore blooms had not been documented previous to 1997 in the eastern Bering Sea, there are satellite images of “white” water from there (Brown and Yoder, 1993).

The first coccolithophore bloom (*Emiliania huxleyi*) recorded from the Bering Sea was initially observed 3 July 1997 in the middle domain (Vance *et al.*, 1998), although *E. huxleyi* cells were present in the water as early as May and June (Stockwell *et al.*, 2001). By early August, the bloom was at least 200 km wide (Tynan, 1998), and by early September it covered $2.1 \times 10^5 \text{ km}^2$

September 1997



25 April 1998



12 September 1999

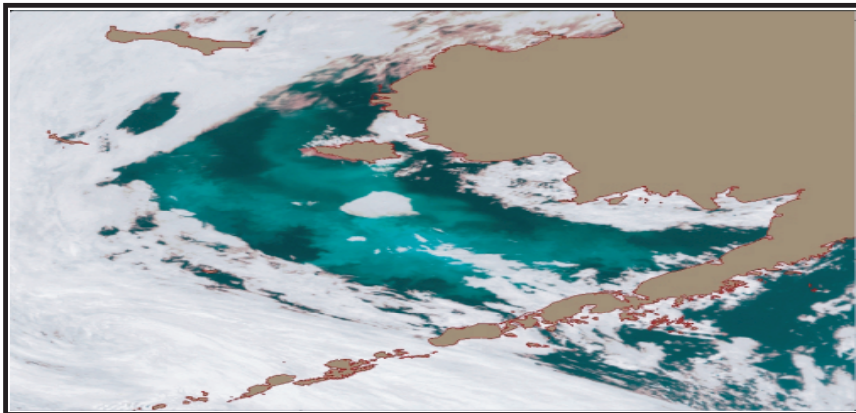


Figure 2.16: Three SeaWiFS views of the Bering Sea coccolithophore bloom.

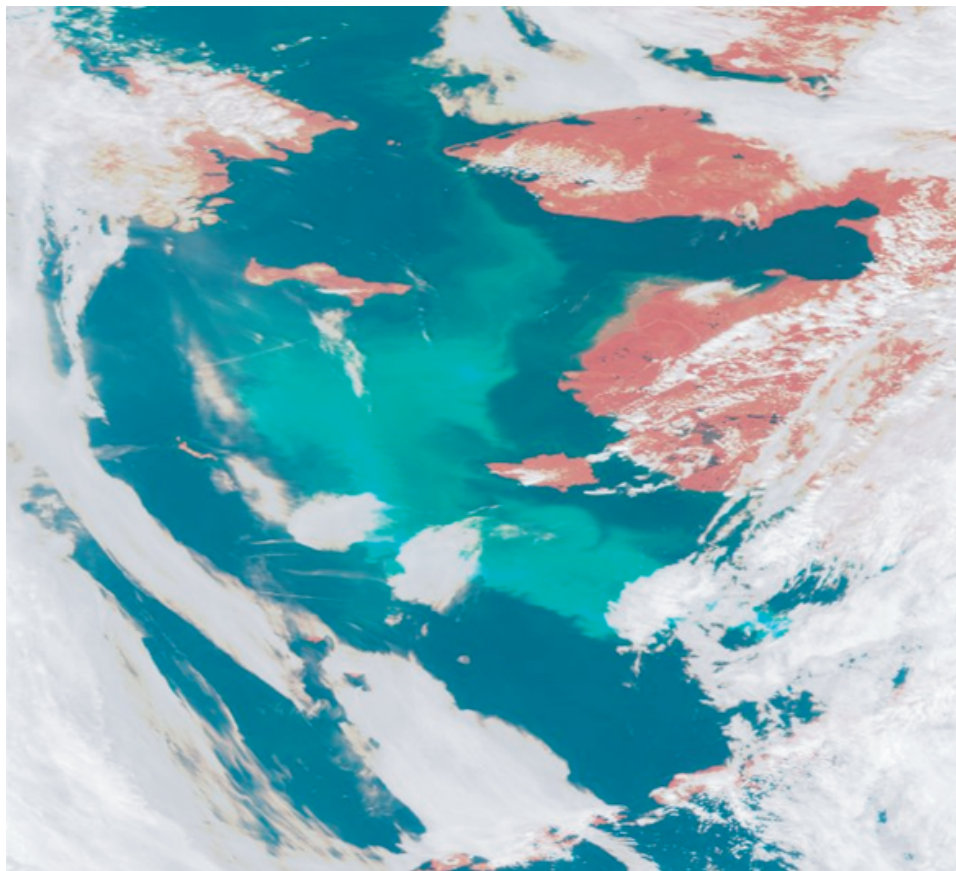


Figure 2.17: SeaWiFS false color image of the coccolithophore bloom, 24 July 1998. Note the trace of coccoliths in the water passing through Shpanberg Strait to the east of St. Lawrence island, and thence northward through the east side of Bering Strait. From Napp and Hunt (2001).

of the middle domain and parts of the inner domain (Sukhanova and Flint, 1998; Vance *et al.*, 1998; Napp and Hunt, 2001). It was apparent in SeaWiFS imagery from 18–25 September, and traces could be detected as late as October. This event was unusually large and long-lived when compared with coastal blooms of coccolithophores described previously (Table 2.2) (Holligan *et al.*, 1983; Balch *et al.*, 1991; Brown and Yoder, 1993; Gower, 1997). Most coastal blooms are on the order of 10^4 km², and persist less than 40 days. Concentrations of coccolithophore cells were as great or greater than those reported from the North Atlantic (Townsend *et al.*, 1994b; Robertson *et al.*, 1994).

The coccolithophore bloom greatly reduced light penetration and visibility in the water. Near Nunivak Island (Fig. 2.2), the depth of the 1% light level, often taken as the maximum limit for net photosynthesis, shoaled from between 18 and 33 m in June to between 5 and 15 m in September in the bloom (Zeeman, University of New England, personal communication). At Slime Bank (Fig. 2.1), outside the bloom, the depth of the 1% light level

Table 2.2: Comparison of large-scale *Emiliania huxleyi* blooms (after Napp and Hunt, 2001).

Characteristic	Measure	Source
Size	km²	
Coastal Blooms	5–10 × 10 ⁴	Holligan <i>et al.</i> , 1983
	5 × 10 ⁵	Balch <i>et al.</i> , 1991
	5 × 10 ⁵	Brown and Yoder, 1993
	5 × 10 ⁵	Brown and Podesta, 1997
Open Ocean Blooms	5 × 10 ⁵	Holligan <i>et al.</i> , 1983
Bering Sea 1997	2.4 × 10 ⁵	Napp and Hunt, 2001
Duration	months	
Gulf of Maine, 1998	≈1	Townsend <i>et al.</i> , 1994
Gulf of Maine, 1989	≈1	Townsend <i>et al.</i> , 1994
NE Atlantic, 1991	1.1	Robertson <i>et al.</i> , 1994
Bering Sea, 1997	4	Napp and Hunt, 2001
Cell Density	cells · ml⁻¹	
Gulf of Maine, 1988	2.4 × 10 ³	Townsend <i>et al.</i> , 1994
Gulf of Maine, 1989	1.5 × 10 ³	Townsend <i>et al.</i> , 1994
NE Atlantic, 1991	1.0 × 10 ³	Robertson <i>et al.</i> , 1994
Bering Sea, 1997	3.1–4.7 × 10 ³	Napp and Hunt, 2001
Lith Density	liths · ml⁻¹	
Gulf of Maine, 1988	1.3 × 10 ⁵	Townsend <i>et al.</i> , 1994
Gulf of Maine, 1989	3.0 × 10 ⁵	Townsend <i>et al.</i> , 1994
NE Atlantic, 1991	3.5 × 10 ⁵	Robertson <i>et al.</i> , 1994
Bering Sea, 1997	3–5 × 10 ⁵	Napp and Hunt, 2001

remained the same (27 m) from spring until fall. Underwater videos near the Pribilof Islands documented cloudy bloom-water ranging in depth from 7 m to 44 m, and extending to the bottom in several locations (Brodeur, NOAA/NWFSC, personal communication).

The eastern Bering Sea coccolithophore bloom recurred yearly from 1997 through 2001, and in most years was comparable in spatial extent and cell density to large-scale coccolithophore blooms in other parts of the world's oceans, though of considerably longer duration (Table 2.2). New algorithms for the analysis of SeaWiFS imagery showed that the coccolithophore blooms started in February as melting began along the ice edge and then spread northward, peaking in April (Iida *et al.*, 2002). The blooms with the largest aerial extent occurred in the warm years of 1998 and 2000, whereas those in the cold years of 1999 and 2001 were smaller (Iida *et al.*, 2002).

The summer of 1997 was marked by unusually warm surface temperatures, a strong thermocline and depletion of nitrate and silicate from the surface waters (Napp and Hunt, 2001). The conditions under which the 1997 bloom commenced were similar to conditions believed to be conducive to coccolithophore blooms elsewhere (Balch *et al.*, 1992; Holligan *et al.*, 1983; Townsend *et al.*, 1994b). However, we do not know why the eastern Bering Sea blooms were initiated, or why they recurred over a several year period when there was great variability in oceanographic conditions (Stabeno and

Hunt, 2002). We also lack information on why they ceased to occur in 2002, and on their role in energy flux to the food webs of the eastern Bering Sea shelf.

2.4.3 Zooplankton

Microzooplankton are protists and metazoan organisms smaller than 200 μm that are present in the plankton (Dussart, 1965). Because they are small and individually inconspicuous, their role in the world ocean has been underappreciated until recently. Although microzooplankton are an abundant element in the food webs of the southeastern Bering Sea, we are only just beginning to investigate their role in this ecosystem (Howell-Kubler *et al.*, 1996; Olson and Strom, 2002). For example, in April 1992, microprotozoan abundances ranged from 300 to 6233 organisms l^{-1} with a biomass of 0.58 to 9.73 $\mu\text{g C l}^{-1}$ (Howell-Kubler *et al.*, 1996). These biomass levels were similar to those of other oceanic regions, and were estimated to be sufficient to meet the metabolic needs of first-feeding larval pollock, though observations to determine if pollock use this resource are not available.

Microzooplankton were an important component of the southeastern Bering Sea food webs in the summer of 1999. Within the coccolithophore bloom, 75% of the total chlorophyll *a* (Chl *a*) came from cells $>10 \mu\text{m}$ (mostly the diatom *Nitzschia* spp.), and average growth rates for cells $>10 \mu\text{m}$ and $<10 \mu\text{m}$ were nearly equal (Olson and Strom, 2002). Within the bloom, microzooplankton grazing rates were only 28% of the growth rates of phytoplankton growth rates. In contrast, for the shelf as a whole, grazing by microzooplankton accounted for 110% of the growth of cells $>10 \mu\text{m}$ and only 81% of the growth of cells $<10 \mu\text{m}$. This preferential grazing on the larger cells may help to explain the persistence of the coccolithophore bloom and is contrary to the belief that microzooplankton are constrained to diets of nannophytoplankton (Olson and Strom, 2002). These findings emphasize the need for a thorough examination of the role of microzooplankton both in the summer, for which we have evidence that they may form an important link between phytoplankton and mesozooplankton, and during the spring bloom, when their role has yet to be evaluated.

Traditionally, calanoid copepods have been believed to be the major agents of energy transfer between large-celled diatoms and upper trophic level consumers such as planktivorous fish (e.g., Hood, 1999). Although emerging data now suggest that in boreal oceans these large copepods have a large dietary component of microzooplankton (Capriulo *et al.*, 1991; Sherr and Sherr, 1992; Rivkin *et al.*, 1999), the large copepods are still important prey for fish, whales and seabirds. In the eastern Bering Sea, the copepod communities of the basin and outer shelf are dominated in spring by large species of *Neocalanus* (*N. cristatus*, *N. plumchrus*, and *N. flemingeri*) and *Eucalanus bungii*, and the middle and inner shelf by the smaller *Calanus marshallae*, *Pseudocalanus* spp. and *Acartia* spp. (Cooney and Coyle, 1982; Smith and Vidal, 1986).

The most complete time series of zooplankton abundances in the eastern Bering Sea depend on data gathered in summer by the T/S *Oshoro Maru*,

which has documented declines in zooplankton biomass from the basin between the late 1960s and the early 1990s (basin, Fig. 2.18) (Sugimoto and Takadoro, 1997). In the basin, they also found a biennial fluctuation in zooplankton biomass that was negatively correlated with the catch of Asian pink salmon (*Oncorhynchus gorbuscha*). Sugimoto and Takadoro interpreted these two patterns as indicating a bottom-up control of the zooplankton on a decadal-scale, and a top-down control on an annual scale. In contrast to the results obtained from the basin, examination of *Oshoro Maru* data from the shelf showed neither a long term trend, nor evidence of biennial cycles in summer zooplankton biomass (Fig. 2.18) (Hunt *et al.*, 2002a; Napp *et al.*, 2002). Although there was considerable interannual variation, no discernable temporal trend was detected.

For spring, two sets of studies show that the abundance of small shelf species of copepods varies with sea temperature. In 1980, the upper layer of the middle and outer shelves of the southeastern Bering Sea warmed slowly as compared to 1981 (Smith and Vidal, 1986). In May 1981, small copepods of the middle shelf were more abundant than in 1980 (Table 2.3), and *Calanus marshallae* was observed to have two generations in 1981, rather than the expected one (Smith and Vidal, 1986). In the 1990s, there was also the opportunity to compare a very cold year (1999) with two years in which water temperatures were high (1997, 1998). For species of small copepods over the inner and middle shelf areas, June abundances in 1999 were reduced by up to 90% compared to the two warmer years (Table 2.4) (Coyle and Pinchuk, 2002b). Although Smith and Vidal hypothesized that differences in predation on the copepods as well as temperature might have affected the differences in abundance between 1980 and 1981, there was no indication in the data of Coyle and Pinchuk (2002b) that chaetognaths were responsible for the declines in copepod abundance observed in 1999. Coyle and Pinchuk (2002b) provide compelling evidence that, even on a station-by-station basis, there was a strong relationship between the numbers of copepods present and integrated water temperatures (e.g., Fig. 2.19). They estimated that secondary production of calanoids in spring 1999 was about 3–4% that which occurred in the warm years of 1997–1998. Interestingly, by August–September, there were no consistent significant differences in the biomass of small copepods between 1999 and the two warmer years (Coyle and Pinchuk, 2002b).

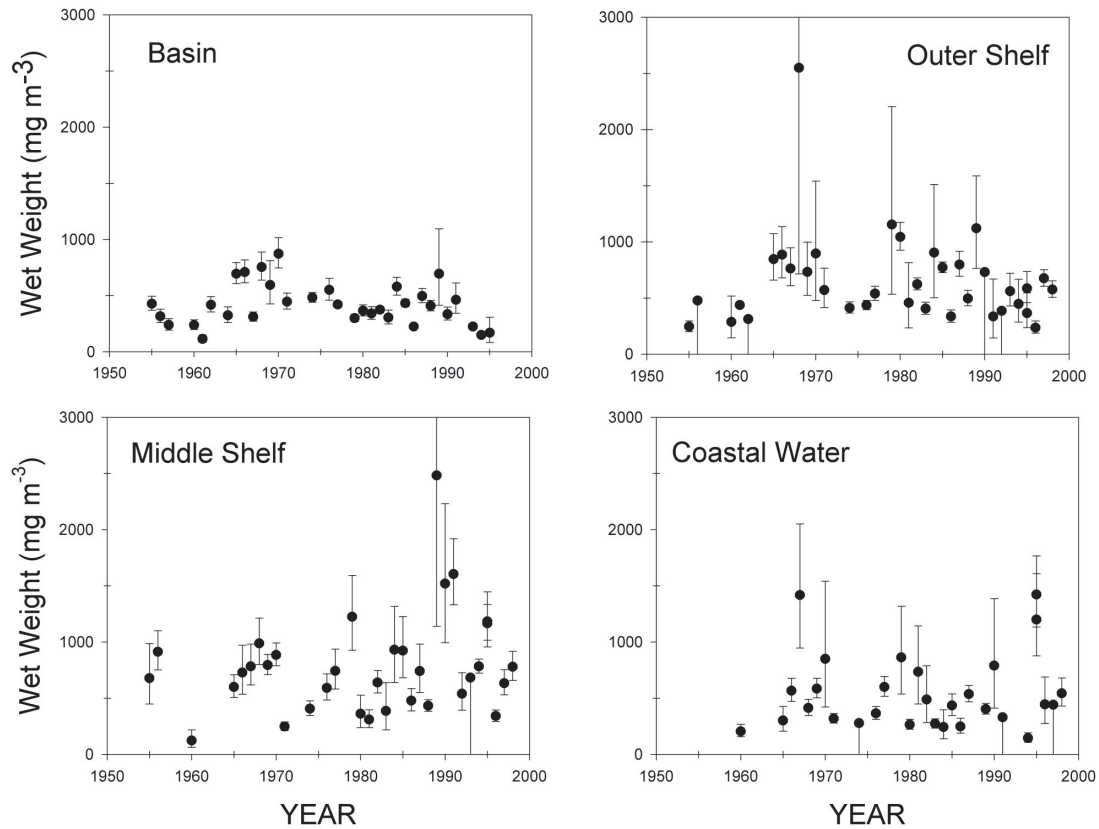


Figure 2.18: Changes in zooplankton biomass in the deep basin and in the outer, middle, and coastal domains of the southeastern Bering Sea sampled by the Oshoro Maru summer cruises. Data from 1994 to 1997 from Sugimoto and Tadokoro (1998). Data from 1995 to 1999 from Dr. N. Shiga (unpublished). Means with standard errors. From Hunt *et al.* (2002a).

Table 2.3: Responses of calanoid copepods to interannual variation in water temperature during the spring bloom in the Bering Sea. Copepod data are numbers m^{-3} from the middle shelf in May 1980 and 1981.

Variable	Year		Difference
	1980	1981	
Onset of Bloom	25 April	5 May	
Termination of Bloom	28 May	29 May	
Temperature ($^{\circ}C$) Prior to Bloom—top 20 m	0.97	3.04	2.07
Temperature During Bloom—top 20 m	2.22	5.06	2.84
<i>Acartia</i> spp. All copepodids	18.9	8.5	-55%
<i>Acartia</i> spp. Adult males and female	9.4	2.8*	-70%
<i>Pseudocalanus</i> spp. All copepodids	83.1	308.5*	+270%
<i>Calanus marshallae</i> All copepodids	31.7	30.6*	-3.5%
<i>Calanus marshallae</i> Adult females	0.1	0.8*	+700%
<i>Metridia pacifica</i> All copepodids	1.6	20.3*	+1169%
<i>Oithona</i> spp.	269.6	233.4	-13.4%

* = difference significant $p < 0.05$. Data from Smith and Vidal (1986).

Table 2.4: Responses of calanoid copepods to interannual variation in water temperature during the spring bloom in the Bering Sea. Copepod data are numbers m^{-3} from the middle shelf and inner shelf in June 1997, 1998, and 1999.

Variable	Year			Change in 1999 from mean of 1997 + 1998
	1997	1998	1999	
Onset of Bloom	Mid April	Early May	Late March	
Temperature during June, integrated water column $^{\circ}C$	3.76	3.45	0.32*	3.29
<i>Acartia</i> spp.	961	711	64*	-92%
<i>Pseudocalanus</i> spp.	1168	893	240*	-77%
<i>Calanus marshallae</i>	34	72	3.7*	-93%
Calanoid nauplii	616	626	322*	-48%
<i>Oithona similis</i>	99	219*	28	-82%
Chaetognaths	43	12*	28	+1.8%

* = difference significant $p < 0.05$. Data from Coyle and Pinchuk (2002b) and Hunt *et al.* (2002a).

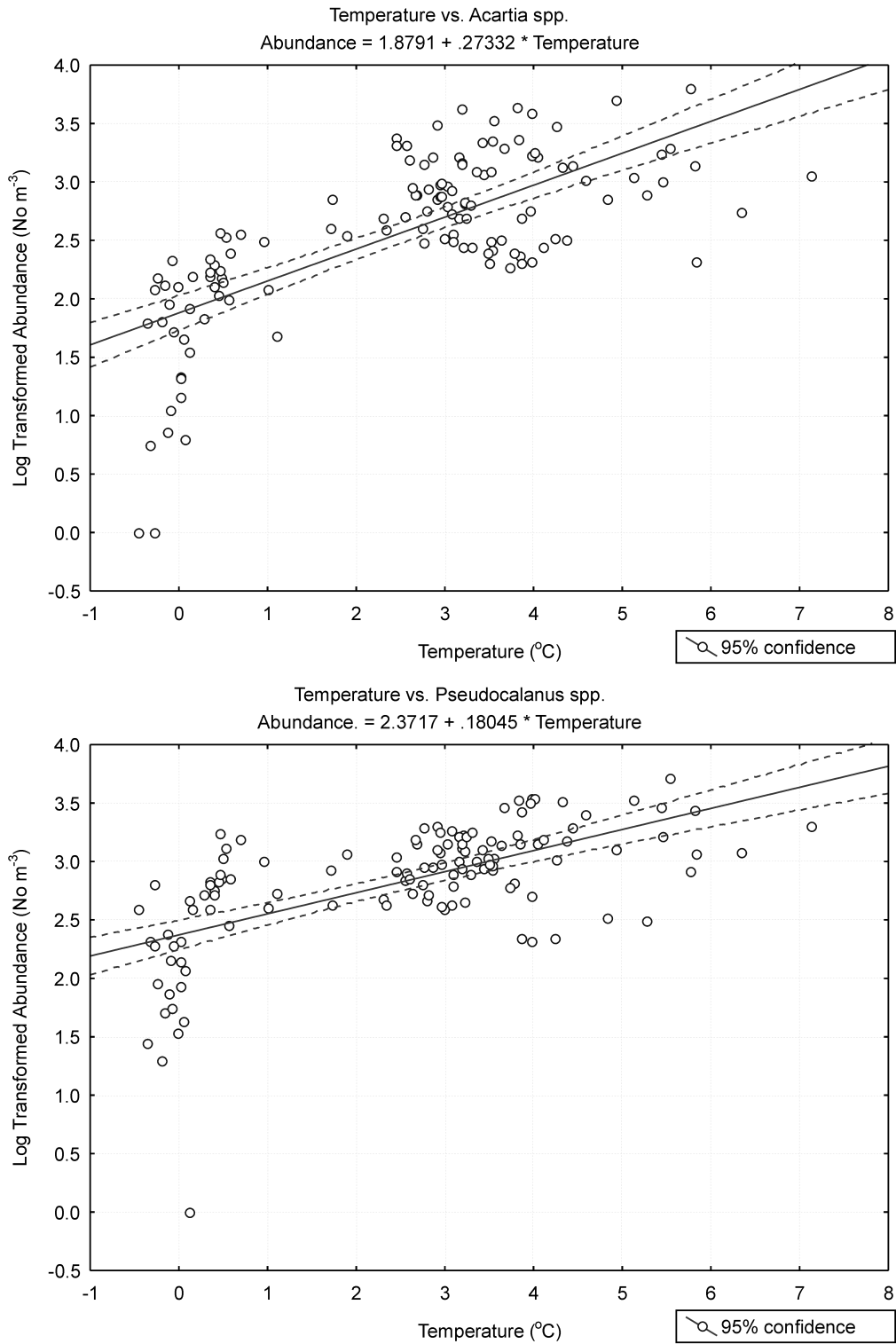


Figure 2.19: June abundances of *Acartia* spp. (top) and *Pseudocalanus* spp. (bottom) in relation to the integrated water temperatures at the stations where they were collected 1997–1999. Dashed lines are 95% confidence intervals around the regressions. Coyle, unpublished data.

Table 2.5: Comparison of acoustically determined euphausiid biomass among the years 1997, 1998, and 1999, mean and 95% confidence interval.

Transect location	June 1997	June 1998	June 1999
	Mean g m ⁻² (95% CI)	Mean g m ⁻² (95% CI)	Mean g m ⁻² (95% CI)
Port Moller, Line A	2.3 (1.94–2.57)	0.77 (0.54–0.99)	17.27* (13.27–21.27)
Port Moller, Line C	2.98 (2.36–3.61)	0.34 (0.25–0.44)	15.76* (14.60–17.46)
Port Moller, Line E	No Data	0.73 (0.62–0.83)	5.29* (4.30–5.65)
Cape Newenham, Line C	1.91 (1.14–1.70)	5.50* (4.71–6.22)	2.75 (1.59–3.91)
Nunivak Island, Line C	1.58 (1.46–1.70)	2.38 (2.26–2.49)	6.82* (5.91–7.72)
Nunivak Island, Line E	1.25 (1.13–1.36)	1.93 (1.62–2.19)	5.64* (4.89–6.02)

* = Statistically significant at $p < 0.05$. Data from Coyle and Pinchuk (2002a).

The effect of temperature on euphausiids appeared to be the inverse of its effect on copepods; in 1999, the acoustically measured biomass of adult euphausiids on the inner and middle shelf was significantly higher than in 1997–1999 (Table 2.5) (Coyle and Pinchuk, 2002a). However, Coyle and Pinchuk point out that this difference may be related to a delay in euphausiid breeding in the cold year, which would result in more adults remaining in the water column when they were sampled in June than in a warm year when most adults would have spawned and died prior to June. Coyle and Pinchuk (2002a) noted that there were significantly higher densities of euphausiid eggs and larvae present in 1999 (the cold year) compared to the warm years of 1997 and 1998. Coyle and Pinchuk (2002a) concluded that there were no significant differences in the biomass of euphausiids over the inner and middle shelf in 1997 and 1998 compared to earlier periods for which data were available. However, if euphausiid spawning is completed in early spring and there is a reduced availability of late spawning adults in summer, this change in the timing of availability could have a negative impact on predators, such as short-tailed shearwaters (*Puffinus tenuirostris*) that depend on euphausiids for a significant portion of their diet (Baduini *et al.*, 2001a,b; Hunt *et al.*, 2002b).

In the last three decades, gelatinous zooplankton, in particular large scyphomedusae, have gone through a remarkable increase in biomass and then crash (Fig. 2.20) (Brodeur *et al.*, 1999a, 2002). The cause (or causes) of the outbreak of jellyfish is not known, though it has been hypothesized that changing climate and ocean temperatures may have been the trigger (Brodeur *et al.*, 1999a). It has also been hypothesized that a decrease in forage fish over the southern portion of the shelf in the early 1980s may have contributed to the jellyfish increase by releasing them from competition (Brodeur *et al.*, 2002). Currently, there are no hypotheses to explain why they suddenly decreased. At the Pribilof Islands, the dominant scyphozoan, *Chrysaora melanaster*, was estimated to consume about one third of the standing stock of crustacean zooplankton and 4.7% of their annual production. Additionally, these jellyfish were estimated to consume about 3% of the standing stock of age-0 pollock in the vicinity of the Pribilof Islands (Brodeur *et al.*, 2002).

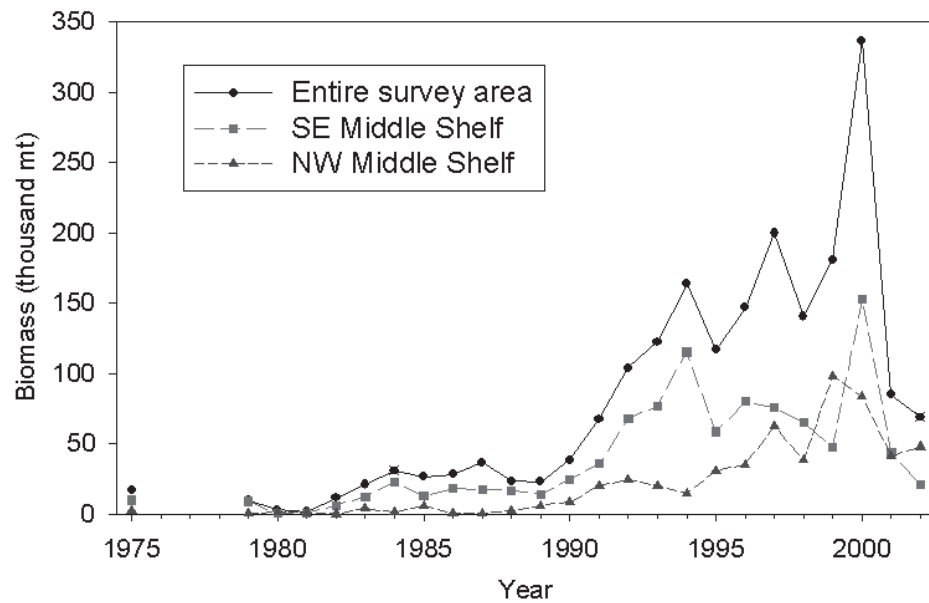


Figure 2.20: Biomass of large medusae in the National Marine Fisheries Service bottom trawl surveys of the southeastern Bering Sea. Data courtesy of G. Walters and R. Brodeur.

2.4.4 Fish

During the late 1970s and early 1980s, several stocks of groundfish and non-crab invertebrates showed strong changes in biomass in the eastern Bering Sea (Conners *et al.*, 2002). Conners *et al.* identified three sites that had been surveyed consistently since about 1965 using comparable gear. Patterns of change in biomass for all species combined were similar across these three areas (Fig. 2.21), and timing of changes in both commercially exploited and non-exploited species were similar. Pacific cod and several species of flatfish showed changes of 300 to 600 percent, whereas the biomass of Greenland turbot decreased by 90 percent (Fig. 2.22). These changes resulted in a marked shift in the species composition of ground fish and benthic invertebrates in shelf waters. Conners *et al.* noted that the timing of the change in CPUE in the trawls was consistent with the timing of the major regime shift of 1976–1977, and that there was little evidence of responses to the later, weaker, regime shifts in 1989 and 1998.

The female spawning biomass of the pollock stock increased strongly in the 1980s because of the growth and survival of the strong year classes that started in 1972 (Fig. 2.23). The biomass continued to be above the long-term average during the 1990s because of the strong year-classes that followed the exceptionally strong 1989 year-class. The increases were apparently due to a combination of favorable ocean conditions and the conservative fishery management practices put in place by the North Pacific Fishery Management Council. The stock showed fluctuations as the young recruits grew in size and were taken by the fishery or died through natural mortality (Fig. 2.22).

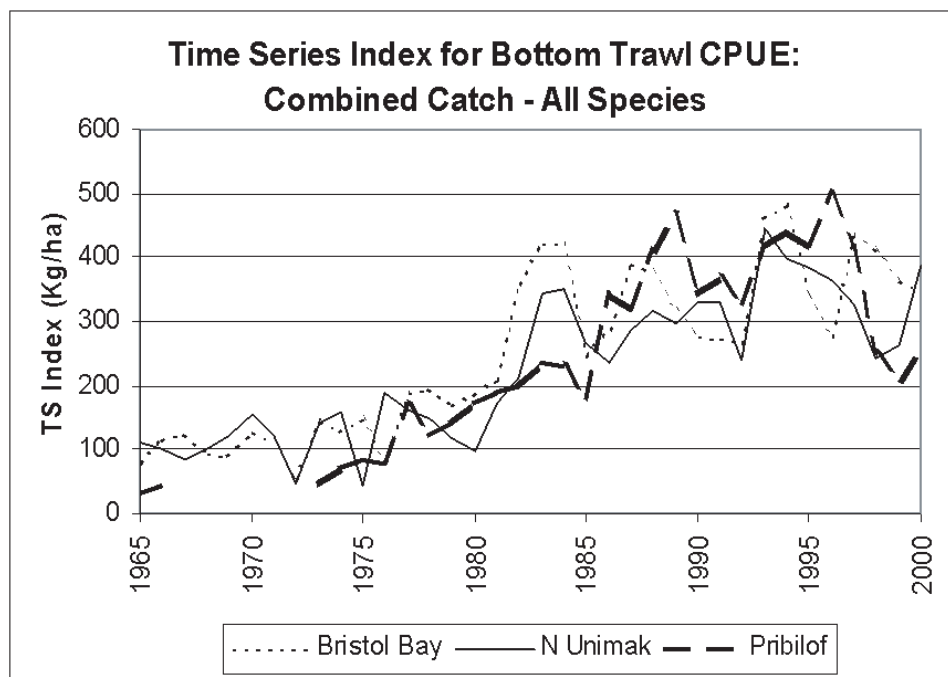


Figure 2.21: Time series of bottom trawl surveys in three regions of the southeastern Bering Sea that have been consistently surveyed with similar gear since the mid-1960s. From Connors *et al.* (2002).

Year-class success represents an annual estimate of productivity and survival for a species. During the period from 1963 to 2001, year-class strength of walleye pollock in the eastern Bering Sea varied from a low of 3.6 billion age-1 fish in 1963 to a high of 66.0 billion in 1978 (Fig. 2.23). Hollowed and Wooster (1995) classified years into those warmer and colder than the long-term mean for the North Pacific Ocean from 1946 to 1990. They found that during a warm period, the year-class strength of many stocks of groundfish were stronger, while during a cool period, the same stocks showed weaker year-class strength. Exceptionally strong year classes of pollock occurred in 10 years (Fig. 2.23, Table 2.6). There were two or three banner year classes per decade with intermediate years showing average to weak year classes (NPFMC, 2000).

Other species of groundfish in the eastern Bering Sea showed the same general pattern as walleye pollock of increase in biomass during the early 1980s due to strong year classes following the 1976–1977 climate regime shift. As examples (Fig. 2.22), Pacific cod (*Gadus macrocephalus*), yellowfin sole (*Limanda aspera*), northern rock sole (*Lepidopsetta polyxystra*), Alaska plaice (*Pleuronectes quadrituberculatus*), flathead sole (*Hippoglossoides elassodon*), arrowtooth flounder (*Atheresthes stomias*) and Greenland turbot (*Reinhardtius hippoglossoides*) follow this pattern (NPFMC, 2000). These trends were due to the increased productivity that was manifest as year-class success (Fig. 2.23).

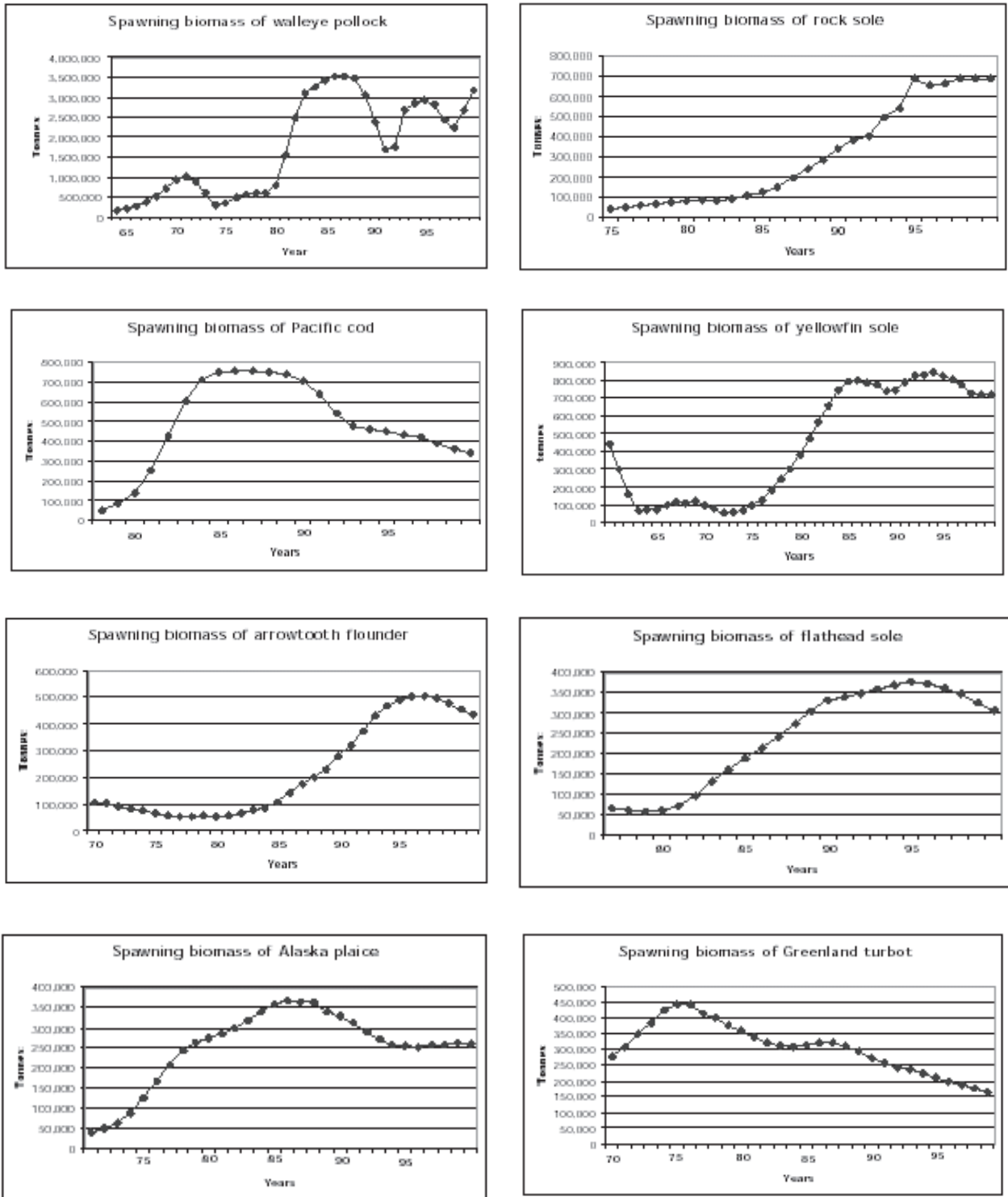


Figure 2.22: Spawner biomass of selected ground fish in the eastern Bering Sea. Data from NPFMC SAFE (2000).

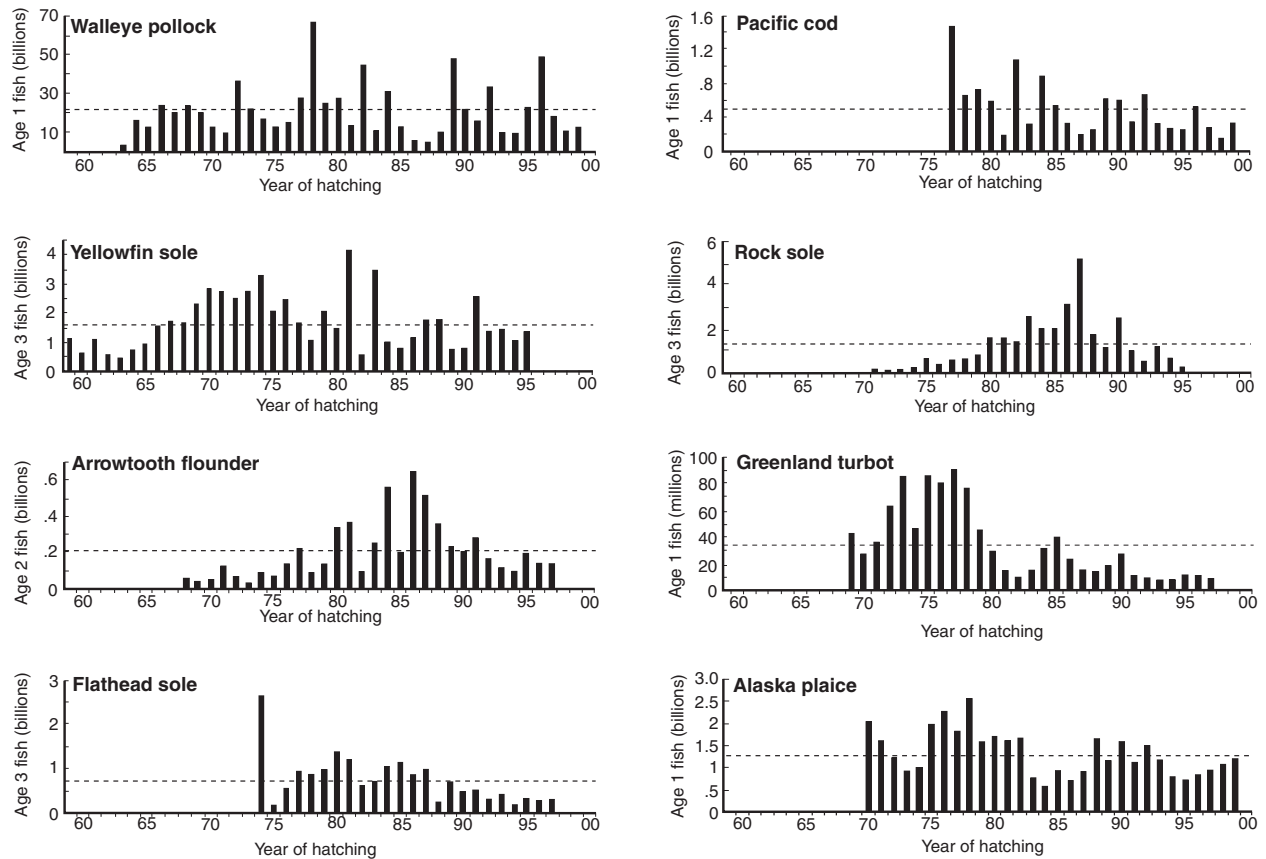


Figure 2.23: Year-class strength for selected species of groundfish in the eastern Bering Sea. Data from NPFMC SAFE (2000).

Table 2.6: Strong year classes ($\geq 20\%$ above the mean from 1975 to 1999) and weak year classes ($\leq 20\%$ below the mean) by species in the Bering Sea. Years not shown had average year classes (mean $\pm 20\%$). Data from NPFMC, 2000.

Group	Strong Year Classes	Weak Year Classes
Group A		
Walleye Pollock	77, 78, 79, 80, 84, 89, 92, 96	75, 76, 81, 83, 85, 87, 88, 91, 93, 94, 98, 99
Alaska Plaice	75, 76, 77, 78, 79, 80, 82, 88, 90	83, 84, 85, 86, 87, 94, 95, 96, 97
Yellowfin Sole	75, 76, 79, 81, 83, 91	78, 82, 84, 85, 86, 89, 90, 94
Flathead Sole	77, 79, 80, 81, 84, 85, 87	75, 76, 88, 90, 91, 92, 93, 94, 95, 96, 97
Pacific Cod	77, 78, 79, 82, 84, 89, 92	81, 83, 86, 87, 88, 91, 93, 94, 95, 97, 98, 99
Group B		
Rock Sole	80, 81, 83, 84, 85, 86, 87, 88, 90	75, 76, 77, 78, 79, 91, 92, 94, 95
Arrowtooth Flounder	80, 81, 83, 84, 86, 87, 88, 91	75, 76, 78, 79, 82, 93, 94, 96, 97
Greenland Turbot	75, 76, 77, 78, 79	81, 82, 83, 86, 87, 88, 89, 91, 92

Two alternative recruitment patterns seem to have emerged. There are those species that show strong year classes in the late 1970s and early 1980s, and there are species with a delayed run of strong year classes beginning in the late 1980s and continuing through the early 1990s (Table 2.6). Both patterns show a reduction of year-class strength in the late 1990s. Fishes with strong year-class productivity in the late 1970s and 1980s include Pacific cod, yellowfin sole, flathead sole, and Alaska plaice. Fishes without strong recruitment in the 1970s, but having strong year classes in the 1980s, are rock sole and arrowtooth flounder (Fig. 2.23). Greenland turbot are unique in that they had strong year classes in the late 1970s, but not in the 1980s and 1990s. There are years that stand out as being characterized as having coincident strong or weak year classes among eight species of groundfish (Table 2.6). The years during which over half of the species had strong year classes were 1977 (5/8), 1979 (6/8), and 1984 (5/8). Two years had weak year classes for over half of the species, 1986 (5/8) and 1994 (7/8).

An important difference between walleye pollock and other groundfish is the continued high biomass levels of walleye pollock in the Bering Sea in the 1990s, which contrasts with patterns of decline for many other economically important species (Fig. 2.22). Walleye pollock is unique in its continued production of young through the decade of the 1990s (Fig. 2.23, Table 2.6).

The pattern of changes in biomass available to the fisheries has followed the availability of recruits, not the catch of the fishery. However, these stock changes greatly affected the fishery landings and sustainable yields. The most notable series of stock increases came after the 1976–1977 regime shift that resulted in favorable ocean conditions north of the state of Washington. During the 1980s, simulations showed that wind-driven surface currents in the southeastern Bering Sea were mostly eastward, and flatfish as well as pollock enjoyed high levels of recruitment (Wilderbuer *et al.*, 2002). However, in the 1990s, surface currents were westerly (seaward), and flatfish recruitment was weaker. For the flatfish, this would have resulted in advection to favorable nursery grounds (Wilderbuer *et al.*, 2002); for pollock,

advection into Bristol Bay would result in separation of larvae and juveniles from cannibalistic adults (Wespestad *et al.*, 2000).

The late 1970s and early 1980s were also a period of major change in the management of the fisheries. In 1977, the extended fishery jurisdiction of the United States and Canada came into force. International fishing was severely curtailed and fishery management became progressively more conservative. There was a transition period of “joint venture” fishing during the late 1970s and early 1980s, after which only domestic fishing was allowed. Also, because of the cooperative interaction between the International Pacific Halibut Commission and the North Pacific Fishery Management Council, the catch of cod and flatfish has been conservative. Thus, fishery takes have affected the total biomass of groundfish in the eastern Bering Sea, and patterns in change appear to be driven by ecological determinants of recruitment.

Another group of species that are of great importance to both the commercial sector and to subsistence users are the Pacific salmon. The world’s largest runs of wild sockeye salmon (*Oncorhynchus nerka*) occur in Bristol Bay (USGS, 2004), and important runs of other species occur in most of the drainages of western Alaska. Several of the runs showed remarkable increases in the 1970s (e.g., Yukon River chum [*O. keta*] and Bristol Bay sockeye), but returns from these and other stocks in western Alaska plunged precipitously in the late 1990s (Fig. 2.24). The reasons for these declines are not apparent, but the most likely hypotheses focus on ocean survival (Kruse, 1998). In recent years, the ocean ecology of salmon in the eastern Bering Sea has received little attention, and we have few data on their impact on the ecosystem there (e.g., Nishiyama, 1974), nor on factors that might affect their ocean ecology. Work recently begun by the North Pacific Anadromous Fish Commission (the BASIS program, NPAFC, 2001), will begin to remedy this lack of information by completing an international survey of Bering-Aleutian salmon.

In addition to work on the commercially important groundfish and salmon species, there have also been significant gains in our knowledge of the distribution, abundance, and ecology of forage fishes. These fish include both small species, such as sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*), smelts, and mesopelagic groups such as Myctophids (lanternfish) and Bathylagidae (deep-sea smelts), as well as the young of larger species such as age-0 and age-1 walleye pollock. These species are eaten by large fish, including Pacific cod, Pacific halibut (*Hippoglossus stenolepis*) and walleye pollock, and are also important components of the diets of marine mammals and seabirds. Brodeur *et al.* (1999b) summarized data collected in 1987 in a joint program with Russian colleagues that resulted in a pair of surveys that covered most of the Bering Sea. They found that age-0 and age-1 pollock were more abundant on the eastern shelf than elsewhere in the Bering, that herring and capelin were most abundant on the northern and western shelves. They also compared the distribution of various species, as sampled in the National Marine Fisheries Bottom Trawl Surveys, in a warm year (1987) and in a cold year (1986). They found that

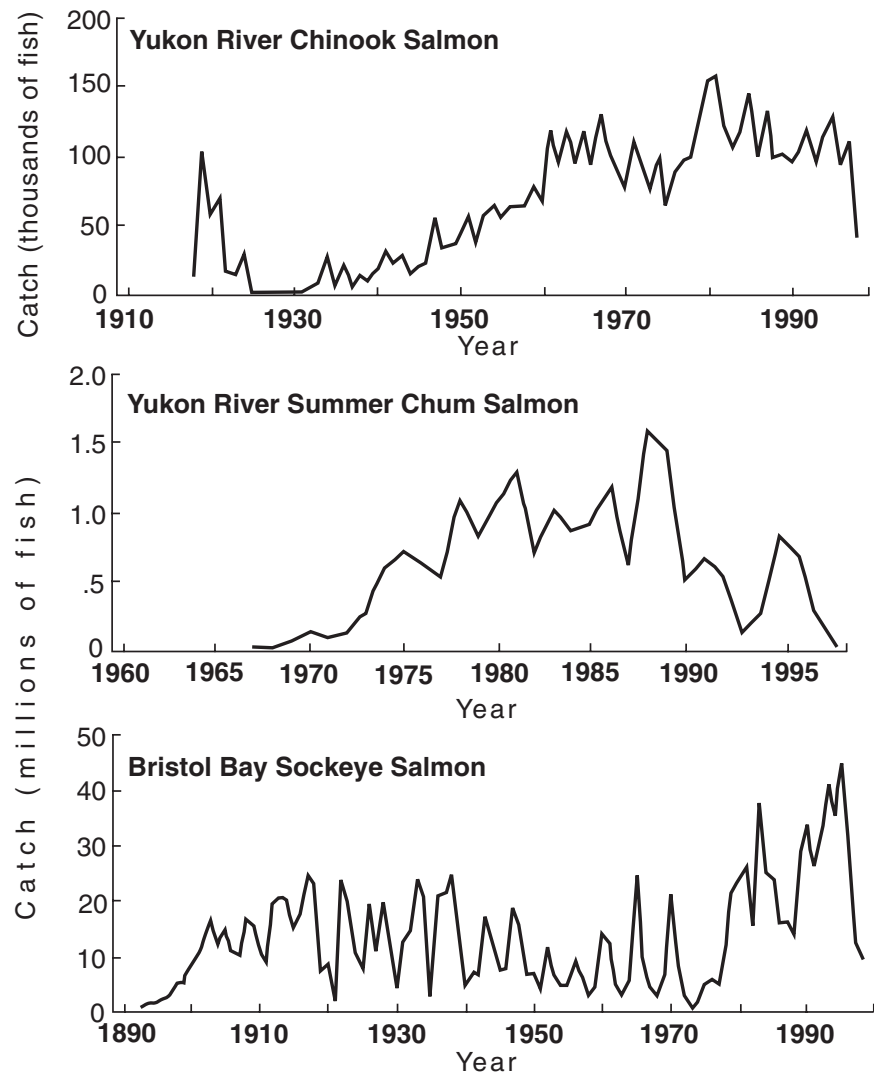


Figure 2.24: Time-series for three western Alaska salmon runs. From Kruse (1998).

some forage fishes, such as age-1 pollock, avoided regions with cold bottom temperatures, whereas others did not (e.g., capelin).

A group of little-studied forage species that deserve particular attention are the mesopelagic fish and squid, which are important forage for upper trophic level consumers including large fish, marine mammals, and seabirds. Many mesopelagic species migrate into the upper mixed layer each night to forage on euphausiids and copepods, returning to depth during the day. This behavior provides a mechanism for rapid downward transport of production from the upper ocean. One species, *Stenobrachius leucopsarus*, perhaps the ecologically most important, may have a biomass of 21 million tons in the North Pacific sub-arctic gyres (including the Bering Sea and the Sea of Okhotsk) (Beamish *et al.*, 1999a). Sinclair *et al.* (1999) assembled data on

mesopelagic fishes and squids from the Bering Sea to provide a description of the species composition, distribution, and relative abundances of members of this important fauna. They noted that, of the squids, members of the families Gonatidae and Cranchiidae appeared in the highest numbers in both trawl surveys and predator diets, while of the fishes, Myctophidae and Bathylagidae were most common. Sinclair and Stabeno (2002) sampled basin waters near the edge of the southeastern Bering Sea shelf. They found unexpectedly high concentrations of biomass, driven primarily by the deep-sea smelt *Leuroglossus schmidti*. Their work revealed a new species of gonatid, a range extension for the snailfish (*Paraliparis paucidens*), and new size records for several species of fish and squid. Discoveries of this nature demonstrate that this ecologically important group of organisms has been neglected. Given their large biomass compared to that of most fish species, we must devote more effort to learning about them. Because of mesopelagics' strongly diel cycles of behavior, study of their ecological role will require examination of trophic relations both during the daylight and at night.

The waters around the Pribilof Islands have been thought to provide a uniquely productive habitat for juvenile pollock because of the potential for enhance production associated with frontal processes there. During the 1990s, several projects examined the ecology of age-0 walleye pollock there. These are referenced in Section 2 (Pribilof Islands) of this report and will not be discussed here.

2.4.5 Marine mammals and seabirds

Dramatic population declines of pinnipeds and seabirds in the eastern Bering Sea and Gulf of Alaska since the mid 1970s contrast with their stability elsewhere in the North Pacific Ocean. Previous studies have proposed a combination of natural (climatic) and anthropogenic (fisheries) factors that may have altered the structure of the food web in the eastern Bering Sea (Piatt and Anderson, 1996; NRC, 1996; Merrick, 1997; Springer, 1998; Anderson and Piatt, 1999; Hunt *et al.*, 2002a) and thus affected population stability of apex predators. Although the mechanisms of change unique to the Bering Sea are not fully understood (Hunt and Byrd, 1999; Hunt *et al.*, 2002a), changes in the populations of marine birds at the Pribilof Islands are likely the result of declines in prey availability, as there is little evidence that these seabird species are subject to significant levels of predation.

Marine mammal populations. Approximately 80% of the world population of northern fur seals (*Callorhinus ursinus*) breeds on the Pribilof Islands where population estimates have been conducted since the turn of the century, and with consistent methodology for the past 60 years (York and Hartley, 1981). There are currently an estimated 800,000 animals remaining from an estimated population of 2 million as recently as the 1950s. The species is listed as depleted under the Marine Mammal Protection Act (NMFS, 1993). Unlike most other apex predators in the Bering Sea, the pattern of decline among northern fur seals is one of steady to severe reductions in population numbers followed by some years of stability (Fig. 2.25). A steep decline began in the mid 1970s that was the effect of either reduced pup

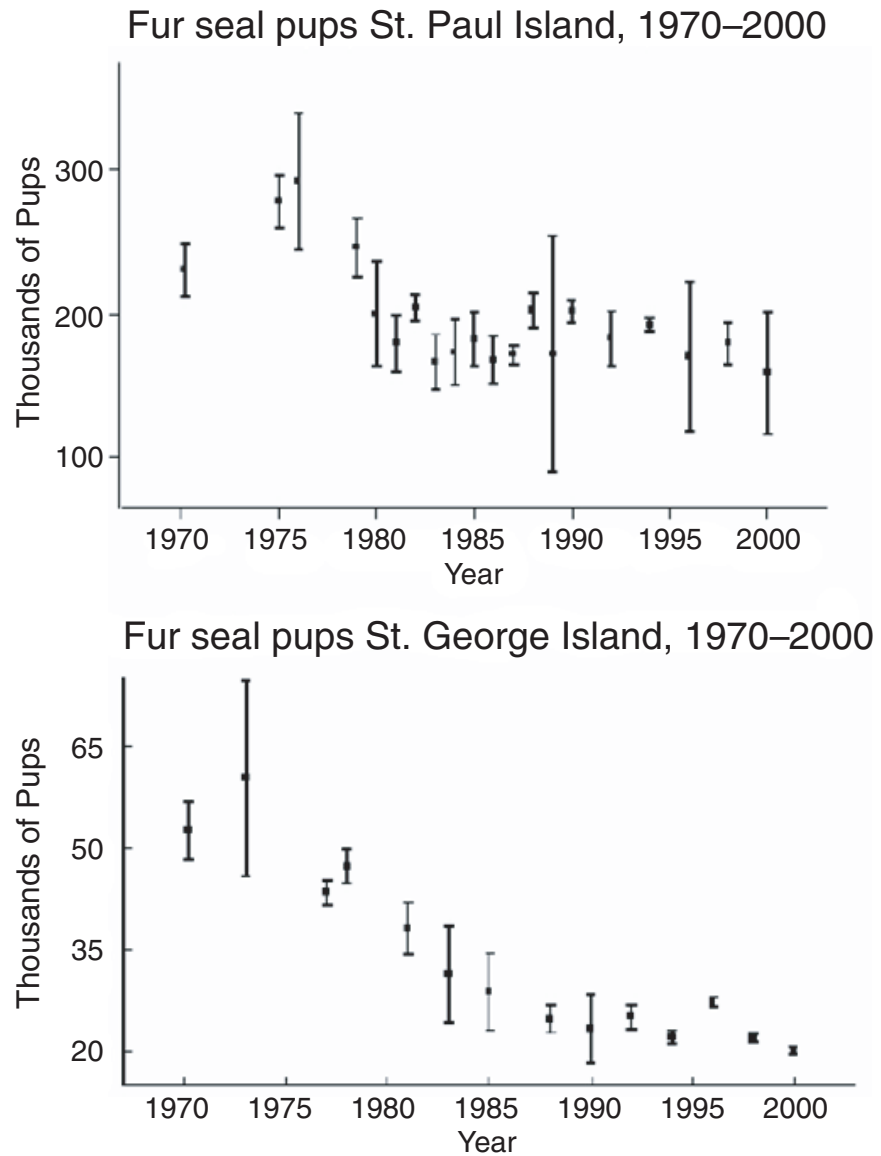


Figure 2.25: Time series of pup counts at St. Paul Island and St. George Island, Pribilof Islands. From NMFS (2002).

production or decreased juvenile survival during their pelagic phase (York and Kozloff, 1987). Declines continued into the mid-1980s, after which the St. Paul Island population remained stable at 33% of its 1970s population, while the smaller population of St. George Island stood at 60% of its 1970s level and continued to decline incrementally into the 1990s (York *et al.*, 2000; Loughlin *et al.*, 1994). The most recent population count in 2002 indicates that an annual decline of 5% has been occurring on both islands since 1998 (NMFS, 2002).

Steller sea lions (*Eumetopias jubatus*) currently are divided into two stocks. The western stock ranges from 144°W in the Gulf of Alaska westward

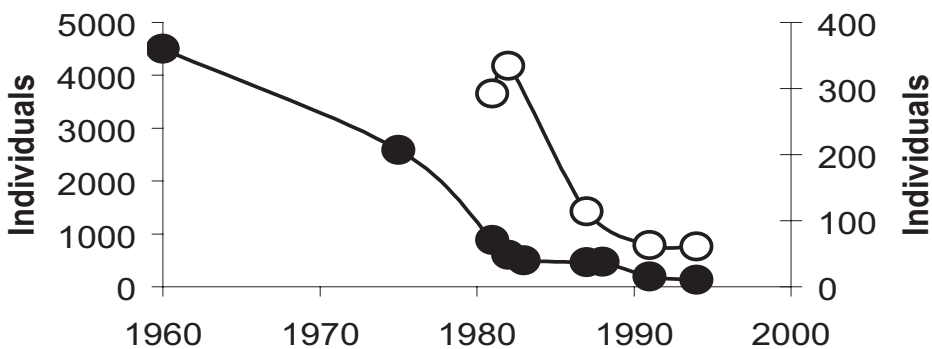


Figure 2.26: Changes in the number of adult (left scale, filled dots) and pup (right scale, open dots) Steller sea lions counted on Walrus Island, Pribilof Islands. Data from National Marine Fisheries Service, National Marine Mammal Laboratory, Seattle, Washington. From Hunt *et al.* (2002a).

across the Aleutian Island chain and includes Walrus Island in the Pribilof Island group. After a continual population decrease of 5% per year since the 1970s, the monitored portion of the stock in the Gulf of Alaska and along the Aleutian Islands chain showed an increase of 5% between 2001 and 2002. The population of Steller sea lions on Walrus Island (Pribilof Island group) has been in steady decline since the 1960s and is considered a nearly extinct rookery (Fig. 2.26). The western stock of Steller sea lions is currently listed as endangered under the U.S. Endangered Species Act. The causes of the decline in the western stock of Steller sea lions remain controversial (NRC, 2003).

Populations of large cetaceans in the eastern Bering Sea were greatly reduced by commercial whaling that continued through about 1970 (NRC, 1996). In contrast to declines in pinniped and seabird populations (see below), populations of large baleen whales, which were almost extirpated in shelf waters of the eastern Bering Sea by the 1960s (NRC, 1996; Merrick, 1997), may be increasing. Although in the mid 1970s it was rare to encounter any large cetacean over the eastern Bering Sea shelf (Leatherwood *et al.*, 1983; Brueggerman *et al.*, 1987), since the 1980s, whales have been encountered over shelf waters with increasing frequency (Baretta and Hunt, 1994). Significant numbers of large cetaceans are now present in shelf waters during summer (Tynan, 1999; Moore *et al.*, 2000, 2002).

Pinniped diets. The composition of the diet of northern fur seals in the Bering Sea has been inferred from material obtained from stomachs of animals shot at sea, from stomach contents and vomits of animals on land, and most recently from analysis of hard parts remaining in scats (feces) (Sinclair *et al.*, in preparation). Although not completely comparable because of differences in the likelihood of detection of different dietary items, the time series for fur seals provide evidence of significant changes in the composition of their diets over the past forty years (see Hunt *et al.*, 2002a for a review of earlier work). Most significantly, in the 1960s, cold-water species such as capelin and Greenland turbot were important, whereas by

the 1980s, these had disappeared from fur seal diets at the Pribilofs, and diets were dominated by pollock ≤ 2 years of age.

During the 1990s, analyses of scats on St. Paul and St. George Islands revealed that fur seals there take at least four species of squid and approximately 30 species of fish. Primary prey (those species that occurred with a frequency of 10% or higher on either island, in any single year) included the four species of squid and five species of fish. On St. Paul Island, only walleye pollock ranked above 10% for all sample years combined. In all years combined on St. George Island, pollock, salmon, and the gonatid squid *Gonatopsis borealis*/*Berryteuthis magister* ranked as primary prey items. Since 1988, the number of northern fur seals on the Pribilof Islands consuming squid has decreased, while the number consuming walleye pollock (*Theragra chalcogramma*) and northern smoothtongue (*Leuroglossus schmidti*) on both islands, and Pacific salmon (*Salmonidae*) on St. George Island has increased (Fig. 2.27). While northern fur seals have relied primarily on juvenile pollock (ages-0 and -1) and to a lesser degree age-2+ since the 1980s (Sinclair *et al.*, 1994, 1996; Antonelis *et al.*, 1997), in the 1990s, there has been an increase in the use of age-3+ pollock, and possibly a decrease in the consumption of age-0 pollock, particularly on St. Paul Island (Fig. 2.28). Over the decade of the 1990s, fur seals on St. George have had a somewhat higher consumption of age-3+ pollock compared to those on St. Paul Island, which is in line with the greater densities of adult pollock around St. George Island relative to St. Paul (NMFS, 1993).

Adult fur seals are typically specific to summer feeding locations (Robson, 2002) depending upon the rookery of their birth; adult females from St. George Island can be generally characterized as off-shelf feeders compared to those from St. Paul Island (Sinclair *et al.*, 1996; Goebel, 2002). Off-shelf feeding is indicated by consumption of salmon, northern smoothtongue, and the Gonatid squid *Gonatopsis borealis*/*Berryteuthis magister*.

Scats collected from Steller sea lions on Walrus Island in 1994 ($n = 43$) and 2001 ($n = 44$) contained 11 species (or taxonomic groups) of fish prey that ranked above 10% in frequency of occurrence (FO) in one or both years. Irish Lord (*Hemilepidotus hemilepidotus*), Pacific cod, walleye pollock, and rock sole ranked above 10% FO in both sample years. With the exception of salmon, all the species consumed by Steller sea lions on Walrus Island are demersal or semi-demersal in habit. Both juvenile and adult pollock were present in Steller sea lion scats with an emphasis of age 5+ in year two.

Seabird populations. During the 1970s and early 1980s, the abundance of piscivorous seabirds breeding at the Pribilof Islands declined (Figs. 2.29, 2.30) (Decker *et al.*, 1995; Springer, 1998; Dragoo *et al.*, 2001). Kittiwake (*Rissa* spp.) and common murre (*Uria aalge*) declines were especially severe on St. Paul Island during the 1970s and 1980s. During that time, common murre became more abundant on St. George Island. It is unclear why population declines in murre were more severe on St. Paul Island than on St. George Island.

Schmutz (Appendix 1 in Sinclair *et al.*, in preparation) partitioned the causes of kittiwake and murre population changes on the Pribilof Islands between reproductive success (productivity) and other factors that include

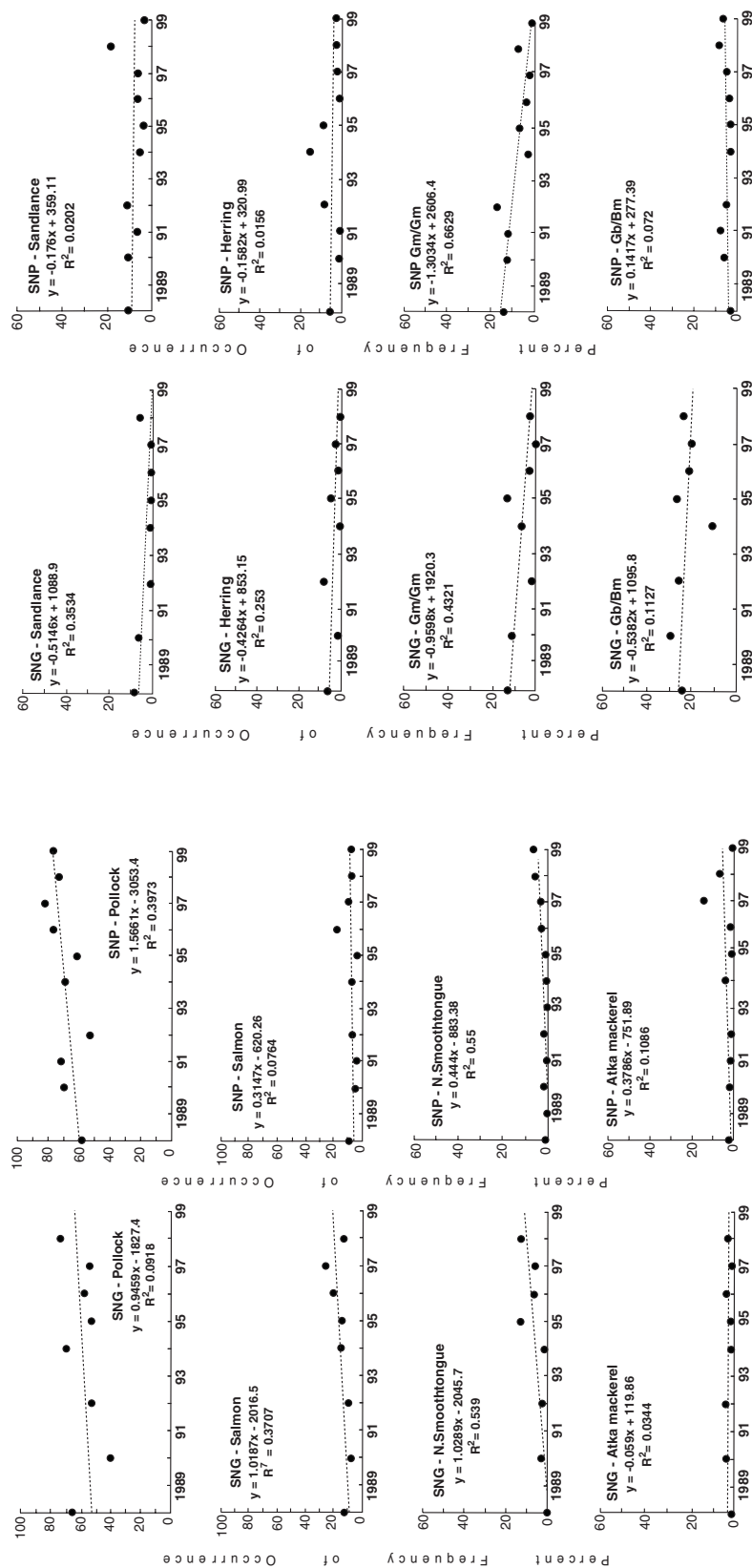


Figure 2.27: Changes in prey composition for northern fur seals on the Pribilof Islands in the late 1980s and 1990s. Gm/Gm: “shelf squid,” one or both of two species *Gonatus middendorffi* and/or *G. madokai*. Gb/Bm: “slope squid” *Gonatopsis borealis* and/or *Berryteuthis magister*. SNP = St. Paul and SNG = St. George. From Sinclair *et al.* (in preparation).

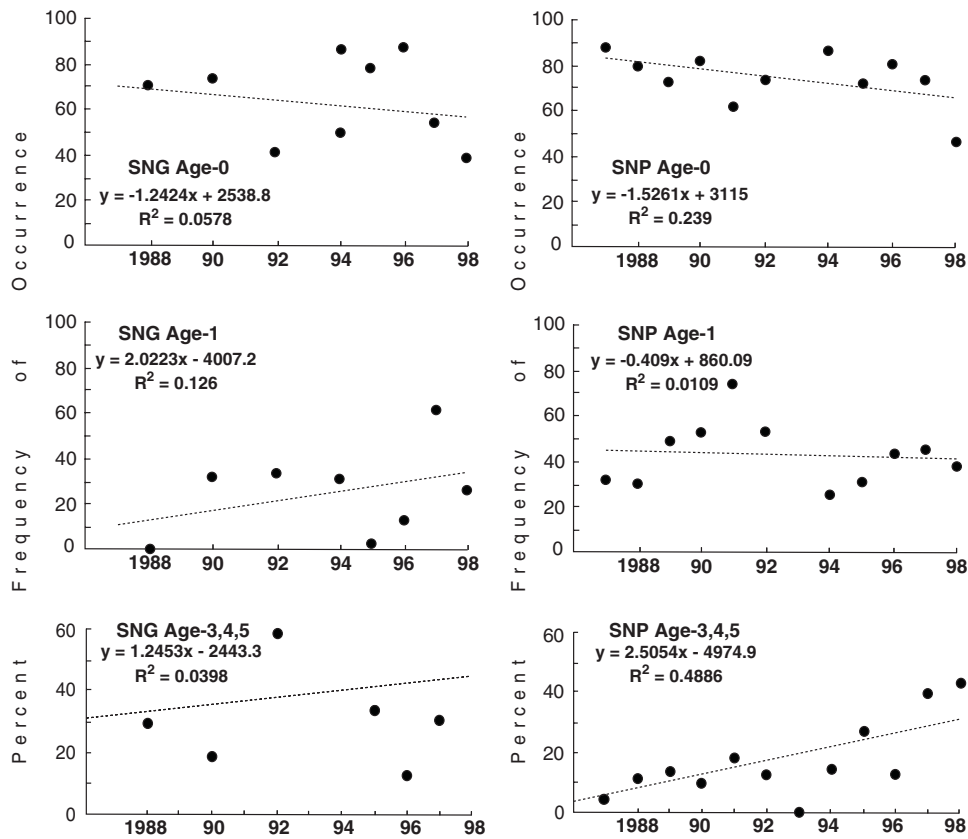


Figure 2.28: Changes in the age composition of walleye pollock in the diets of northern fur seals on the Pribilof Islands in the late 1980s and 1990s. Data from Sinclair *et al.* (in preparation).

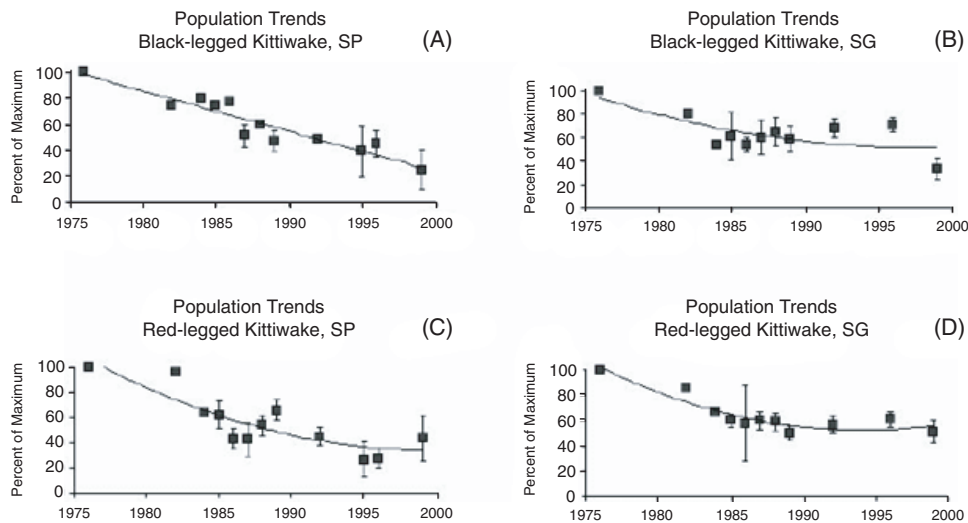


Figure 2.29: Population trends in black-legged kittiwakes and red-legged kittiwakes on the Pribilof Islands. From Dragoo *et al.* (2001).

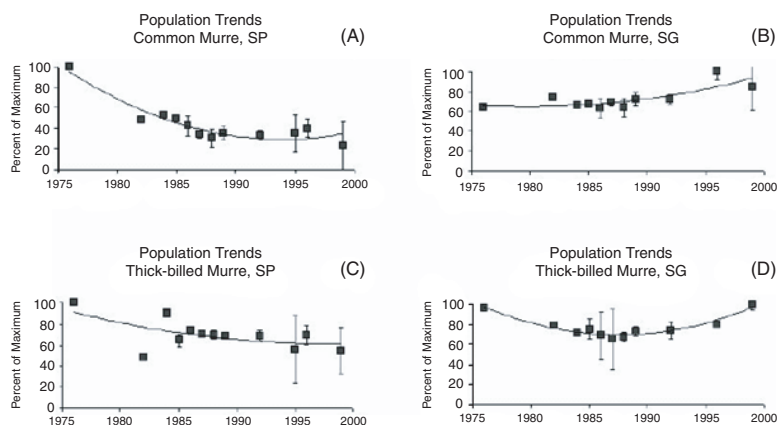


Figure 2.30: Population trends of common and thick-billed murres on the Pribilof Islands. From Dragoo *et al.* (2001).

post-fledging mortality and emigration. He found that for the four species of kittiwakes and murres, productivity accounted for one-third (34%) of the variation in population change. The majority (66%) of variation in population growth rate was attributable to mortality and emigration, but distinction between these two demographic processes was not possible for most species due to lack of data. However, other survival and population data for the geographically restricted red-legged kittiwake (*Rissa brevirostris*) indicated that, for this species, variations in survival have likely been a principal demographic force.

Marine bird diets. Sampling of marine bird diets has shown that there are consistent, significant differences in diet components between seabirds nesting on St. George and St. Paul islands, and that, since the mid 1970s, there have been significant changes of diet components for seabird species nesting on St. George and St. Paul islands (Sinclair *et al.*, in preparation). During the 1970s and 1980s, black-legged kittiwakes (*R. tridactyla*) and common and thick-billed murres (*U. lomvia*) used more invertebrates (e.g., euphausiids, squid) on St. George than on St. Paul Island. Similarly, during the 1990s, the proportion of black-legged kittiwake and thick-billed murre diets consisting of invertebrates was higher on St. George than on St. Paul Island. During the 1970s and 1980s, there were also differences in the proportions of four species of forage fishes used (Sinclair *et al.*, in preparation). Capelin composed a higher proportion of kittiwake diets on St. Paul Island than on St. George Island. Sand lance were a larger proportion of murre diets on St. George Island than on St. Paul Island. During the 1990s, all four seabird species took a higher percentage of gadids on St. Paul Island than they did on St. George Island.

The differences in diets between the islands are important. They indicate that kittiwakes and murres on St. George have had access to a wider variety of prey, in particular, invertebrates including squids and euphausiids, than seabirds on St. Paul Island. And, seabirds on St. Paul Island have been more dependent on juvenile gadids and capelin than birds on St. George Island

where seabirds apparently had more ready access to a wider variety of forage fishes including sand lance and myctophids.

During the 1970s and 1980s, gadids (mainly walleye pollock) were the primary component of black-legged kittiwake, common murre, and thick-billed murre diets. Red-legged kittiwakes took mainly lanternfish. There was a significant decline between the 1970s and 1980s in the proportion of gadids in kittiwake diets on St. Paul, but not St. George Island (Fig. 2.31), and in thick-billed murre diets on St. George Island. Likewise, the diet of red-legged kittiwakes during the early season contained a higher proportion of gadids during the 1970s than they did during the 1980s.

Seabird reproduction in an ecosystem context. Sinclair *et al.* (in preparation) evaluated the spatial scale at which causal factors appeared to have influenced demographic parameters in Pribilof Islands' seabirds. If population declines were related to processes that operate on large (regional) spatial scales, such as prey availability over the shelf, then seabird reproductive success and colony attendance should have been correlated between St. Paul and St. George Islands. If populations responded to processes that operated on small (local) spatial scales, such as prey availability associated with oceanographic features near an island, then seabird demography should have differed between the islands. Because colony attendance and reproductive success of black-legged kittiwakes and red-legged kittiwakes were correlated between populations on St. Paul and St. George Islands, as were interannual variations in the diets of these species on the two islands, Sinclair *et al.* (in preparation) concluded that population dynamics in kittiwakes were influenced by processes that occurred over large spatial scales (shelf-wide), rather than at the local (island) level. In contrast, for both common and thick-billed murres, interannual variability in colony attendance, and reproductive success in thick-billed murres, were not correlated between islands, suggesting that the sizes of populations of two murres were influenced by factors that operated on a local scale.

At about the time of the 1976–1977 regime shift, and concurrent with the declines in piscivorous pinnipeds and seabirds at the Pribilof Islands, there were significant decreases in the biomass of age-1 walleye pollock on the Bering Sea shelf (Brodeur *et al.*, 1999b; Hunt *et al.*, 2002a; Sinclair *et al.*, in preparation). In some areas, abundance decreased by as much as 95% (Springer, 1992; Sinclair *et al.*, 1996; Brodeur *et al.*, 1999b; Hunt *et al.*, 2002a). Likewise, there is evidence for significant declines in the abundance of capelin, an important forage fish for seabirds (Hunt *et al.*, 1996a). Because seabirds whose populations declined had diets consisting primarily of age-1 pollock (Springer, 1992; Decker *et al.*, 1995; Hunt *et al.*, 1996c, 2002a), and the proportion of these declined in their diets, it was hypothesized that declines in the abundance of age-1 pollock and other forage fishes reduced the foraging success and, consequently, reproductive success and population size of kittiwakes and murres at the Pribilof Islands (Hunt and Byrd, 1999). A shift from use of age-1 to age-0 pollock during this period (Hunt *et al.*, 1996b) would have been particularly challenging, as age-0 pollock are both smaller (about 2 g) than age-1 pollock in spring (about 19 g) and of lower energy density (about 2% fat vs. about 5% fat) (Iverson *et al.*, 2002).

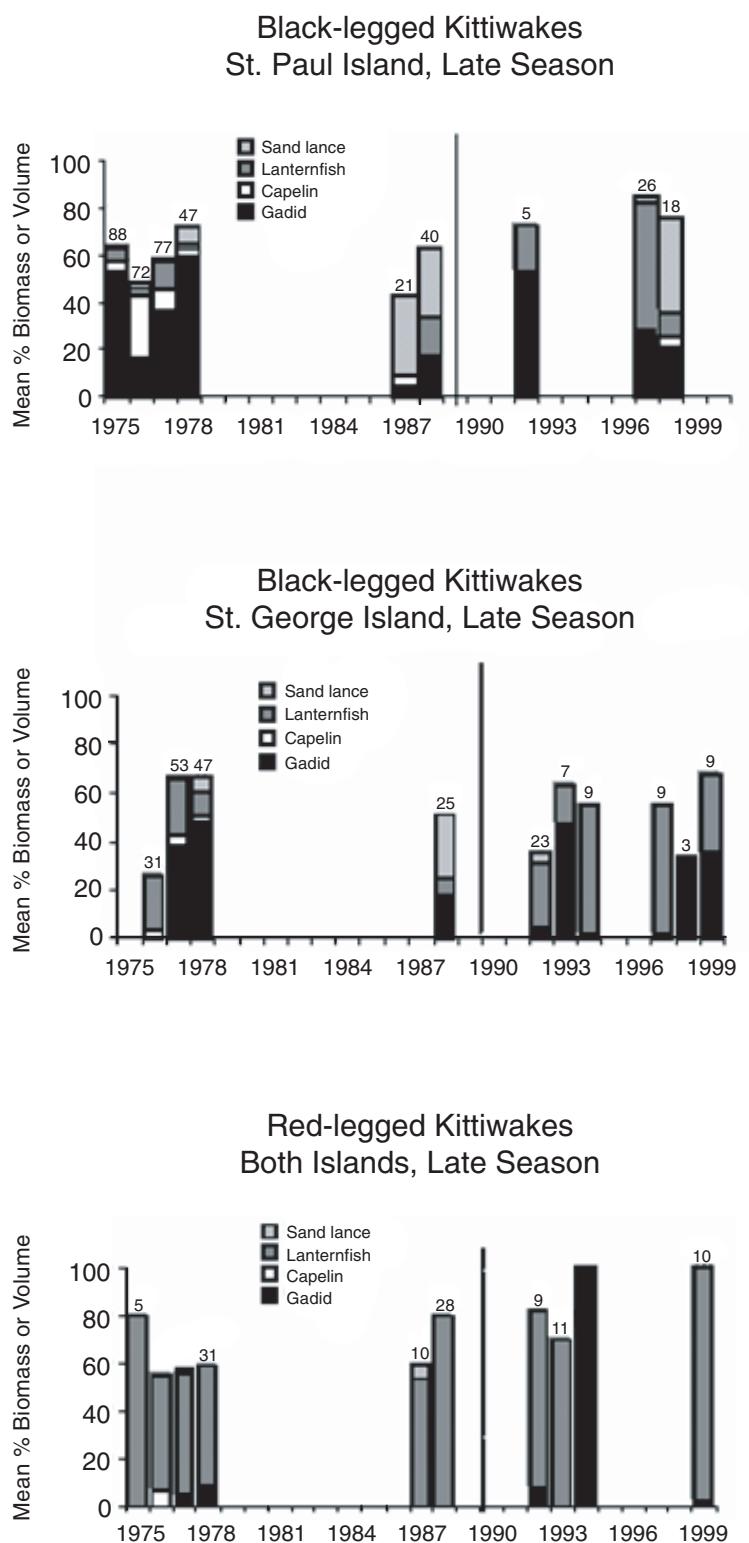


Figure 2.31: Changes in the species composition of the diets of black-legged and red legged kittiwakes at the Pribilof Islands, 1975–1999. Data from Sinclair *et al.* (in preparation).

The decreases in at least black-legged kittiwakes may be related to an increase in adult pollock on the shelf and competition with these fish for age-1 pollock and other forage fish. The biomass of adult (age 3+) walleye pollock on the Bering Sea shelf increased during 1976–1999 ($r^2 = 0.30$, $P = 0.006$, $n = 24$), with the steepest increase in their biomass occurring during 1979–1982 (Sinclair *et al.*, in preparation). The annual variability in reproductive success in black-legged kittiwakes was negatively correlated with the biomass of adult walleye pollock on the Bering Sea shelf ($r = -0.68$, $p < 0.001$) (Livingston *et al.*, 1999; Hunt and Stabeno, 2002; Sinclair *et al.*, in preparation). There was no correlation between reproductive success in red-legged kittiwakes ($r = -0.35$, $p = 0.160$), common murre ($r = 0.18$, $p = 0.626$), or thick-billed murre (St. Paul: $r = -0.419$, $p = 0.136$; St. George: $r = 0.19$, $p = 0.440$) and the biomass of adult walleye pollock on the shelf (Sinclair *et al.*, in preparation).

Prey availability and seabird mortality at the Pribilof Islands.

Although Sinclair *et al.* (in preparation) found little correlation between juvenile pollock abundance on bottom trawl surveys and seabird reproductive success on an interannual basis, changes in the availability of young pollock (and possibly other prey) to seabirds during the late 1970s probably *did* result in poor foraging conditions for seabirds. Inter-colony comparisons suggest that seabird productivity at the Pribilof Islands is limited by the availability of food. For example, since the mid 1970s, the long-term (1976–1999) mean reproductive success of black-legged kittiwakes on St. Paul Island is 0.28 chicks nest⁻¹ year⁻¹, and on St. George Island, it is 0.22 chicks nest⁻¹ year⁻¹. In contrast, mean reproductive success over the same period for black-legged kittiwakes at Cape Lisburne, northern Bering Sea, is 0.80 chicks nest⁻¹ year⁻¹, and in some areas, black-legged kittiwakes raise two or more chicks per year. At the Pribilofs, kittiwakes raise at most one (Dragoo *et al.*, 2001). Likewise, reproductive success is also low among murre at the Pribilof Islands relative to murre at other colonies in the North Pacific. Since the mid 1970s, common murre on St. Paul Island fledged an average of 0.53 chicks nest⁻¹ year⁻¹, and, on St. George Island, the average is 0.52 chicks nest⁻¹ year⁻¹. In contrast, common murre at Cape Thompson, in the northern Bering Sea, fledged an average of 0.70 chicks nest⁻¹ year⁻¹. At Kodiak Island (E. Amatuli), in the Gulf of Alaska, they fledged an average of 0.71 chicks nest⁻¹ year⁻¹ (Dragoo *et al.*, 2001). The ability of kittiwakes and murre at other colonies to consistently raise more young than they do at the Pribilof Islands suggests that competition for food is greater around the Pribilofs or foraging conditions around the Pribilofs are poor relative to other regions in the Bering Sea.

If prey availability to seabirds at the Pribilof Islands is relatively low during the breeding period, as suggested in the preceding discussion, reproduction may be an especially stressful time for Pribilof seabirds. Kitaysky and colleagues (1999a,b, 2000, 2001a) demonstrated the exacerbating effect that a limited food supply can have on acute stress to seabirds during the reproductive phase. Kitaysky *et al.* (1999b) found that adult black-legged kittiwakes breeding at a colony in Cook Inlet, Alaska, had elevated corticosterone levels during reproduction, and that stress levels were nega-

tively associated with food availability near the breeding colony (Kitaysky *et al.*, 1999b). In addition, corticosterone concentrations in birds increased throughout the breeding season, indicating that stress can become increasingly severe for seabirds as they progress from the egg-laying to the chick-rearing periods (Kitaysky *et al.*, 1999b). Using captive kittiwakes, Kitaysky *et al.* (1999a, 2001a) showed that food scarcity and food of poor nutritional quality increased circulating concentrations of a stress-response hormone, corticosterone, in black-legged and red-legged kittiwake chicks. Corticosterone indicates catabolic activity of metabolic pathways, signaling reliance by seabirds on endogenous energy reserves.

Increasing levels of corticosterone in plasma may affect not only the behaviors of the birds involved, but also their probability of survival. Kitaysky *et al.* (2000) showed experimentally that adult black-legged kittiwakes with elevated levels of corticosterone had significantly lower probability of returning to their colonies over the 2 years subsequent to implantation of corticosterone than did birds with sham operations. These results support the hypothesis that when adults have to work hard to raise chicks, either because food may be in short supply (Kitaysky *et al.*, 2000), or because the begging of hungry chicks forces them to work harder (Kitaysky *et al.*, 2001b), adult survival may be compromised (Golet *et al.*, 1998; Golet and Irons, 1999; Kitaysky *et al.*, 2001b). In the laboratory, Kitaysky *et al.* (2003) showed that young red-legged kittiwake chicks with elevated levels of corticosterone resulting from implants were less able at learning to find food than were birds that were sham-operated. Here the implication is that young kittiwakes that have had less food than optimal while growing may have difficulty learning to feed themselves once fledged and independent. These birds would be exceptionally vulnerable to starvation during the first few months of independence. There is considerable evidence that young seabirds have a more difficult time catching prey than adults. Learning deficits imposed by lack of adequate feeding in the nest and the consequent high stress levels would exacerbate this situation.

Thus, mortality among seabirds at the Pribilof Islands may have varied with the abundance of prey near the islands and may have been most severe during the post-breeding period, when deaths were difficult to observe. By that time, adults would have spent a considerable amount of energy on reproduction and fledglings would have had to learn to forage for themselves or perish. Storm activity is also greater during the post-breeding period (i.e., autumn), and inclement weather can have both direct and indirect implications for chick survivorship and adult mortality, as stormy weather impairs foraging by some seabirds. At the Pribilof Islands, Braun and Hunt (1983) found that in black-legged kittiwakes on St. Paul Island, chick loss due to ejection of second-hatched young by an older sibling happened more often than expected by chance during inclement weather. Work by others has shown that these behaviors result from the older chick being unable to satisfy its nutritional needs (Mock *et al.*, 1990; Irons, 1992).

Inability to obtain adequate prey has also affected migrant, non-breeding species in the Bering Sea. Each year millions of short-tailed shearwaters (*Puffinus tenuirostris*) migrate from Australia to the Bering Sea to forage

over the inner shelf. The evolution of this annual trans-equatorial migration implies that usually extraordinary amounts of prey must be readily available to these birds in the Bering Sea. During summer and fall of 1997, possibly as many as 10% of the 16 million short-tailed shearwaters present in the southeastern Bering Sea died (Vance *et al.*, 1998; Baduini *et al.*, 2001a,b). Between 1 August and 1 September, reports of moribund and dead shearwaters came from both sides of the Alaska Peninsula, the Aleutian Islands as far west as Adak, Bristol Bay, the Bering Sea north to Cape Anadyr (Russia), and the eastern Chukchi Sea. At least several hundred thousand shearwaters washed ashore. Compared with previous large-scale seabird die offs in the Bering Sea (Bailey and Davenport, 1972; Oka and Maruyama, 1986; Hatch, 1987; Piatt and Van Pelt, 1997), the 1997 event in the southeastern Bering Sea was probably one or two orders of magnitude larger (10^5 – 10^6 vs. 10^4 birds dying). Apparently they were unable to obtain sufficient of the usual prey, euphausiids, in 1997. In 1998, shearwaters were again emaciated, but few died, perhaps because the summer was windier, and they needed less energy to fly between places where food was obtainable. Their diets also shifted, with a greater proportion of fish and zooplankton being taken than was true in the same region in earlier years (Hunt *et al.*, 2002b).

In spring 1998, shearwaters had lower body masses than in spring 1997. Because the seasonal progression of stratification, bloom, and euphausiid mating occurred earlier in 1997, foraging for shearwaters arriving in May 1997 was apparently good, and birds were fat in June. In contrast, in 1998, the seasonal progression was late, and euphausiids were only beginning to form mating swarms in June. Consequently, shearwaters did not put on the level of fat reserves seen in June 1997. Perhaps because euphausiid mating came early in 1997, by late July, few near-surface swarms of mating euphausiids were available to shearwaters. If we are correct in our assessment that euphausiid maturation was delayed in 1999, and that the biomass of euphausiids was large compared to 1997, then swarms should have been available late into the summer and late-season body mass of shearwaters should be high. In the cold spring of 1999, euphausiids were abundant well into summer (Coyle and Pinchuk, 2002a), and shearwaters gained mass through the summer. Thus, it appears that temperature, through its effects on the timing of the availability of prey, may have important impacts on the survival of top predators.

2.5 What Controls Recruitment of Walleye Pollock?

Walleye pollock dominate the biomass of the eastern Bering Sea ecosystem and the trophic guilds in which they participate (Schumacher *et al.*, 2003). They are harvested in greater quantity than any other species of fish or shellfish, and made up >65% of the total groundfish biomass harvested during the 1980s (Napp *et al.*, 2000). Pollock, because of their vast numbers, are a nodal species for the Bering Sea, i.e., they are an integral part of the food chain for lower and higher trophic prey and predators. Thus, in any examination of the ecosystems of the eastern Bering Sea, factors that influ-

ence the abundance, distribution, and ecology of walleye pollock are of key importance for understanding the function of the ecosystem as a whole.

Walleye pollock were not always so abundant. In the early 1960s, their populations were small by comparison with those of the 1980s and 1990s. The reason for their initial increase in the mid to late 1960s is not known, but one hypothesis is that the increase was a result of a trophic cascade that occurred when large, plankton-eating whales and Pacific Ocean perch (*Sebastes alutus*) were harvested to “commercial extinction” in the late 1960s and early 1970s, thereby releasing vast amounts of zooplankton from consumption (Merrick, 1997; NRC, 1996). This newly available zooplankton resource then fuelled the expansion of the pollock population. The removal of the whales may also have released age-0 and age-1 pollock from predation pressure, as fin (*Balaenoptera physalus*) and minke (*B. acutorostrata*) whales would have most likely consumed young pollock along with zooplankton.

During the 1970s and early 1980s, the biomass of walleye pollock first declined and then increased explosively. In the mid 1970s, excessively high harvest rates imposed by the foreign fishing fleets caused the stock to decline. This foreign fishery ceased as of the establishment of the 200-mile Exclusive Economic Zone in 1977. In 1978, pollock produced an enormous year-class that numbered 63.5 billion age-1 fish in 1979 (NMFS, 2002). As these fish grew to adult size, their biomass came to dominate the eastern Bering Sea ecosystem. The reasons for this second spurt in population growth are not known. It is possible that this was a continuation of the ecological release of the pollock population subsequent to the removal of the whales and fish with which they are believed to have competed for prey. An alternative, but not mutually exclusive, hypothesis for this population growth is that the strong year classes of 1977 and 1978 were the result of the 1976–1977 regime shift that resulted in earlier ice retreat and warmer water temperatures in spring, conditions favorable for zooplankton production that would have provided abundant prey resources for growing pollock (Francis *et al.*, 1998; Hunt *et al.*, 2002a). Indeed, there is a general acknowledgment that warm years are conducive to enhanced pollock recruitment (Bulatov, 1995; Hollowed and Wooster, 1995; Bailey *et al.*, 1995, 1996; Quinn and Niebauer, 1995; Walsh and McRoy, 1986; Blood, 2002). The cessation of the foreign fishery did not cause the strong year class of 1978. The increase was driven by exceptional early survival and recruitment. Had the fishery continued into the mid 1980s, there might not have been as great a growth in pollock biomass, but the 1978 year class still would have been exceptional.

Throughout the 1980s, the biomass of walleye pollock in the eastern Bering Sea remained high, though between 1990 and 1998 there was a substantial decline (Fig. 2.32) (NMFS, 2002). During the 1980s, there were three strong year classes, and during the 1990s, there were two (Table 2.6; Fig. 2.32). It is these strong year classes, as they matured, that sustained the biomass of the stock and its ability to support commercial fisheries. Understanding of the determination of year-class strength is a key to understanding much of what occurs in the southeastern Bering Sea marine ecosystem. Section 4 of this report discusses some factors in detail.

Table 2.7 lists several hypotheses that have been put forward as expla-

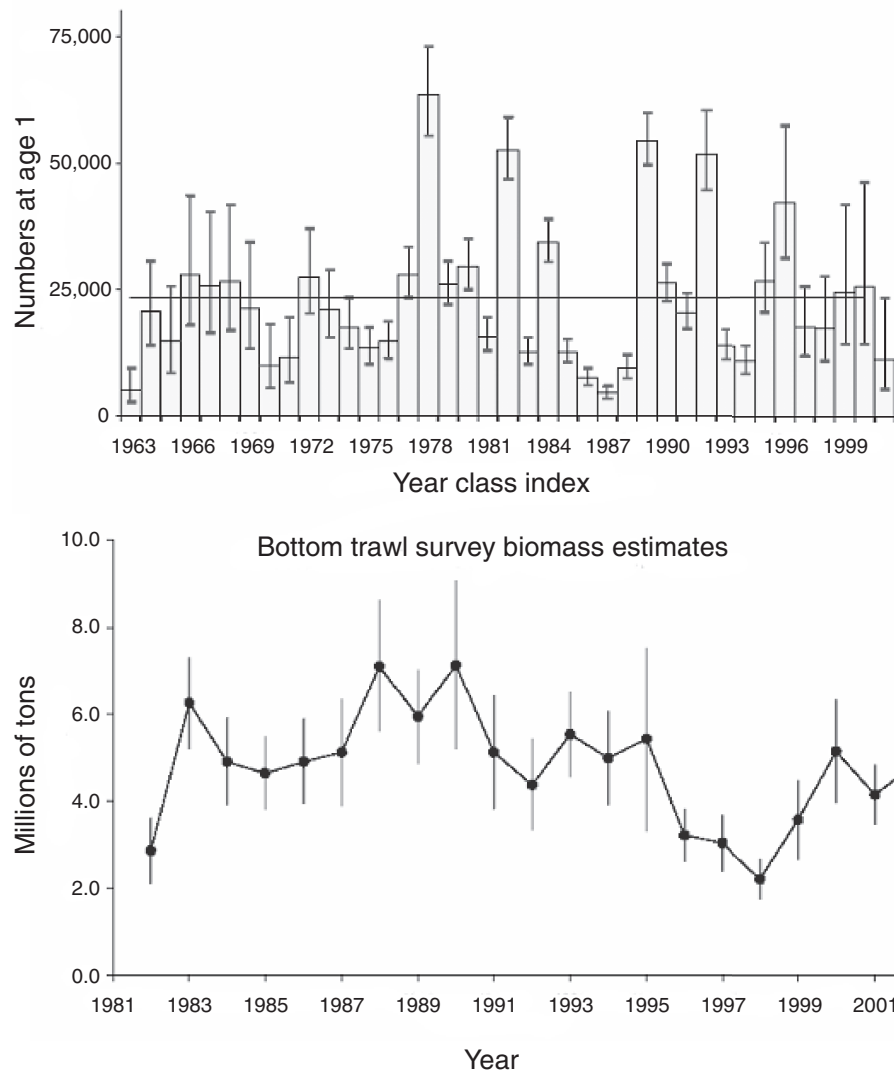


Figure 2.32: **Top:** year class strength of walleye pollock; **Bottom:** biomass of pollock on the eastern Bering Sea shelf (NPFMC, 2002).

nations for variation in pollock year-class strength. They can be divided into four groups. Group A focuses on the importance of primary or secondary production for the survival of young pollock; Group B focuses on the importance of cannibalism and mechanisms that result in the separation of adult and juvenile pollock; Group C hypothesizes that variation in risk of predation and variation in the abundance of zooplankton are causal, and Group D relates survival of young pollock to variation in the amount of turbulence when feeding. Ladd *et al.* (ms) have modeled the amount of mixing across the seasonal pycnocline expected during each summer over the past decades, and a preliminary comparison of their results with the distribution of strong and weak year classes in Table 2.6 suggests that variations in primary production forced by summer entrainment of nutrients is not likely a

good predictor of year-class strength in pollock. The abundance of small shelf copepods does vary significantly with integrated water temperature (Tables 2.3 and 2.4), and if prey is a limiting factor in pollock year-class strength, then this remains a viable hypothesis. Cannibalism is recognized as a major source of mortality for young pollock (Dwyer *et al.*, 1987; Wespestad, 1994; Balykin, 1996; Livingston and Lang, 1996; Wespestad and Quinn, 1996; Livingston and Methot, 1998; Lang *et al.*, 2000; Livingston and Jurado-Molina, 2000), and mechanisms for separating vulnerable individuals from cannibalistic older fish, such as on-shelf advection (Wespestad *et al.*, 2000), are likely to be of importance, regardless of what other factors are at play. For instance, Cooney *et al.* (2001) found that in Prince William Sound, adult pollock would feed on large *Neocalanus* copepods in spring if the copepods were abundant, but if not, the adult pollock would prey upon juvenile salmon and herring. Finally, variations in the amount of turbulence may influence foraging success of larval pollock by either enhancing the encounter rate with food particles at intermediate rates of turbulence, or depressing foraging success with either too much turbulence or insufficient turbulence (Megrey and Hinckley, 2001). Most of these hypotheses remain to be tested in the field, and it is likely that some combination of them together will provide the key to understanding the occurrence of strong year classes.

It is also likely that, as pollock populations wax and wane, the mechanisms responsible for population control will shift. Hunt *et al.* (2002a) hypothesized that under environmental conditions in which zooplankton were scarce, such as during a prolonged series of cold springs, walleye pollock populations would be controlled from the bottom-up because there would be insufficient zooplankton for larval or juvenile pollock (Fig. 2.33). In contrast, in years when pollock populations were large, cannibalism would exert strong top-down control on the population, as it apparently does at present. In periods under top-down control, large year classes could still occur, but to do so there would have to be some mechanism to promote separation of the young fish from the adults (e.g., Hypotheses 3 and 4, Table 2.7). When there is a switch from a period of years with cold springs to warm springs, one can expect large year classes, as there should be plentiful zooplankton and low risk of cannibalism, while during a switch from a prolonged period of warm springs to cold springs, year-class strength might be expected to be low because of both bottom-up and top-down effects.

The distributions and abundances of adult and juvenile pollock (age-0 and age-1) have important impacts on other elements of the eastern Bering Sea ecosystem. Juvenile pollock are a major source of prey for not only large piscivorous fishes such as adult pollock, Pacific cod and arrowtooth flounder, they are also staples in the diets of several species of marine birds and pinnipeds, such as northern fur seal, harbor seal, and Steller sea lions (see above). There is evidence for a negative relationship between the reproductive success of black-legged kittiwakes on St. George Island and the biomass of adult pollock on the eastern Bering Sea shelf (Livingston *et al.*, 1999; Hunt and Stabeno, 2002; Sinclair *et al.*, in preparation). During the period of population decline in the 1990s, northern fur seals at St. Paul

Table 2.7: Hypotheses for explaining variation in year-class strength of walleye pollock in the eastern Bering Sea.

	Hypothesis	Citations	Tests
A. Production-Based Hypotheses			
1.	Decreases in wind mixing negatively influence post-bloom primary production.	Sambrotto <i>et al.</i> (1986) Hunt <i>et al.</i> (2002a) Springer, this report, Part 4	Compare wind mixing in years with strong and weak year classes; Ladd <i>et al.</i> (unpublished manuscript). Probably no significant relationship with summer mixing. Determine if there is strong coupling between spring and summer primary production, zooplankton abundance, and pollock year-class strength.
2.	Late ice retreat results in cold water blooms and reduced zooplankton production.	Stabeno <i>et al.</i> (1998) Hunt <i>et al.</i> (2002a) Hunt and Stabeno (2002)	Compare zooplankton abundances in years with early and late ice retreat; Coyle and Pinchuk (2002b) show significant differences. Determine if zooplankton abundance limits age-0 or age-1 pollock survival.
B. Cannibalism-Based Hypotheses			
3.	When the cold pool is large, age-1 pollock move to the shelf edge where adults abound.	Dwyer <i>et al.</i> (1987) Ohtani and Azumaya (1995) Wyllie-Echeverria (1995)	Compare cold pool size in years with strong and weak year classes.
4.	Favorable winds in early spring may transport eggs, larvae, and small age-0 pollock deep onto the shelf, thus separating them from adults.	Wespestad <i>et al.</i> (2000)	Compare wind forcing in years with strong and weak year classes.
C. Mixed Production/Cannibalism Hypothesis			
5.	Adult pollock switch prey types such that when zooplankton are scarce in spring, they increase cannibalism.	Cooney <i>et al.</i> (2001)	Since zooplankton are less abundant in cold years, compare the amount of cannibalism in years with cold and warm spring temperatures.
D. Mixing Process Hypothesis			
6.	Intermediate levels of turbulence are required for optimal foraging conditions.	Megrey and Hinckley (2001)	Compare turbulence levels in years with strong and weak year-classes.

Oscillating Control Hypothesis

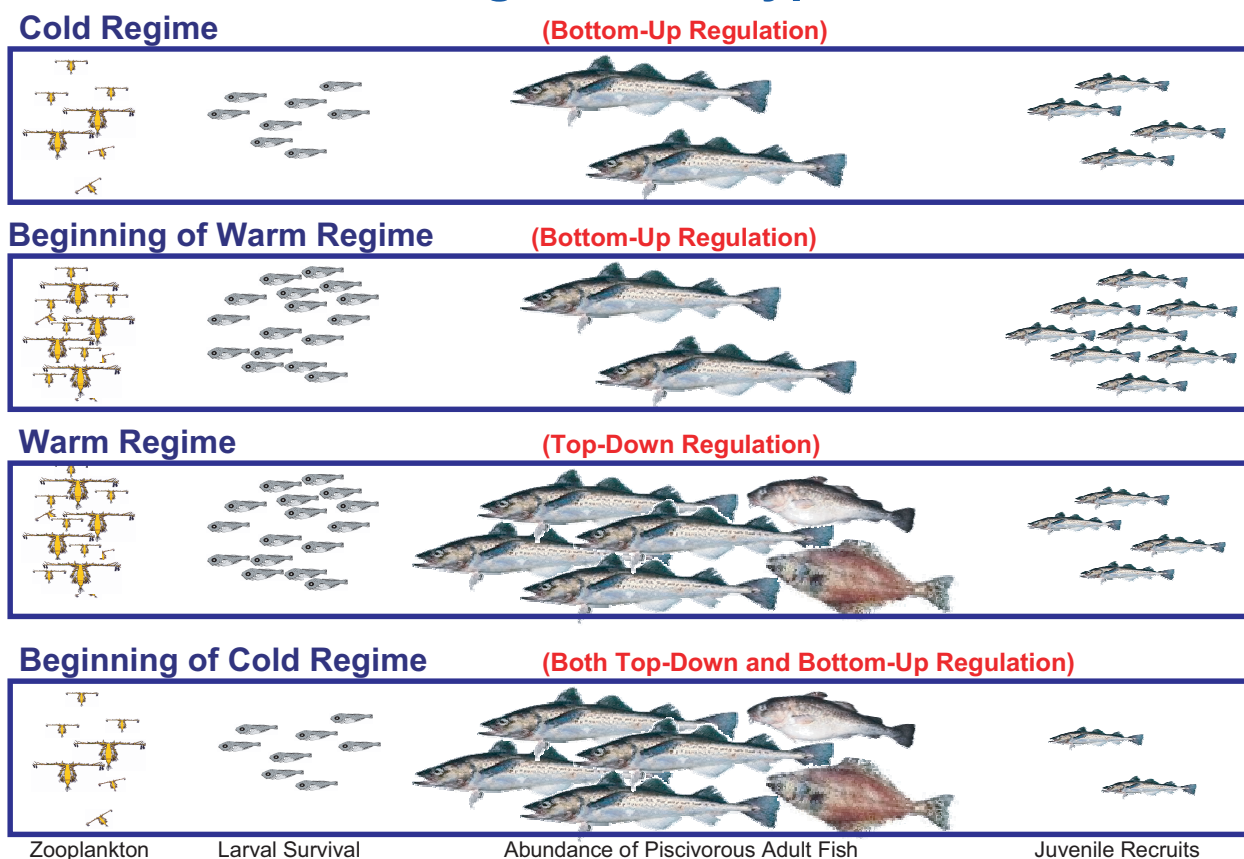


Figure 2.33: Schematic of the function of the Oscillating Control Hypothesis. For an explanation, see text. (From Hunt *et al.*, 2002a).

Island reduced their use of age-0 and age-1 pollock, sand lance, and slope squids, but increased their use of age-3, -4, and -5 pollock. It is difficult to know the causes of these shifts in fur seal diets.

The distribution of age-1 pollock may be affected by not only water temperature (Hypothesis 3, Table 2.7), but also their exposure to predation, either through removals, or through behavioral responses to the presence of predators (Sogard and Olla, 1993). Displacements of juvenile pollock from surface waters will make them unavailable to predators such as kittiwakes that are restricted in their foraging to the very surface of the water column, while displacements in the horizontal from the vicinity of rookeries and colonies will diminish their value to central place foragers as a function of the distance travelled from the central place. After the biomass of adult pollock increased near the Pribilof Islands, the biomass of age-1 pollock there dropped precipitously (Hunt *et al.*, 2002a, Fig. 2.12). There remains a need to understand the role that adult pollock play in determining not only the abundance, but also the distribution of forage fishes, including age-1 pol-

lock, and their availability to upper trophic level predators including marine mammals and seabirds.

2.6 Summary of Advances

Many of the important advances in our understanding of the coupling of regional atmospheric processes, physical processes in the Bering Sea, and biological responses to these forcing mechanisms have been the subjects of recent review (Stabeno *et al.*, 2001; Overland *et al.*, 2002; Schumacher *et al.*, 2003). Among these advances in our knowledge are:

2.6.1 Marine climate

1. A new understanding of the importance of warm-season climate (Overland *et al.*, 2001; Bond and Adams, 2002).

2.6.2 Basin and slope waters

1. An improved understanding of the function of the Aleutian North Slope Current and the Bering Slope Current (Reed and Stabeno, 1999; Stabeno *et al.*, 1999a; Johnson *et al.*, 2004), and their potential importance to fish (Reed, 1995);
2. Documentation of eddies over the slope (Schumacher and Stabeno, 1994; Okkonen, 2001) and along the outer shelf (Reed, 1998) and their importance as habitats for fish and for the transport of small pollock onto the shelf (Schumacher and Stabeno, 1994);
3. Development of a model that resolves eddies and suggests that the source of eddies in the southeastern Bering Sea basin is in the Bering Slope Current (Hermann *et al.*, 2002).

2.6.3 Shelf waters

1. Discovery of mean flows across the shelf (Reed and Stabeno, 1996; Reed, 1998), which for short intervals in summer can result in replenishment of salts and transport of oceanic zooplankton to the Inner Front (Stabeno *et al.*, 2001; Coyle and Pinchuk, 2002b);
2. A clarification of the role of the timing of ice retreat for the timing and fate of the spring bloom (Stabeno *et al.*, 2001; Hunt *et al.*, 2002a; Hunt and Stabeno, 2002);
3. Understanding of the relative importance of winter and warm season conditions for determining the timing and strength of spring stratification and the potential for summer mixing across the pycnocline (Ladd *et al.*, unpublished manuscript);
4. An understanding of the temporal and spatial variability of the Inner Front and its role in nutrient fluxes from depth (Kachel *et al.*, 2002);

5. A greater appreciation for the role of water temperature in the distribution of fish, especially pollock (Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1996; Wyllie-Echeverria and Wooster, 1998), the hatching time of pollock eggs (Blood, 2002), and the population dynamics of zooplankton (Coyle and Pinchuk, 2002a, b);
6. A greater appreciation for the role of episodic events in structuring the ecosystem;
7. A new hypothesis concerning the role of wind-forced transport for the survival of juvenile walleye pollock (Wespestad *et al.*, 2000).

2.6.4 Biological components of the ecosystem

1. Evidence that the net annual primary production in the northern Bering Sea may be declining (Schell, 2000; Grebmeier and Cooper, 1994; Grebmeier and Dunton, 2000), whereas in the southeastern Bering Sea, increases in standing stocks of fish and non-crab benthic invertebrates do not suggest a decline in production (Connors *et al.*, 2002);
2. Commencement of research on the role of nanno- and microplankton, including coccolithophores, in the marine ecosystem of the southeastern Bering Sea (Howell-Kubler *et al.*, 1996; Olson and Strom, 2002);
3. Re-examination of the *Oshoro Maru* zooplankton time series shows no evidence for a significant decline in zooplankton biomass within samples stratified by the domain in which they were collected (Hunt *et al.*, 2002a; Napp *et al.*, 2002);
4. Immense increases in the biomass of large jellyfish and then a rapid decline to levels seen in the early 1980s (Brodeur *et al.*, 1999a, 2002);
5. Observations of responses of crustacean zooplankton to variations in water temperature, including apparent shifts in the timing of breeding in shelf euphausiids (Coyle and Pinchuk, 2002a), and the abundance of small shelf copepods (Coyle and Pinchuk, 2002a; Napp *et al.*, 2002);
6. Determination that large cetaceans are now encountered more frequently in shelf waters than in the 1970s, and that substantial numbers are present over the shelf (Baretta and Hunt, 1994; Moore, 2000);
7. Progress in developing understanding of climate effects on flatfish recruitment (Wilderbuer *et al.*, 2002);
8. Progress in defining multiple hypotheses concerning the control of year-class strength in walleye pollock (Table 2.7; Section 4 of this report);
9. Improved understanding of the foraging habits and diets of marine birds, northern fur seals, and Steller sea lions at the Pribilof Islands; the potential relationships between the abundance of adult pollock over the shelf and the reproductive success of black-legged kittiwakes at the Pribilof Islands (Sinclair *et al.*, in preparation);

10. Evidence that sub-lethal food stress during the breeding season can lead to elevated levels of corticosteroids, and possibly elevated levels of post-breeding season mortality in seabirds (Kitaysky *et al.*, 1999b, 2001a, 2002);
11. Development of a mechanistic explanation of how variations in climate could cause shifts in the mechanisms controlling walleye pollock populations (Oscillating Control Hypothesis, Hunt *et al.*, 2002a).

2.7 Areas of Research Requiring More Attention

Although a great deal of progress in understanding the forcing mechanisms and the ecosystem responses of the southeastern Bering Sea has been made since the early 1990s, there are still many unanswered questions that demand attention if we are to provide good stewardship for the resources of the Bering Sea shelf. Answers to these questions go beyond academic value; we need to understand the processes and mechanisms that determine how changes in global climate and the associated physical forcing affect the flow of energy to upper trophic level organisms including commercially valuable fish and shellfish, marine mammals, and seabirds. Below are listed a number of questions that require attention.

1. How do atmospheric forcing mechanisms influence the distribution and transport of salts, heat, nutrients, and organic matter in the eastern Bering Sea?
 - (a) How does atmospheric forcing influence the distribution, abundance, and magnitude of eddies?
 - (b) How does atmospheric forcing affect cross-shelf flow? Do the mechanisms whereby climate affects cross-shelf flow vary seasonally? What are the time scales of primary importance?
 - (c) How does one scale up and down between large-scale atmospheric processes and the biological processes critical to the production regimes of the eastern Bering Sea?
2. How is the timing and magnitude of cross-shelf flux controlled?
 - (a) What are the relative contributions of summer and winter cross-shelf fluxes for renewal of nutrients on the eastern Bering Sea shelf?
 - (b) What is the relative importance of flow up canyons, movement in eddies, and other mechanisms of cross-shelf flux?
 - (c) What is the relative importance of nutrients provided by winter-time on-shelf advection and nutrients that have been remineralized by benthic processes? Are the estimates provided by Sambrotto *et al.* (1986) still useful?
3. How do different patterns in the formation, thickness, extent, and melt-back of sea ice influence the ecosystems of the eastern Bering Sea shelf?

- (a) How does the pattern of ice melt-back affect the timing and type of phytoplankton bloom? Do these mechanisms work in similar ways in the southern and northern Bering Sea?
 - (b) Do open-water blooms occur in the northern Bering Sea? If so, are they as important as the ice-related blooms?
 - (c) Are ice-related blooms shorter and more intense than open-water blooms? When both are potentially present, which is likely to fix more carbon?
 - (d) How do ice formation and melt-back interact with cross-shelf advection of warm water in winter to determine the temperature and extent of the southern cold pool?
4. What controls the amount and fate of primary production?
- (a) Has primary production decreased over the southeastern Bering Sea shelf?
 - (b) For the cold-adapted species of the Bering Sea, are zooplankton growth and production more sensitive to temperature than phytoplankton productivity, as is assumed in the hypothesis of Walsh and McRoy (1986)?
 - (c) Does significantly more phytoplankton sink to the bottom in cold years than in warm years, as hypothesized by Walsh and McRoy (1986)?
 - (d) How do the nanno- and microplankton affect the flow of energy in the southeastern Bering Sea? Are they directly or indirectly important prey for either larval or juvenile walleye pollock?
 - (e) How do coccolithophores affect energy flow in the southeastern Bering Sea? Why did they suddenly bloom, and then as suddenly disappear after blooming consecutively for 5 years?
5. What controls the biomass and productivity of upper trophic level organisms?
- (a) How do plankton predators such as chaetognaths, ctenophores, and larger jellyfish affect the flow of energy in the eastern Bering Sea? Why did the population of large jellyfish increase and then crash? Are they significant competitors or predators on juvenile pollock and other forage fish?
 - (b) How does temperature affect the role of chaetognaths, ctenophores and larger jellyfish as predators of crustacean zooplankton?
 - (c) How can one account for the simultaneous increase of round-fish, flatfish, and non-crab invertebrates over the shelf of the southeastern Bering Sea (Conners *et al.*, 2002)?
 - (d) How variable is the abundance of mesopelagic fish and squids in the eastern Bering Sea? What are the ramifications of this variability for their use by commercially valuable fish, marine mammals and seabirds?

6. How can we translate information about Bering Sea ecosystems into products useful to those who are managing the fisheries of the eastern Bering Sea?
 - (a) What factor or factors control year-class size in walleye pollock? The most promising hypotheses, such as those listed in Table 2.7, need to be tested systematically.
 - (b) There is a need to test the underlying assumptions and predictions of the Oscillating Control Hypothesis (Hunt *et al.*, 2002a). In particular, are zooplankton grazers closely coupled with phytoplankton in any season, and does this coupling affect their availability to larval or juvenile pollock? Likewise, are larval or juvenile pollock closely coupled to zooplankton in any season?

2.8 Acknowledgments

Many scientists provided text and figures that have been incorporated into this report. Included are Nick Bond, Ric Brodeur, Liz Connors, Susan Heinrichs, Anne Hollowed, Jim Overland, Beth Sinclair, Phyllis Stabeno, and Al Tyler. Financial support for this review was provided in part by the NOAA Coastal Ocean Program, Southeast Bering Sea Carrying Capacity program.

Part 3—Forecasting Abundance of Walleye Pollock: Indices for Juvenile Abundance

RESULTS FROM THE INDICES WORKING GROUP: DEVELOPMENT AND APPLICATION TO FISHERY MANAGEMENT AND ECOSYSTEM INFORMATION ISSUES OF ENVIRONMENTAL INDICES IN THE EASTERN BERING SEA

Principal Authors: J.D. Schumacher and S.A. Macklin

With participation and contributions from the Indices Working Group:

Kerim Aydin, Nick Bond, Cathy Ferrar, Al Hermann, Anne Hollowed, Jim Ianelli, Nancy Kachel, Carol Ladd, Pat Livingston, Allen Macklin, Bern Megrey, Jeff Napp, Ron Reed, Dylan Righi, Sigrid Salo, Jim Schumacher, Alan Springer, Phyllis Stabeno, Peggy Sullivan, Terry Whitledge, and Tom Wilderbuer

3.1 Introduction

The goal of the Southeast Bering Sea Carrying Capacity program was to document the role of juvenile pollock in the eastern Bering Sea ecosystem. This included examination of factors that affect their survival and development and testing of annual indices of pre-recruit (age-1) abundance (SEBSCC, 1995). Within this framework, the purpose of the Indices Working Group (IWG, which was developed at the SEBSCC Principal Investigators meeting held in January 2001; membership as listed above) was defined as follows. Based on the best understanding of ecosystem dynamics, identify potential single- or multi-parameter constructs or indices (e.g., wind mixing, time of spring bloom, etc.) that lead to development of survival indices for pollock in the egg, larval, and young-of-the-year life history stages. Further, this information will provide input to the National Marine Fisheries Service (NMFS) stock assessment model and/or models of juvenile pollock for use by fisheries scientists at the Alaska Fisheries Science Center (AFSC)/NMFS and others interested in changes in the ecosystem.

In Section 3.2, we first present the conceptual framework for development of indices, including discussion of the time series of estimates of age-1 pollock recruitment (Fig. 3.1), which provides a base time series that indices can be evaluated against. Section 3.3 contains contributions from IWG members regarding development of potential indices (Table 3.1). Using a one-dimensional mixed layer model, Ladd and Stabeno (Section 3.3.1) developed an index of stratification. Stratification can influence larval and juvenile pollock survival through its impact on nutrient limitation, temperature and its inherent effects on physiological processes of the pollock and of their zooplankton prey. Megrey and Bond (Section 3.3.2) examine the potential impact of wind speed, a surrogate for mixing, as it might affect the ability of pollock larvae to feed. Napp and Kachel (Section 3.3.3) present time series of average net short wave radiation that has a direct impact on the timing of the spring phytoplankton bloom. This, in turn, has ramifications throughout the entire ecosystem (Hunt *et al.*, 2002a) and thus serves managers of components of this ecosystem by providing an index of the status and po-

Table 3.1: Environmental indices described in Section 3.3.

Index	1996	1997	1998	1999	2000	2001	2002
Wind Mixing							
Low	0.35	0.61	0.35	0.35	0.45	0.42	0.26
Optimum	0.65	0.26	0.58	0.61	0.42	0.58	0.55
High	0.00	0.13	0.06	0.03	0.13	0.00	0.19
Stratification							
Maximum	0.692	0.855	0.770	0.679	0.677	0.709	0.852
Date	May 17	ice bloom	June 16	ice bloom	May 19	May 15	June 4
Mixing Events	6	1	1	0	3	0	1
Temperature	1.6	ice bloom	2.9	ice bloom	1.0	1.9	2.5
Light							
[60°N, 170°W]	-150.3	-153.9	-141.2	-143.1	-145.5	-152.9	#N/A
[57.5°N, 165°W]	-180.6	-196.3	-176.2	-187.1	-187.0	-188.7	#N/A
[58°N, 159°W]	-185.0	-188.6	-175.3	-168.5	-181.0	-180.3	#N/A
Sea Ice							
	0.012	0.466	0.002	0.346	0.055	#N/A	#N/A
Cold Pool							
T1	1.9	7.3	3.2	6.3	2.1	#N/A	#N/A
T2	1.0	5.3	0.0	16.8	8.9	#N/A	#N/A
Advection							
	#N/A	0.059	0.003	0.000	0.045	0.003	#N/A
Age-0 Index							
	2.68	0.14	0.75	1.13	#N/A	#N/A	#N/A
Age-1 Abundance							
	26.6	42.3	17.5	17.5	24.5	25.7	11.1

Explanation of Indices

Wind Mixing: Fraction of period May 15 to June 15 when daily average surface wind speed (m s^{-1}) was <4.8 (low), 4.8–9.5 (optimum), >9.5 (high). [Estimated from NCEP winds.]

1-D Mixed Layer Model:

Stratification: Maximum (May–June) modeled stratification ($^{\circ}\text{C m}^{-1}$) (3-y running mean).

Date: When maximum stratification occurred.

Mixing Events: Number of times between stratification setup date and August 31 that modeled 3-day smoothed mixed layer depth increased >5 m in a day.

Temperature: Mixed layer temperature at max stratification date.

Light: Average net shortwave radiation (W m^{-2}) from April 1 through June 30 at [60°N, 170°W], [57.5°N, 165°W], and [58°N, 159°W] [from NCAR/NCEP Reanalysis].

Sea Ice: Average per cent concentration of sea ice within the region bounded by [58°N, 170°W] and [57°N, 165°W] during the period 15 March to 15 April.

Cold Pool: Estimated vertical areal slice of cold pool ($<2^{\circ}\text{C}$) water (km^2) contained along transect (on T1 during 1996 and 1999, the cold pool continued into shallower water).

Advection: Fraction of 735 simulated drifters that arrived after 90 days in the region between 57°–58°N and 165°–170°W.

Age-0 Index: Young-of-the-year abundance estimate (arbitrary units) from independent Pribilof survey.

Age-1 Abundance: Abundance estimates of 1-year old eastern Bering Sea pollock (billions) from Model 1 [2002 Stock Assessment].

tential trends in ecosystem structure. Sea ice influences the ecosystem via bottom-up (e.g., timing of peak phytoplankton production) and top-down (e.g., habitat) impacts. Salo and Stabeno (Section 3.3.4) developed time series of sea ice concentrations in various strata that establish the existence of strong spatial and interannual patterns. Because the extent and timing of sea ice largely determine the extent and yearly thermal characteristics of the cold pool, Sullivan (Section 3.3.5) developed time histories of water column temperature from the annual bottom trawl survey. These provide a different and more direct measure of the thermal field than does the sea ice index. The extent and magnitude of the cold pool may have implications for the distribution of adult pollock and hence cannibalism on young of the year fish (Wylie-Echeverria and Ohtani, 1999; Wylie-Echeverria, 1996; Wylie-Echeverria and Wooster, 1998). In Section 3.3.6, Ianelli considers using the estimated abundance of age-0 pollock from the Pribilof Islands area of the annual stock assessment as an index for juvenile pollock abundance. Hermann (Section 3.3.7) then provides a description of the Northeast Pacific Regional Ocean Modeling System (NEPROMS), as hydrodynamic model simulations can provide underpinning for the development of various indices. Righi (Section 3.3.7) presents an application of NEPROMS to the transport of pollock eggs and larvae. The connection to survival in these scenarios is the extent of overlap between the transported animals and older cannibalistic pollock. Importantly, the transport trajectories from the simulations more closely simulate actual conditions over the shelf than those used by Wespestad *et al.* (2000) in their examination of year-class success of pollock. Macklin (Section 3.3.8) presents a framework for cataloging indices.

Ianelli (Section 3.4) demonstrates how an index of early life history success is being used by NMFS for annual stock assessments. He presents an index of separation between juvenile and adult fish. Importantly, he points out that variation in location and timing of spawn, as well as the location in the water column of eggs and larvae must be accounted for in the development of more robust transport- and cannibalism-related indices. Springer (Section 3.5) examines changing relationships between climate and biological indices throughout the eastern Bering Sea, implying that different relationships likely apply during different phases of the climate regime. These results demonstrate the potential for using environmental indices (e.g., selected sea surface temperatures) as measures of ecosystem trends. Section 3.6 contains a synthesis of results from indices development and provides a road map for future development of indices. Section 3.6.3 presents concluding remarks that call for the development of informational products from the NEPROMS oceanographic model that would permit access to various model products by resource managers and users.

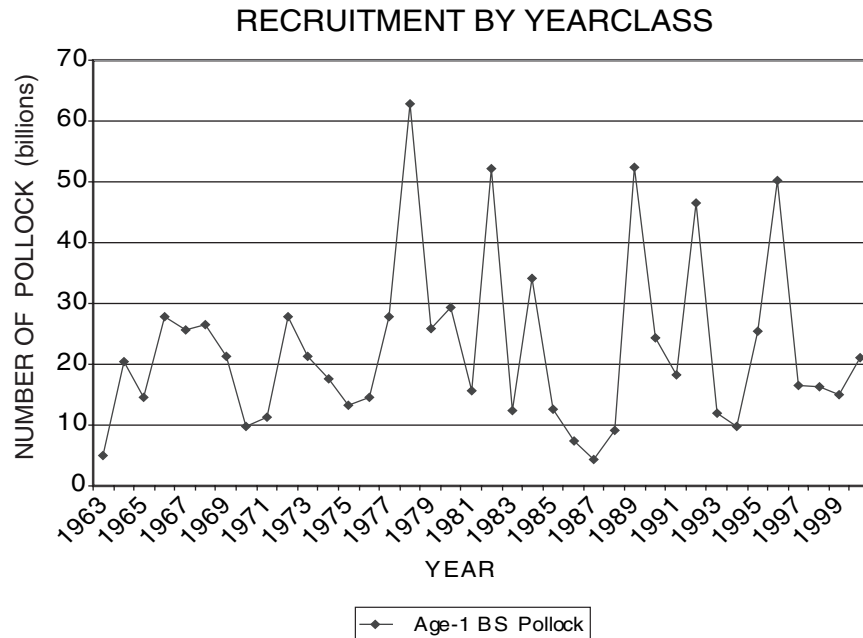


Figure 3.1: Recruitment of age-1 pollock in the eastern Bering Sea estimated as number of fish (from SAFE Report, 2001).

3.2 Conceptual Framework for Development of Indices

3.2.1 A pollock-centric perspective of the southeastern Bering Sea ecosystem

As noted by Napp *et al.* (2000), pollock is the most abundant species harvested in the Bering Sea, accounting for >65% of the total groundfish biomass during the 1980s when the total biomass exceeded 20 million tons. The biomass trends of three major trophic guilds in the eastern Bering Sea from 1979 to 1998 (Schumacher *et al.*, 2003) show that while the total biomass of pollock in the 1990s is less than in the 1980s, they still dominate biomass in any of the guilds which include marine birds, mammals, other fishes, and crabs. Walleye pollock is a nodal species in the food web (NRC, 1996) with juveniles being the dominant prey of fishes, seabirds, and marine mammals (Springer and Byrd, 1989; Livingston, 1993; Brodeur *et al.*, 1996). It is natural that pollock have been the focus of the Coastal Ocean Program's SEBSCC. The choice of developing a survival index for the early life history stages (eggs through young of the year) allows an early forecast of potential recruitment to the fishery and a metric that can be compared to existing time series of age-1 abundance (Fig. 3.1).

A switch model was developed for survival of pollock in the eastern Bering Sea (Megrey *et al.*, 1996). The model identifies candidates for cause of mortality by life history stage, the mortality variability of each stage, and indication of the stage contributing the most variability in recruitment to the fishery (Fig. 3.2). In this model, transport and turbulence have their greatest

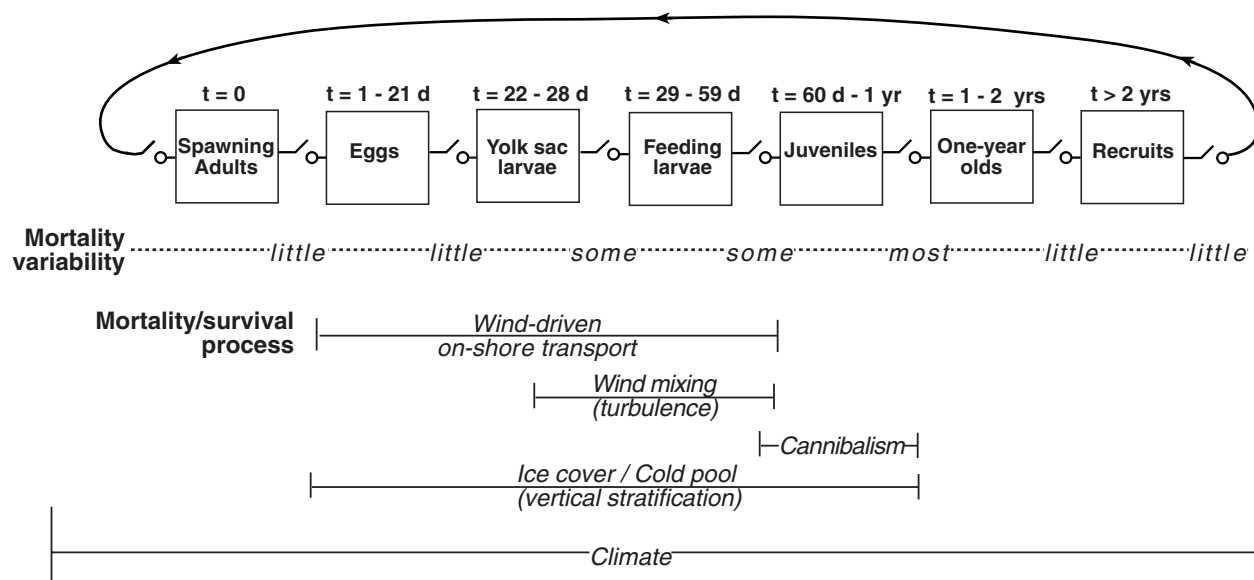


Figure 3.2: Switch model of pollock dynamics in the eastern Bering Sea. Processes thought to be important regulators of survival variability are shown and the span of their interaction is indicated.

impact on mortality of yoke-sack through feeding larval stages. It is the vertical structure and horizontal distribution of temperature, however, through their suggested influence on cannibalism, that have the greatest impact on recruitment (see Section 3.4 for more detail on egg/larval transport and the subsequent potential impact on cannibalism).

In a later version of the switch model, Napp *et al.* (2000) augmented the candidates that regulate survival by adding the timing of preferred prey production and the absence or presence of ice over the shelf region. Most recently, these have been woven together with other environmental factors to develop the Oscillating Control Hypothesis (OCH, Section 2.5), which examines how energy flow through the ecosystem may vary in different climate regimes (Hunt *et al.*, 2002a).

3.2.2 A generic model of pathways of energy flow through the ecosystem

Although the focus on pollock is reasonable, and models that have pollock as the central feature helped focus research in SEBSCC, a more inclusive perspective also has value. This is particularly true when considering questions on the ecosystem scale, e.g., the dramatic decline in abundance of the Steller sea lion. Identifying and understanding mechanisms that transfer climate change via the ocean to biota is essential if we are to understand ecosystem dynamics (Francis *et al.*, 1998). Fluctuations in the physical environment can impact the ecosystem through both changes in the nutrient-phytoplankton-zooplankton sequence (i.e., bottom-up control), and/or by altering habitat resulting in changes in abundance and/or composition of higher trophic level animals (i.e., top-down control). Hunt *et al.* (2002a) hy-

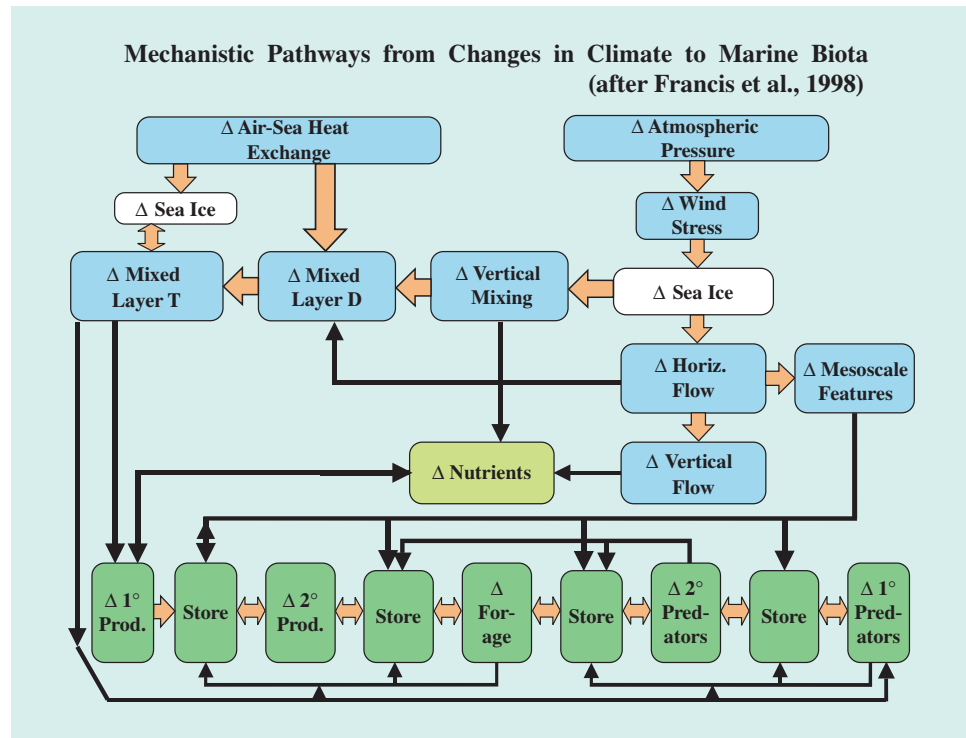


Figure 3.3: Conceptual model showing the pathways through which changes in atmospheric features can influence oceanic and biological components of the ecosystem of the eastern Bering Sea (from Schumacher *et al.*, 2003).

pothesize that the control of energy flow on the shelf (either top down or bottom up) depends on the timing of the nutrient-phytoplankton-zooplankton sequence related to the presence/absence of sea ice.

More inclusive and general conceptual models have been developed for the eastern Bering Sea and North Pacific Ocean. Schumacher *et al.* (2003) adapted the Francis *et al.* (1998) conceptual model of the pathways by which climate phenomena influence the biota to include sea ice, a dominant feature of the ecosystem of the eastern Bering Sea shelf (Fig. 3.3).

This model shows that there are numerous ecosystem elements (Section 3.5 discusses relationships between adjacent and more widely separated ecosystem elements) and connecting processes to consider when attempting to understand the impact of changes in atmospheric pressure on survival of young pollock. For example, a change in characteristics of the Aleutian Low will alter wind stress and the ensuing horizontal flow field (upper layer currents). It also will impact vertical mixing and air-sea heat fluxes and, thereby, the temperature of the upper mixed layer. These changes in transport, turbulence and temperature can impact the biological ecosystem element of interest either by enhancing or limiting survival, or both.

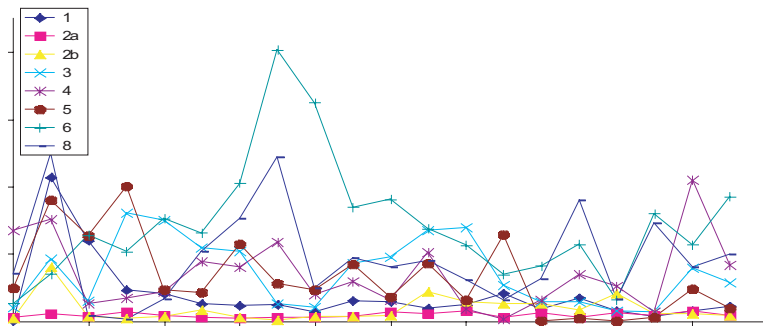


Figure 3.4: Abundance of adult pollock in the unequal areas used in the development of the ice index (Section 4.3.4).

3.2.3 Other aspects of indices development

As expected, many questions were generated and addressed during IWG workshops. One area of critical interest related to the potential time/space scale mismatch or match among features of the ecosystem. From a physics perspective, the eastern shelf has distinct regions or strata that are dominated by different physical processes. This is strongly evident in an across-shelf direction going from the more oceanic-like outer shelf waters to the strongly two-layered middle shelf and then shoreward into a water column that often is without vertical structure. (Stabeno *et al.*, 1999a) show that differences in advection occur within the previously defined latitudinal strata (southeastern, central and northern shelf; Schumacher and Stabeno, 1998). For this reason, some of the physical observations were partitioned into areas within the NMFS strata (Section 3.3.4). Some data sets, however, would become too noisy if the spatial domain is reduced beyond some limit. For example, the estimates of pollock abundance from the bottom trawl survey (Fig. 3.4) can be grouped in the same areas used for the ice index. However, it was the consensus of the IWG that this time series contains too much variation and that the integrated values (i.e., the commonly used time series of adult or age-1 pollock throughout the eastern Bering Sea) provided the appropriate time series of abundance.

The IWG members also felt that it was important to consider the local/regional impact of larger-scale indices, seeking relationships between physics and biology. For example, when using a hemispherical index (e.g., Arctic Oscillation, PDO, NPI), one should first consider how it is manifested on the regional or local scale. This also applies on finer spatial scales, e.g., how representative are winds measured at St. Paul Island to mixing processes in inner Bristol Bay? While zero-order approaches have some value, their results can be misleading. For example, several studies use the OSCURS model to transport planktonic stages of various species. In these simulations, only one release site is used to initialize trajectories. As results from the NEPROMS model have shown (Section 3.3.7), changes in initial location can result in significantly different trajectories.

3.3 Development of Environmental Indices

3.3.1 *Indices of stratification, potential supply of nutrients to the upper mixed layer, and turbulence experienced by larval pollock (Carol Ladd and Phyllis Stabeno)*

We used the Price-Weller-Pinkel (Price *et al.*, 1986) one-dimensional, mixed layer model to simulate the establishment of stratification and subsequent mixing over the southeast Bering Sea shelf during summer. We selected the location (56.9°N, 164.1°W) to coincide with the site of FOCI biophysical mooring 2. Observations collected at this mooring provide 7 years of data that were used to validate model results. The possible mechanisms that could relate mixed layer depth to differential survival of young-of-the-year pollock include: (1) food limitation due to lack of renewal of nutrients from deeper waters or mixing of food particles through a larger volume of water, and (2) changes in the upper layer thermal field that impact physiological processes (timing of prey production and duration of the development of larvae to the first feeding stage) and community composition (appearance of new predators).

The model calculates the density and wind-driven velocity profile in response to imposed atmospheric forcing (discussed below using the method of Price *et al.*, 1986). Model simulations were initialized with a vertical temperature profile derived from the NCEP Reanalysis (Kalnay *et al.*, 1996). We used the sea surface temperature (SST) from May 1 combined with a weak thermocline ($\Delta T = 0.5^\circ\text{C}$) between 10 and 20 m. The model is then forced with winds and heat fluxes from the reanalysis and run from 1 May through 30 September 30 of each year. Comparisons with data show that the model reproduces mixed layer depth, timing of stratification set-up, and mixing events quite well.

The following assumptions and caveats should be noted:

- The model is one-dimensional. Hence, advection is assumed unimportant. Advection over the middle shelf is generally weak (Schumacher and Kinder, 1983; Schumacher and Stabeno, 1998). At times, however, currents have resulted in transport of salt and nutrients at this location (Stabeno *et al.*, 2001). In general, the assumption of no advection is likely good at this site, but it would have to be evaluated for other locations.
- The model is initialized with 1 May SST from the NCEP reanalysis. This time series has errors on the order of $\pm 0.5^\circ\text{C}$ when compared to in situ observations collected at site 2 between 1996–2001. These errors are well within the magnitude of interannual variability in the NCEP SST (the standard deviation over 40 years is $\sim 1^\circ\text{C}$). Summer heat content and SST of the model results, however, are dependent on the initial temperature profile and will reflect errors in that profile.
- Based on comparisons between model simulations and observations at site 2, salinity appears to have only a minor impact on stratification and mixing processes. Waters of the middle shelf domain exhibit weak

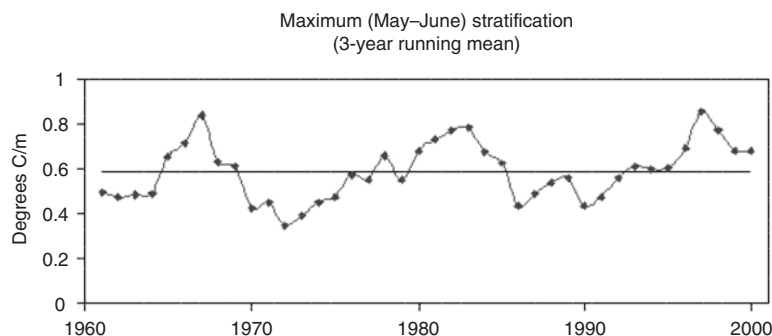


Figure 3.5: Maximum over May/June of vertical stratification maximum.

horizontal and vertical gradients in salinity (Coachman, 1986), and the time series of salinity measurements are sparse. Therefore, salinity is kept constant (31.65 psu) throughout the model runs.

- The model includes a diffusive term that results in a slightly weaker thermocline than observed. Without diffusion, the thermocline becomes too strong, resulting in SSTs that are too warm.
- Although the model simulates mixing processes in the upper layer quite well, the bottom mixed layer is not reproduced. Over the middle shelf, the water column exhibits a strongly stratified two-layer structure (in temperature) with a wind-mixed surface layer and a tidally mixed bottom layer (Schumacher and Stabeno, 1998). The model does not include any tidal mixing.

Results. Table 3.1 contains the stratification indices developed from this research. Interannual variability in mixing conditions can be evaluated using the model hindcasts. Model results show that the stratification maximum during May/June of each summer has varied on an approximately decadal time scale (Fig. 3.5) with maxima in 1967, the early 1980s, and 1997, and minima in the early 1970s and late 1980s. We note that this signal is not in phase with the accepted regime shifts (1976–1977, 1989, and perhaps 1998) observed in physical and biological time series for the eastern Bering Sea (Hare and Mantua, 2000).

When stratification is established in the spring, it provides an index of the timing of the spring bloom (Fig. 3.6) based on classical critical depth theory (Sverdrup, 1953). Interannual variability in the date of stratification is high with little indication of variability on decadal time scales. The stratification date averages 18 May and ranges between 10 May and 25 June.

The number of mixing events over the summer (Fig. 3.7) provides an index of the potential (some nutrients must still exist in the lower layer) amount of nutrient entrained into the mixed layer and of conditions that relate to decreased survival of pollock larvae (Bailey and Macklin, 1994). A high number of mixing events in a given year may indicate higher primary production and increased mortality of pollock larvae.

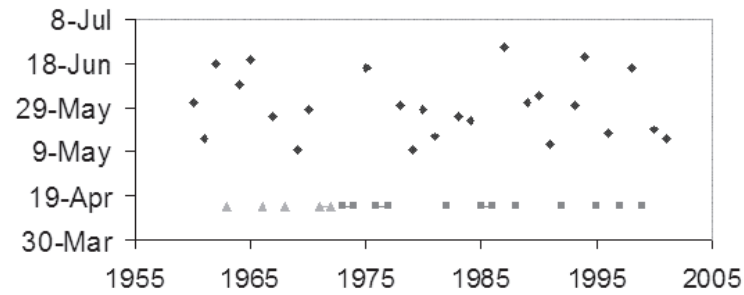


Figure 3.6: Date when maximum $\Delta T/\Delta z$ first is $>0.2^\circ\text{C}/\text{m}$ and occurs at a depth that is <25 m, for more than 1 day. Squares (ice data based on satellite images) and triangles (ice data based on shipboard observations) represent years when there was ice after 1 April, and an ice-associated bloom would have been expected (Stabeno *et al.*, 2001).

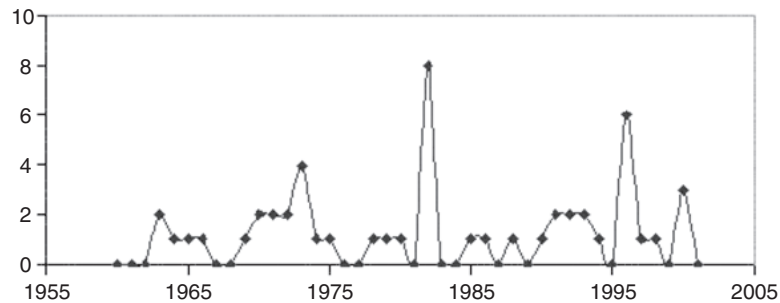


Figure 3.7: Number of times between the stratification setup date and 31 August when 3-day smoothed MLD increases >5 m in a day.

Temperature is important to the development of pollock eggs with eggs being slower to hatch in colder conditions (Blood, 2002). Temperature also affects the production of zooplankton (Coyle and Pinchuk, 2002b). The water column temperature on the stratification date (Fig. 3.8) may influence the coupling between the spring phytoplankton bloom and zooplankton prey for first feeding and older pollock larvae. Water column temperature on the stratification date varies between less than 1°C in 1991 to over 4°C in 1987 with high interannual variability, especially after 1980.

Future work. In order to expand on the present results, the model is being modified to track entrainment of water into the mixed layer. This will enable quantitative estimates of nutrient flux into the mixed layer over the summer. Another option would be to include a nutrient-like tracer, kept constant in the bottom layer and depleted over some time scale in the mixed layer.

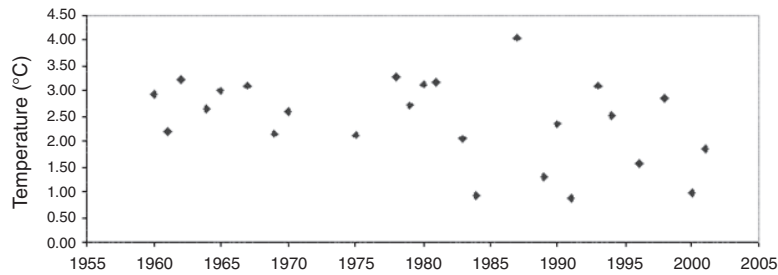


Figure 3.8: Water column average temperature on the stratification date. No temperature is shown for years when ice was present after 1 April.

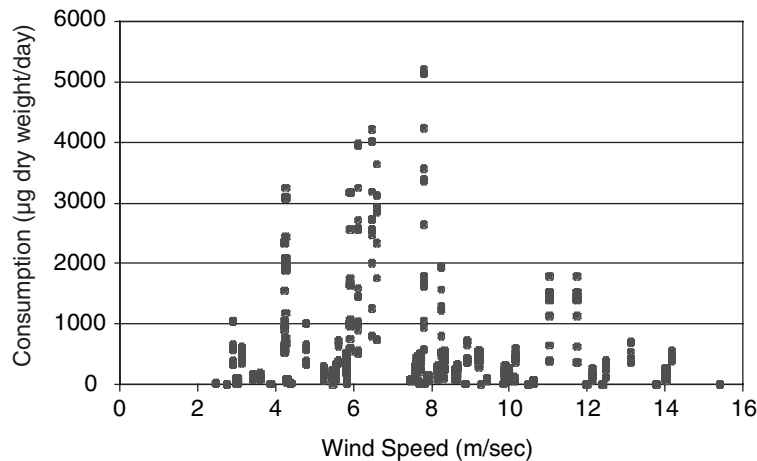


Figure 3.9: IBM output showing consumption as a function of wind speed.

3.3.2 An index related to wind turbulence and feeding success (Bern Megrey and Nick Bond)

Using a process-oriented, individual-based model (IBM) of pollock fish larvae, which incorporated a detailed description of the turbulence/contact rate/feeding success process (Megrey and Hinckley, 2001), we evaluated the relationship between the model-predicted influences of wind-generated turbulence and feeding. Output from the model (Figs. 3.9 and 3.10) conforms nicely to the theory (MacKenzie *et al.*, 1994) by the indication of a well-defined peak in consumption at intermediate wind speeds. Because of the high variability in the model data, we estimated the wind speed that generated optimum consumption (Fig. 3.11) by fitting a quadratic line through wind speed and consumption data, averaged by Julian day over the period DOY 102-164, the period when pollock are in their early larval stage. The wind speed that generated maximum consumption was derived by taking the derivative of the fit quadratic equation and setting it to zero. Optimum feeding (540 μg dry weight per day per individual) was at a wind speed of 7.1 m s^{-1} .

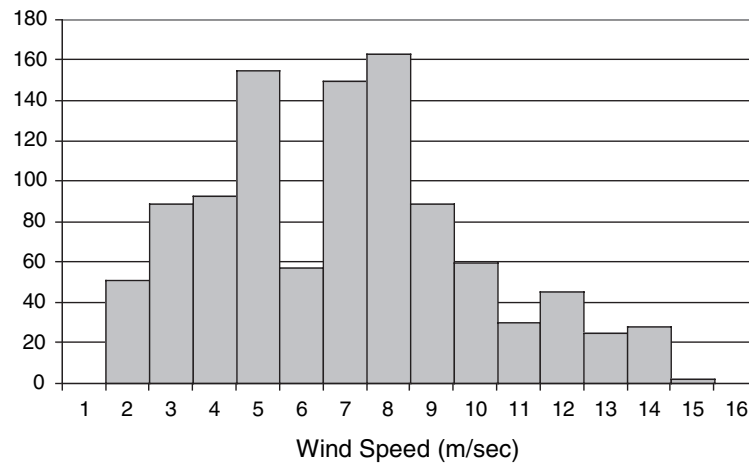


Figure 3.10: Frequency histogram of wind speeds used to force the IBM model.

Using Fig. 3.11, we arbitrarily defined the range of optimum feeding to be $\pm 15\%$ of the optimum level ($486 \mu\text{g}$ dry weight per day per individual). The wind speeds corresponding to a feeding level of $486 \mu\text{g}$ were 4.8 and 9.5 m s^{-1} . These points are indicated in Fig. 3.11 by the two circles on either side of the optimum circle. Thus, the range of wind speeds that provide “favorable feeding” would be 4.8 to 9.5 m s^{-1} . At wind speeds $>9.5 \text{ m s}^{-1}$, increased turbulence negatively affects feeding, and at wind speeds $<4.8 \text{ m s}^{-1}$, feeding is less than optimal because wind speeds are not sufficient to enhance the prey contact rate. Table 3.1 presents the indices developed for wind mixing.

There are some caveats that must be considered concerning this research. First, results are from a model experiment, not a laboratory experiment. Simulations were carried out on Shelikof Strait walleye pollock. However, results should be applicable to Bering Sea pollock as the feeding/contact-rate/turbulence processes should still be valid. Wind induced turbulence was not the only major process in the IBM model. The IBM was very detailed and included many other biological processes that would have affected the outcome of the simulations.

3.3.3 Variations in net short wave radiation: Toward development of an index of when sufficient light exists for primary production (Jeff Napp and Nancy Kachel)

The timing of the spring phytoplankton bloom is quite variable in the southeastern Bering Sea. It can occur anytime from the late winter to late spring, but it appears potentially to be predictable from prevailing environmental conditions (i.e., presence or absence of sea ice, frequency of storms, and erosion of the water column stability; Sambrotto *et al.*, 1986; Niebauer *et al.*, 1995; Stabeno *et al.*, 1998; Eslinger and Iverson, 2001; Hunt *et al.*, 2002a). Thus, it is conceivable to model the initiation of the spring phytoplankton bloom, which has significance to ecosystem dynamics. The dominant path-

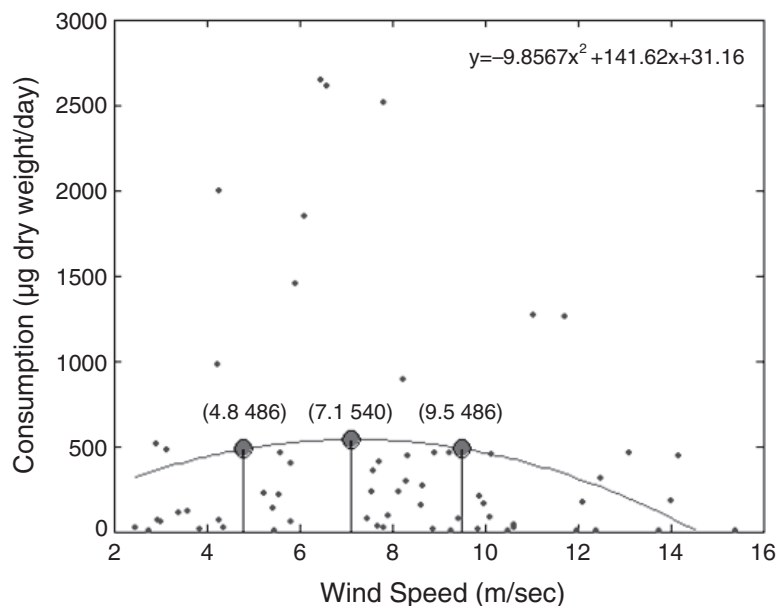


Figure 3.11: Estimates of the wind speeds required to generate optimum feeding.

ways of carbon cycling (pelagic versus benthic) as well as the temporal match or mismatch of larval pollock and their prey are dependent on the timing of the spring phytoplankton bloom (Napp *et al.*, 2000; Hunt *et al.*, 2002a). A strong case has been made that the timing of the bloom is dependent on the current atmospheric regime, and that it plays a key role in determining whether the ecosystem is controlled by bottom-up or top-down processes. Thus, prediction of the timing of the spring bloom would assist ecosystem managers in their assessment of the status and trends of the Bering Sea ecosystem (Hunt *et al.*, 2002a). The goal of the present exercise was to predict the earliest date that available light is sufficient to support a bloom and to begin an examination of interannual variation in this date.

Daily average net short wave radiation (NSWR) was extracted from the National Center for Atmospheric Research/National Center for Environmental Prediction (NCAR/NCEP) Reanalysis data set. We examined average NSWR for the period April 1–June 30 during 1972–2001 for three sites: inner Bristol Bay (IBB) at 58°N , 159°W , middle shelf domain (MSD) at 57.5°N , 165°W , and northwest central shelf domain (NWCSD) at 60°N , 170°W . The effect of latitude is evident, with the northernmost station receiving about 19% less energy (W m^{-2}) from 1981 onward (Fig. 3.12, Table 3.1). The MSD and IBB time series appear coherent, and are in phase with the NWCSD station from 1972–1983 and 1995–2001. During the intervening period, the time series appear to be out of phase by $\sim 180^\circ$. Correlation between the MSD and other two stations is significant and positive, although the amount of variance explained between the MSD and IBB is higher ($R^2 = 0.58$) than the MSD and NWCSD ($R^2 = 0.43$).

From our analysis, several conclusions can be drawn. First, if monitoring

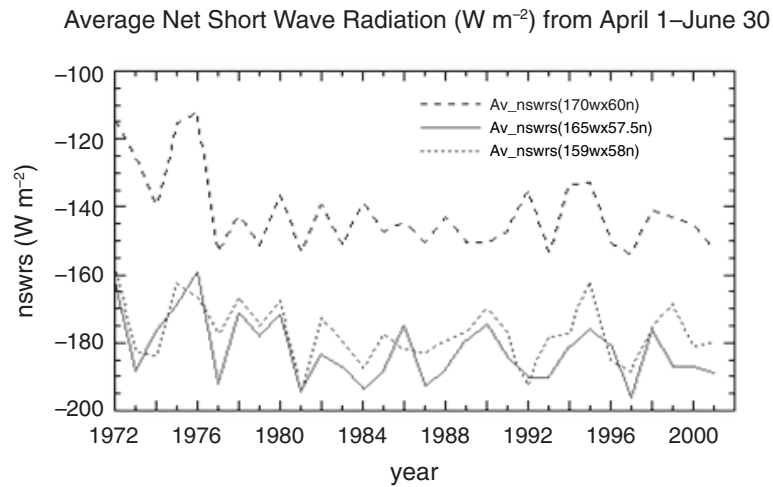


Figure 3.12: Average net short wave radiation from 1 April–30 June (W m^{-2}).

of a smaller set of stations is desired, then it is recommended that there is at least one station in both the southeast and northwest portions of the eastern Bering Sea shelf. This is due to both latitudinal and local meteorological conditions, which appear to drive the southeast and northwest systems in or out of phase. The second feature seen in the data is the large degree of interannual variability. The data show frequent positive and negative deviations from the long-term daily mean. Of these two fluctuations, the negative deviations qualitatively appear to be more frequent and pronounced than the positive ones. The sustained positive deviations will tend to promote an earlier bloom (ignoring wind mixing), and prolonged negative deviations will tend to delay the bloom. See Section 3.6 for suggested further research.

3.3.4 Indices related to sea ice (Sigrid Salo and Phyllis Stabeno)

Sea ice is a prominent feature of the eastern Bering Sea shelf, and several mechanisms exist that connect sea ice to biological processes. The phytoplankton bloom associated with the presence of sea ice (Stabeno *et al.*, 1998) influences the timing of zooplankton prey availability for first feeding pollock larvae. The size and magnitude of the following summer's cold pool depend on sea ice cover (timing and persistence) and can influence adult fish distribution and intensity of cannibalism.

Several indices exist for assessing the annual influence of sea ice on the continental shelf of the eastern Bering Sea. Niebauer (1998) and Niebauer *et al.* (1999) used the percentage of ice cover over the entire shelf. Another index, used to relate physical characteristics to changes in fish populations, was based on the presence of ice along the longitude of 169°W (Wyllie-Echeverria and Wooster, 1998). Both have shortcomings. The percent ice cover provides no information regarding changes in the spatial patterns of the sea ice, and the longitudinal index is not always spatially representative.

To examine sea ice characteristics on a finer spatial scale, we calculated

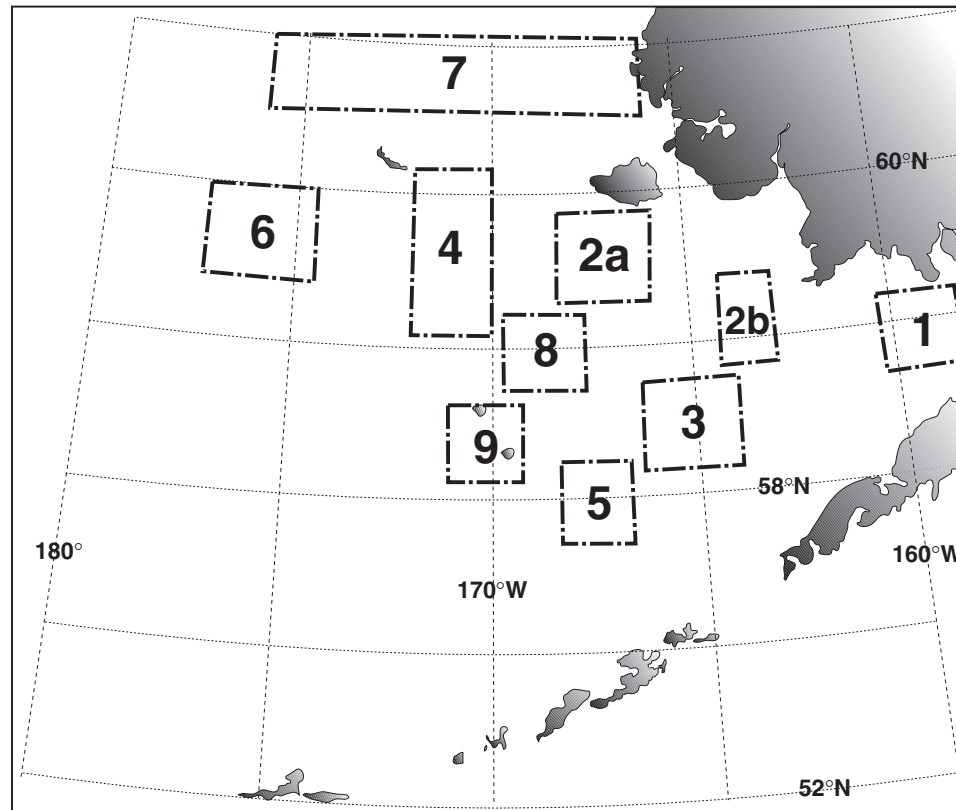


Figure 3.13: Strata used to calculate ice concentration.

ice concentration in the ten strata shown in Fig. 3.13. The ice concentration data are on a 0.25° grid and were obtained from two sources. Data from 1972 to 1994 came from the compact disk of Arctic and Antarctic ice concentrations produced by the National Ice Center, Fleet Numerical Meteorology and Oceanography Detachment (FNOC), and the National Climatic Data Center. To extend the time series to 2001, we digitized charts from the Anchorage Weather Service Forecast Office. The National Ice Center offers one chart of ice concentrations per week, and we continued to use that interval.

Using the results from area 9 (which includes longitude 169°W that was used in a previous index) and area 3, strong differences are evident as shown in Figs. 3.14 and 3.15. This comparison clearly shows some common features, i.e., the years of greatest ice extent occurred prior to the 1976–1977 regime shift. For the most part, however, the sea ice concentration is much less in Area 9 than in Area 3. Analyses of spatial patterns in sea ice cover have revealed both earlier transition to spring over the middle and outer shelf. The ice concentration results for all strata are presented in some detail below in order to highlight the rich nature of the original time series and the inherent spatial variability that exists over the shelf:

Area 7: Ice remains for a long period, occurs earlier and retreat is latest

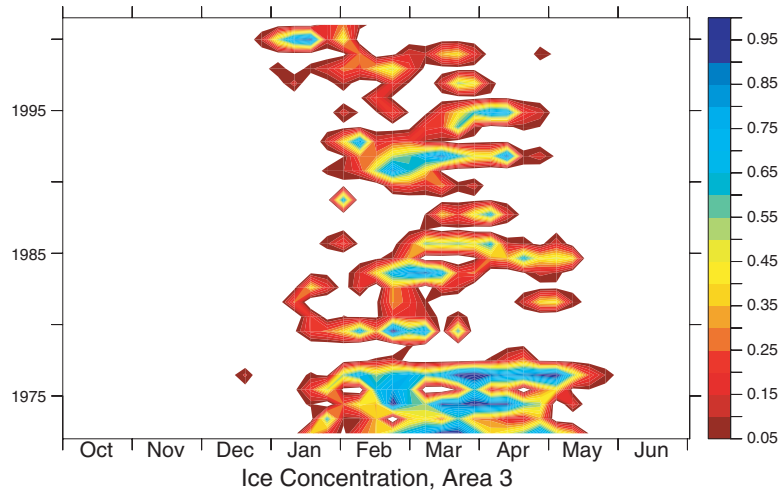


Figure 3.14: The time series of sea ice concentration in Area 3.

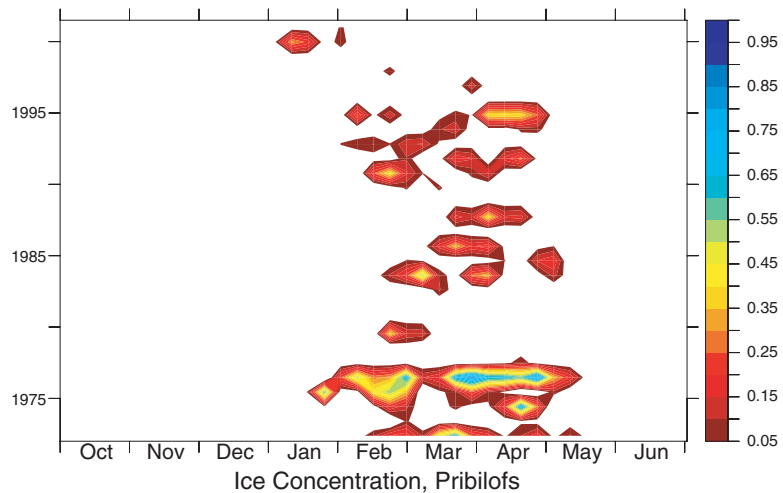


Figure 3.15: The time series showing ice concentration in Area 9.

of all the areas. The date of last ice is typically about 15 June, with the ice disappearing over a long period (about 1 month from full to no coverage). Most of the change among years occurs on the interannual time scale rather than decadal.

Area 2b: Some decadal period in the ice coverage, and disappearance occurs quicker than in Area 7.

Area 2a: very similar to 2b.

Area 4: Ice concentration shows the greatest variability here of all the areas. There is similarity in ice concentration with patterns in 2a. There appears to be little difference between these two areas in the length of time that the ice remains; the major difference is the later arrival of ice in Area 4.

The above are the four areas with the most extensive ice.

Area 6: The concentration of ice changes immensely each year. This area is dominated by interannual variation, and it has distinctly less ice than the other areas. In some years, there is little or no ice at all.

Area 8: (contains mooring site 4) The concentration of ice here shows large variability in percent of concentration. The time of maximum concentration varies throughout the years: one year it occurred in January, while in another year it occurred about May 1.

Area 3: (contains mooring site 2) We know most about what is occurring at this location from the long-term moored instruments. Interannual variability is the dominant mechanism in the spectrum of ice concentration here.

Area 1: This area is in a region where ice can form locally. The ice observations show that there is huge interannual variability in the concentration of ice, which provides a most surprising result.

Pribilof I.: Some of the variation in ice concentration here occurs because of the influence of the islands on regional and tidal currents. St. George Island typically has minimal ice compared to St. Paul Island. The patterns of ice concentration are very distinct from other areas. For example, in Area 7 there is ice 5–6 months of year, while there may be none at all around the Pribilof Islands.

Area 5: The warmer slope waters bathe this area, and ice is a transient feature. There were significant concentrations in the early 1970s (cold period), and, after the regime shift of 1976/77, ice was an infrequent visitor to this area. The dominant energy of this area occurs in the year-to-year variability.

For indices of sea ice (Table 3.1), the average percent concentration of sea ice within a rectangular region bounded by 58°N, 170°W and 57°N, 165°W was computed during the period 15 March to 15 April over the active research years of SEBSCC.

Sea ice has a marked impact on the ecosystem of the eastern Bering Sea. It provides habitat for marine mammals, and its presence is related to timing and magnitude of primary production (e.g., Stabeno *et al.*, 1998; Hunt *et al.*, 2002a). While a single index of ice can provide an indication of ecosystem characteristics, this analysis demonstrates that a single index of ice concentration is not valid for the entire SEBSCC study area. Because time series observations exist, indices can be created for any region of interest over the shelf.

3.3.5 Indices related to the cold pool and adjacent fronts (Peggy Sullivan)

Cooling and mixing associated with sea ice advance help to condition the entire water column over the Middle Shelf Domain, generating the cold lower layer of water known as the “cold pool” (Schumacher and Stabeno, 1998; Stabeno *et al.*, 1998). With seasonal heating, the lower layer becomes insulated and temperatures often remain below 2.0°C. The area of this cold pool varies by $\sim 2.0 \times 10^5$ km² between maximum and minimum extent. The

mechanisms that connect the cold pool to biota include changing habitat location (species composition) and alteration of biological rates.

Temperature cross sections along two southeastern Bering Sea transects are assessed over the years, 1996, and 1998–2000. MicroBathythermograph (MBT) temperature profile data from the Alaska Fisheries Science Center (AFSC) annual trawl surveys were used. Fig. 3.16 shows the areal extent and well-gridded structure of the trawl survey data, with data-collection sites shown by blue triangles, and red triangles marking the two transects which were processed and used for present purposes. The transects were chosen to represent distinctive regions near the perimeters of the trawl area, while still residing within solid data-coverage range for the entire area. Transect 1 (T1), the more northwesterly line, optimally contains nine data-collection points, while Transect 2 (T2), the more southeasterly line, optimally contains 11 data-collection points. Not all points exist for each year. Kachel *et al.* (2002) provide insight into processes related to the cold pool and inner front based on temperature, salinity, and dissolved nutrient observations, and Stabeno *et al.* (2002) provide insight into processes along the 70-m isobath.

Observing successive years across the same transects allows a comparative view of the behavior of the middle shelf cold pool, its year-to-year variations and overall shelf temperatures. The cold pool is well defined for all years along T1 (Figs. 3.17–3.20). This transect is not close to shore, so the coastal shelf is not well represented. The warm years of 1996, 1998, and 2000 had relatively warmer surface waters. During 1999, overall temperatures are colder, and the cold pool is cooler and shifted more shoreward. For both 1999 and 2000, the cold pool is shallower than in 1996 and 1998.

At transect 2, Fig. 3.21 shows a well-defined cold pool in 1996, deeper than in subsequent years, with horizontal temperature variability and moderately warm temperatures. During 1998–2000 (Figs. 3.22–3.24), the cold pool is more horizontally dispersed. The year 1998 had warmer overall temperatures, and the colder years 1999 and 2000 showed cold water more shoreward into the vertically mixed coastal shelf. The cold pool index in Table 3.1 shows the estimated area (km²) of water colder than 2°C in the vertical section of the T1 transect.

It should be noted that MBT trawl survey data from the AFSC are the subject of a data rescue, and, when completed, will be a rich data resource. Data profiles from 1992 through 2000 number approximately 3000. The physical data portion of the survey is being processed with normal PMEL methodologies, quality control, and web placement.

3.3.6 Pribilof age-0 pollock as an index of pollock year-class strength (Jim Ianelli)

Each year the EBS pollock stock is analyzed for fishery management purposes. This analysis consists of an integrated statistical assessment based on several different types of observations. The primary data analyzed include annual bottom-trawl surveys of the entire shelf area (within the U.S. EEZ), bi-annual echo-integration trawl (EIT) surveys of this region, annual fishery catch data from scientific observers aboard fishing vessels, and estimates of

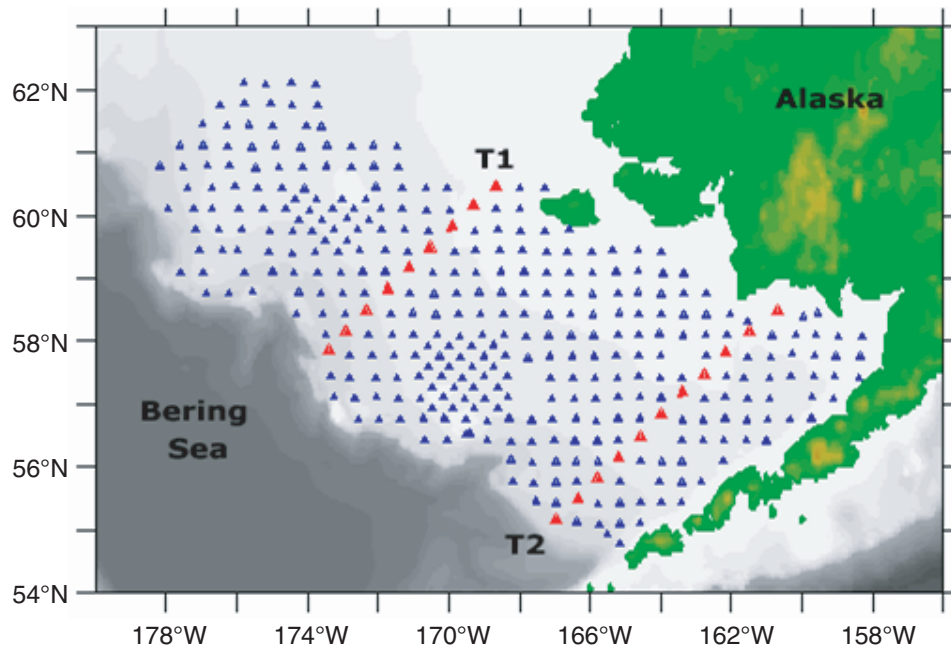


Figure 3.16: Trawl survey data collection grid in the Bering Sea. Data locations from the 1996 data set were used. Red triangles indicate transects 1 and 2.

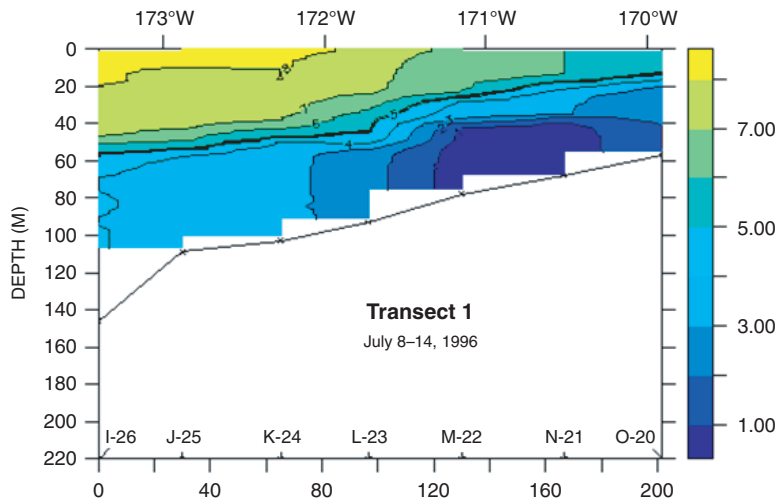


Figure 3.17: Temperature contours along T1 for 1996.

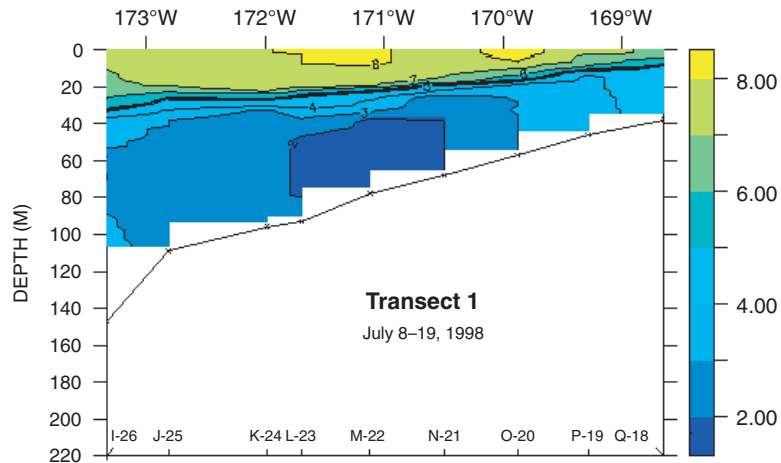


Figure 3.18: Temperature contours along T1 for 1998.

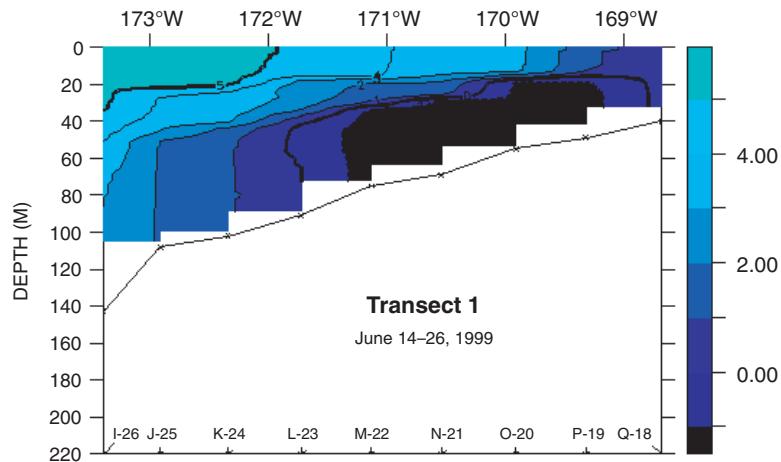


Figure 3.19: Temperature contours along T1 for 1999.

biological characteristics (e.g., age composition, growth, and maturation). These assessment analyses lead to recommendations on risk-averse harvest levels for the coming year.

The risk-averse aspects of harvest recommendations include levels of uncertainty in both the observations and the physical processes affecting the population. For example, pollock in this region are well known to have highly variable year classes (coefficients of variation on the order of 60%). As this variability propagates through the population, a key variable in quota determination is affected: estimated pollock biomass. It is therefore useful to be able to estimate reliably the abundance of incoming (pre-recruit) pollock.

One suggestion is that for a relatively small sampling effort, abundance of age-0 pollock around the Pribilof Islands can provide a useful index of year-class strength. Preliminary comparisons (Swartzman *et al.*, 2002) of such an

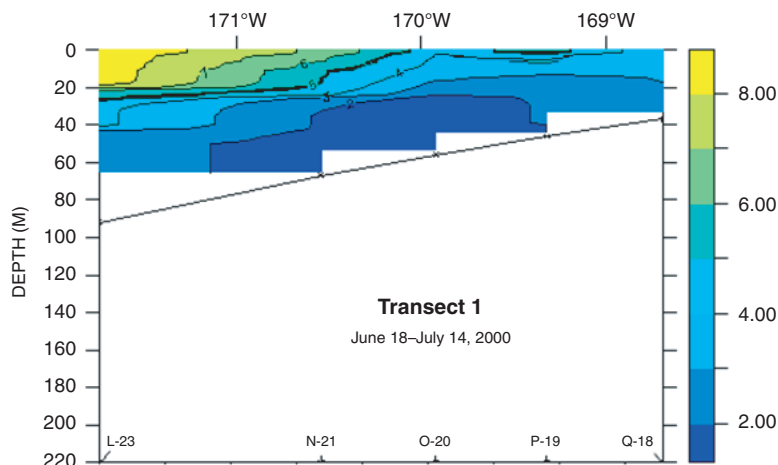


Figure 3.20: Temperature contours along T1 for 2000.

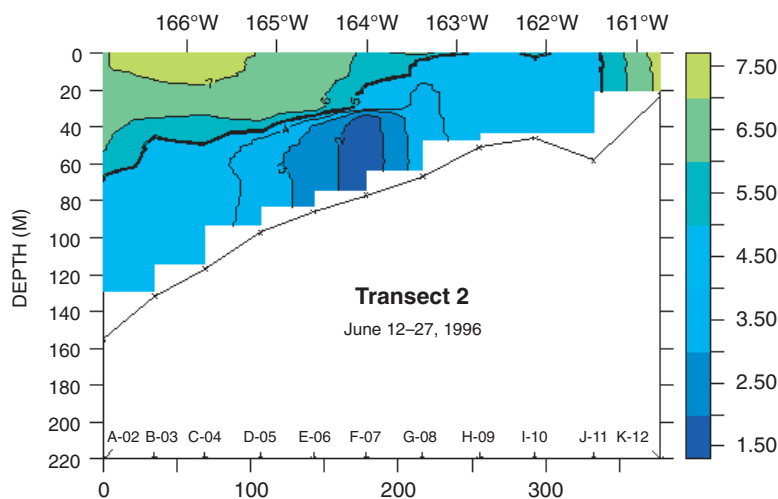


Figure 3.21: Temperature contours along T2 for 1996.

index with results from assessment analysis (based on age compositions from the fishery and two independent surveys, abundance indices from two surveys, growth rates, maturity information, natural mortality rates, and catch of the fishery; Ianelli *et al.*, 2001) suggest that an index of this type might prove useful (Fig. 3.25, Table 3.1). This is particularly appealing when one examines similarly constructed indices with other pollock surveys since both the bottom trawl and EIT surveys provide some indication of pre-recruit abundance at later stages (Figs. 3.26 and 3.27). The root mean squared errors for these three indices (relative to the assessment model prediction in log-space) are:

Note that in the assessment analyses, the overall abundance estimates (e.g., the area-swept estimate of total population numbers) are treated in-

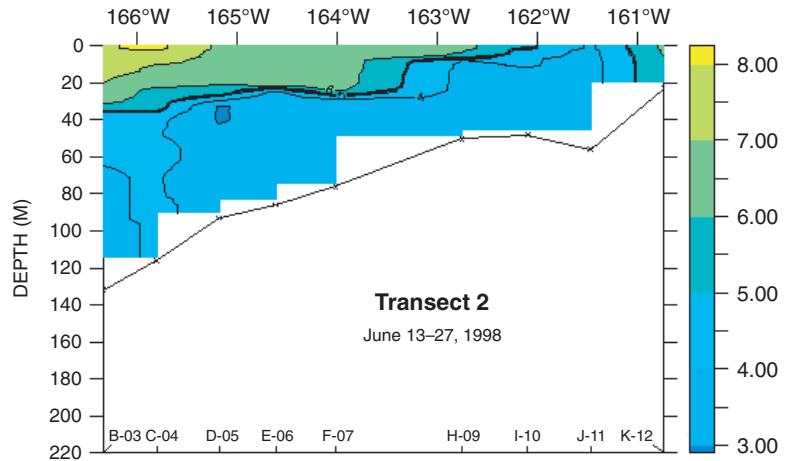


Figure 3.22: Temperature contours along T2 for 1998.

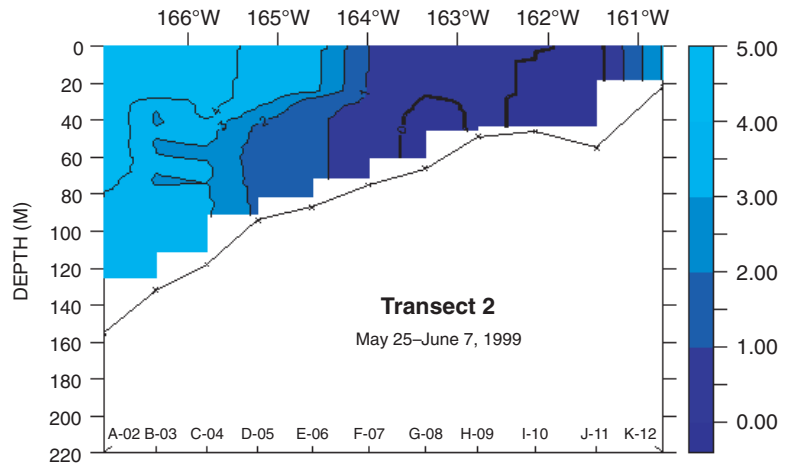


Figure 3.23: Temperature contours along T2 for 1999.

Pribilof Age 0	Age 1 Bottom trawl survey	Age 3 EIT survey
0.725	0.532	0.713

dependently from estimates of the age composition. This appeals to the way the population is sampled and sub-sampled for age compositions and avoids independence problems of statistically fitting several separate sets of indices-at-age. Furthermore, the indices as presented above are only for representation and do not reflect the fact that the assessment model allows for changes in age-specific availability over time (Ianelli *et al.*, 2001).

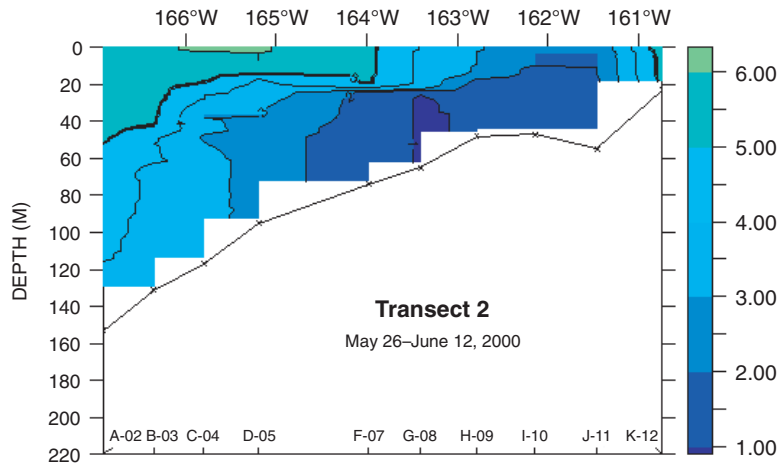


Figure 3.24: Temperature contours along T2 for 2000.

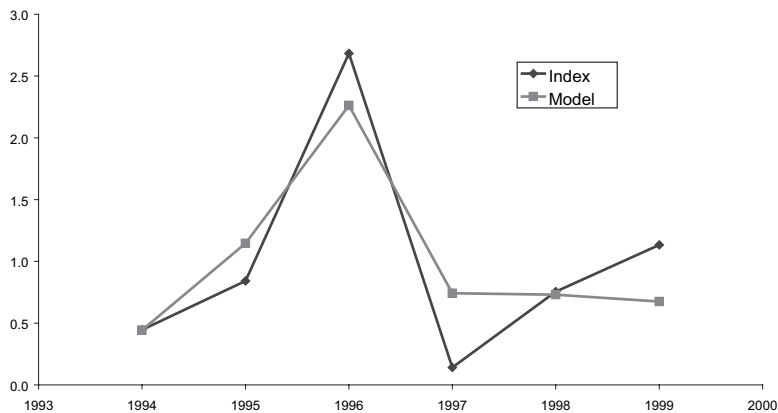


Figure 3.25: Pribilof young-of-the-year index relative to assessment results from Ianelli *et al.* (2001). Units are arbitrary.

3.3.7 Model simulations

What is NEPROMS? (Al Hermann). The Regional Ocean Modeling System (ROMS) is a versatile, state-of-the-art, free-surface, hydrostatic, primitive equation, ocean circulation model developed at Rutgers University and UCLA. Details can be found in Haidvogel *et al.* (2000), Shchepetkin and McWilliams (1998), and Marchesiello *et al.* (2001), and on the ROMS web site (<http://marine.rutgers.edu/po/index.php>). The ROMS user community now numbers more than 200 scientists worldwide. The version of ROMS used for our simulations achieves distributed memory parallelism using the Scalable Modeling System developed at NOAA's Forecast Systems Laboratory.

Using this parallel version of ROMS, we have been implementing a suite of basin-, regional-, and local-scale circulation models, linked via one- (and

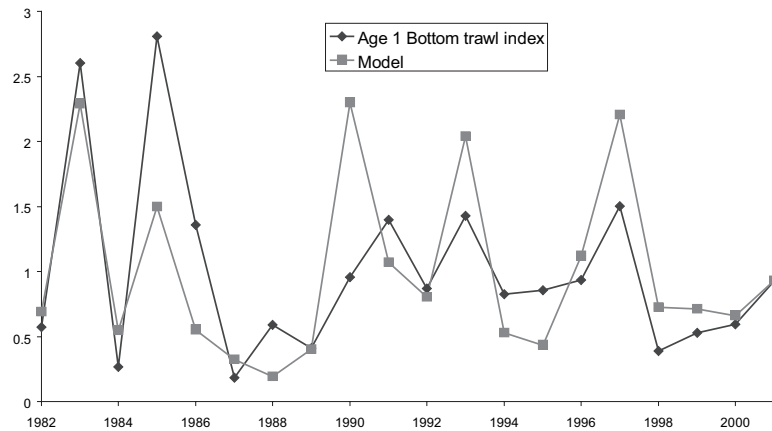


Figure 3.26: NMFS bottom trawl survey age-1 index relative to assessment results from Ianelli *et al.* (2001). Units in numbers rescaled to have a mean value of 1.

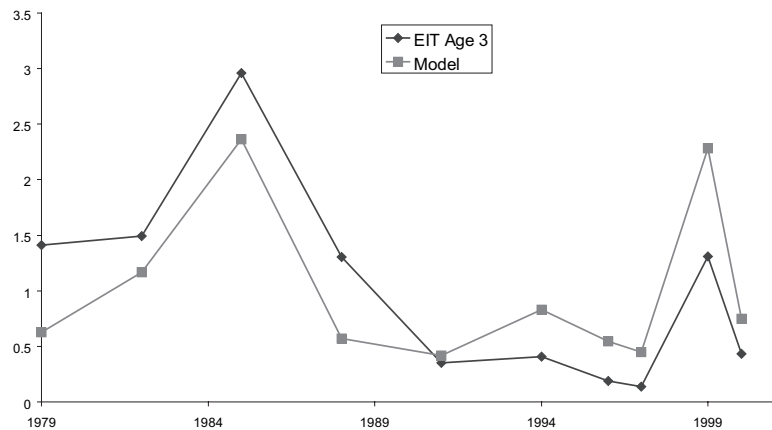


Figure 3.27: NMFS EIT survey age-3 index relative to assessment results from Ianelli *et al.* (2001). Units in numbers re-scaled. Note that the observations do not occur in every year.

eventually two-) way coupling. Figure 3.28 shows the set of nested modeling domains in current use, including: a basin-scale model encompassing the North Pacific Basin at 20–40 km resolution (NPac), a regional model at ~10-km resolution spanning the Northeast Pacific (NEP), and finally local models at ~3-km resolution in regions of specific interest [California Current System (CCS) and the Coastal Gulf of Alaska (CGOA)]. The NEP grid spans the area from Baja California up through the Bering Sea at approximately 10-km resolution, and was used for the simulations of the Bering Sea reported here. Additional information on these models (with snapshots and animations of model output) is available at <http://www.pmel.noaa.gov/~dobbins/nep.html>.

The NEP model is forced with daily average wind (converted to wind stress) and heat fluxes (sensible, latent, longwave, and shortwave) from the

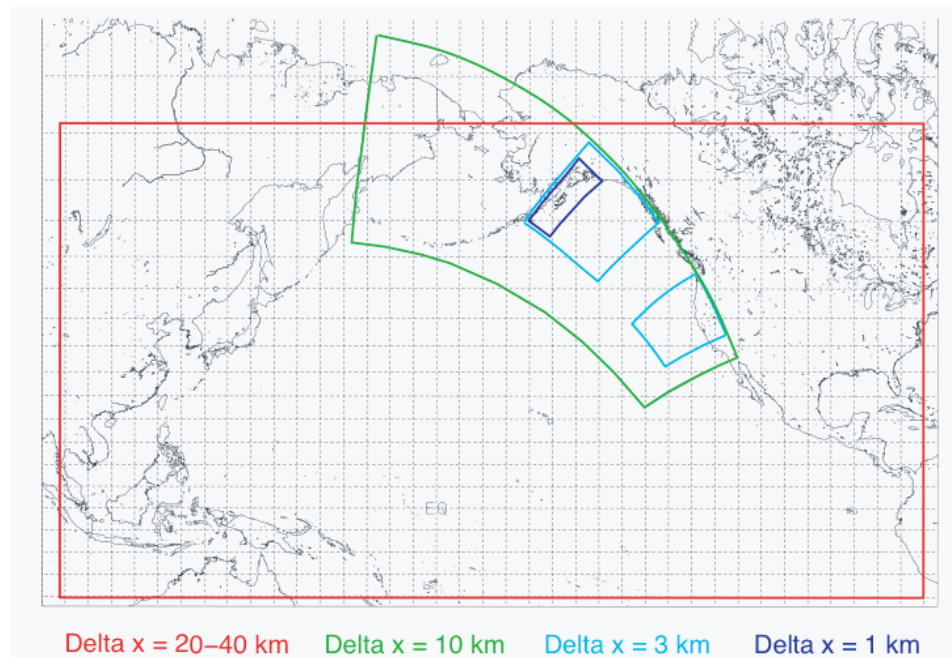


Figure 3.28: Nested modeling domains in current use for Pacific modeling, including: a basin-scale model encompassing the North Pacific Basin at 20–40 km resolution (NPac, red), a regional model at ~ 10 km resolution spanning the Northeast Pacific (NEP, green), and finally local models at ~ 3 km resolution in regions of the California Current System (CCS, light blue) and the coastal Gulf of Alaska (CGOA, light blue).

NCEP reanalysis project. No tidal forcing is included in these simulations. Model runs were initialized with Levitus monthly climatology for T and S fields. Hindcasts for a particular year were achieved by spinning up the NEP model from January of the previous year; for example, the model was spun up using daily NCEP values from January 1999–March 2000 for hindcasts of the period April–July 2000. Although even longer spin up would be preferable, 15 months is a sufficiently long period to evolve the appropriate mesoscale detail in the boundary currents and gyres (which is not contained in the coarse-scale Levitus-based initialization). It is also long enough to allow NCEP forcing to produce conditions (e.g., SST and currents) appropriate to the hindcast year (Fig. 3.29). Buoyancy input for the Gulf of Alaska was derived from the analyses of Royer (1982 and Old Dominion University, personal communication) and is added at the surface of the water column along the coast in the CGOA. The weakly dissipative algorithms for tracer advection in ROMS obviate the need for strong explicit mixing; here, explicit Laplacian horizontal mixing coefficients were set at $50 \text{ m}^2 \text{ s}^{-1}$ for momentum and $25 \text{ m}^2 \text{ s}^{-1}$ for temperature and salinity.

ROMS includes algorithms for passive float tracking in three dimensions. Floats can be seeded at arbitrary locations and times, and re-seeded as required for the numerical experiment. Output includes Lagrangian time

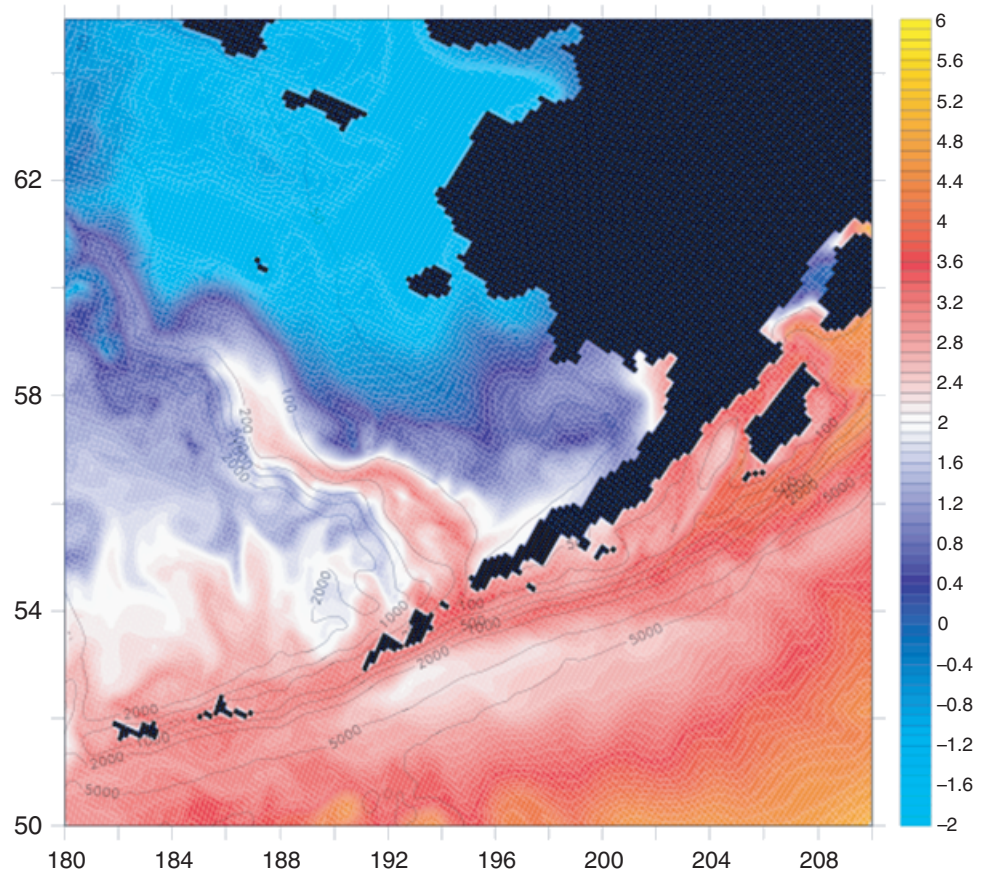


Figure 3.29: Model-generated sea surface temperature in the southeastern Bering Sea for 15 April 2000. Axes denote latitude ($^{\circ}$ N) and longitude ($^{\circ}$ E). Bathymetry is contoured in meters. Note the penetration of warmer waters from the Gulf of Alaska through Unimak Pass.

series of position, depth, salinity, temperature, and density. We have utilized this feature to track the temperature history of passive particles during NEP runs, as an approximation to the life history of passive planktonic organisms, e.g., pollock larvae.

ROMS simulations of pollock egg and larvae transport (Dylan Righi). Several mechanisms can connect transport of eggs and larvae to survival, including: transport to regions where predation is great due to cannibalism, and transport to regions where primary and secondary production is minimal (reduced prey availability). In this contribution, only the characteristics of the transport itself are addressed. The Northeastern Pacific Regional Ocean Model System (NEPROMS) was used to simulate drifter trajectories in the southeastern Bering Sea. Drifter tracking in ROMS is done using a fourth-order, predictor-corrector scheme. Drifters are allowed to move vertically. We currently have results for the years 1997–2001.

The simulated drifters are initialized over the eastern Bering Sea shelf just north of Unimak Island and to the northeast of Unimak Pass. This region

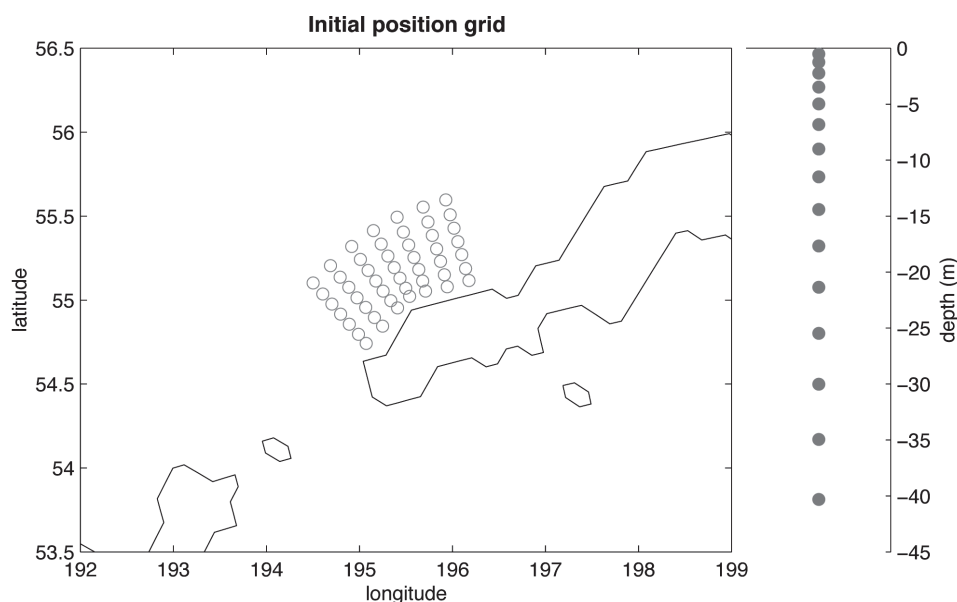


Figure 3.30: Simulated drifter initial horizontal (left) and vertical (right) positions.

is known to be an area of strong spawning for walleye pollock. The initial drifter positions fill out a 7×7 grid with horizontal separations of about 10 km (Fig. 3.30). Vertically, there are 15 drifters initialized at each grid point with maximum depths just over 40 m. The drifter initial positions are denser near the surface, replicating vertical egg distribution data collected in the Bering Sea (Kendall, 2001). Drifters are released on 1 April of each year and are tracked for 90 days.

Endpoints after 90 days for drifter trajectories from the 1997–2001 runs are shown in Fig. 3.31 (this plot shows all drifters at all depths). In all years, there is a strong tendency for trajectories to move to the northeast up the Alaskan Peninsula. The other common path is movement to the northwest along the 100-m isobath. These patterns are qualitatively similar to circulation schematics that were constructed from current, satellite-tracked drifter and hydrographic observations (e.g., Schumacher and Stabeno, 1998). The split between these two paths is seen clearly in the 1998, 1999, and 2001 drifter endpoints. In 1997, the full trajectory plots (not presented here) show that a subset of the drifters begin following the standard 100-m isobath path, but then currents change and drive them up the shelf to the northeast. The endpoints in 2000 are the result of strong turning to the northwest of trajectories that previously had been moving up the Alaskan peninsula. Further study of possible forcing mechanisms is needed to understand what leads to these years departing from the archetypal two-limbed flow.

The initial goal of this work was to compare simulated trajectories from a full primitive equation model with those from the Ocean Surface Current Simulations (OSCURS) numerical model. OSCURS computes daily surface current fields using daily sea level pressure and long-term mean geostrophic

current data. As such, it is a simpler model in terms of the physics involved and is much less computationally expensive. Wespestad *et al.* (2000) used OSCURS to create simulated trajectories in the Bering Sea. The initial grid used here was centered on the initial release point they used. Our trajectories for drifters released near the surface (0 to 5 m depth) show good agreement with the OSCURS results. However, our results show variation of trajectory endpoints with changes in both horizontal and vertical initial position. Figure 3.32 shows the full trajectories for the 2001 simulated drifters.

The upper left panel of Fig. 3.32 shows the tracks of all the drifters released for the run. The upper right and the bottom panels show drifter tracks as a function of their release depth. The first facet of these plots is that a drifter's endpoint depends largely on its initial horizontal placement.

The next point is that there is a strong dependence on release depth. The OSCURS 2001 trajectory moves a short distance to the northeast up the Alaskan Peninsula, as do the majority of the NEPROMS drifters released in the upper 5 m of the water column (upper right panel of Fig. 3.32). Nevertheless, with deeper release points comes a stronger divergence of the trajectory fates. In the 5–20 m and 20–40 m release bins, there are significant numbers of drifters that join the 100-m isobath flow to the northwest, with some even moving through Unimak Pass before turning back. OSCURS results completely miss this variation in particle fates.

As a working index of advection, Table 3.1 shows the fraction of each year's 735 simulated drifters that landed in the region bounded by 57°–58°N, 165°–170°W after 90 days.

3.3.8 A matrix for cataloging indices (Allen Macklin)

Early in the brainstorming process, members of the Indices Working Group suggested that a matrix would be a valuable data cataloging tool and an aid in developing and testing indices. At a minimum, a matrix would help with the housekeeping tasks of data tracking. At its fullest development, a matrix would be a multi-dimensional catalog of SEBSCC (and other relevant) data, accessible through the Internet, with direct links to referenced data collections. Presently, the character of the matrix is somewhere between the extremes. It is viewed as a dynamic document that is one of SEBSCC's legacies for future research in the region.

Figure 3.33 illustrates the Microsoft Excel version of the matrix. It is available by linking to "Phase III Working Groups" on the SEBSCC web site at <http://www.pmel.noaa.gov/sebscc>. Note that each index or data variable in column 1 (scrollable) is cataloged in two dimensions: time and space. Each index also contains a description, e.g., the yellow box in Fig. 3.33 describes the "Thermocline" index. Passing the computer's mouse over the cell containing the index name activates the description. To the right of column 1 are scrollable, color-coded columns for the years contributing to the matrix, 1972–2001. Each color-coded column is divided into four sub-columns: annual average, spring bloom, summer, fall overturn. These represent the important time scales and seasonal periods for the matrix. Cells

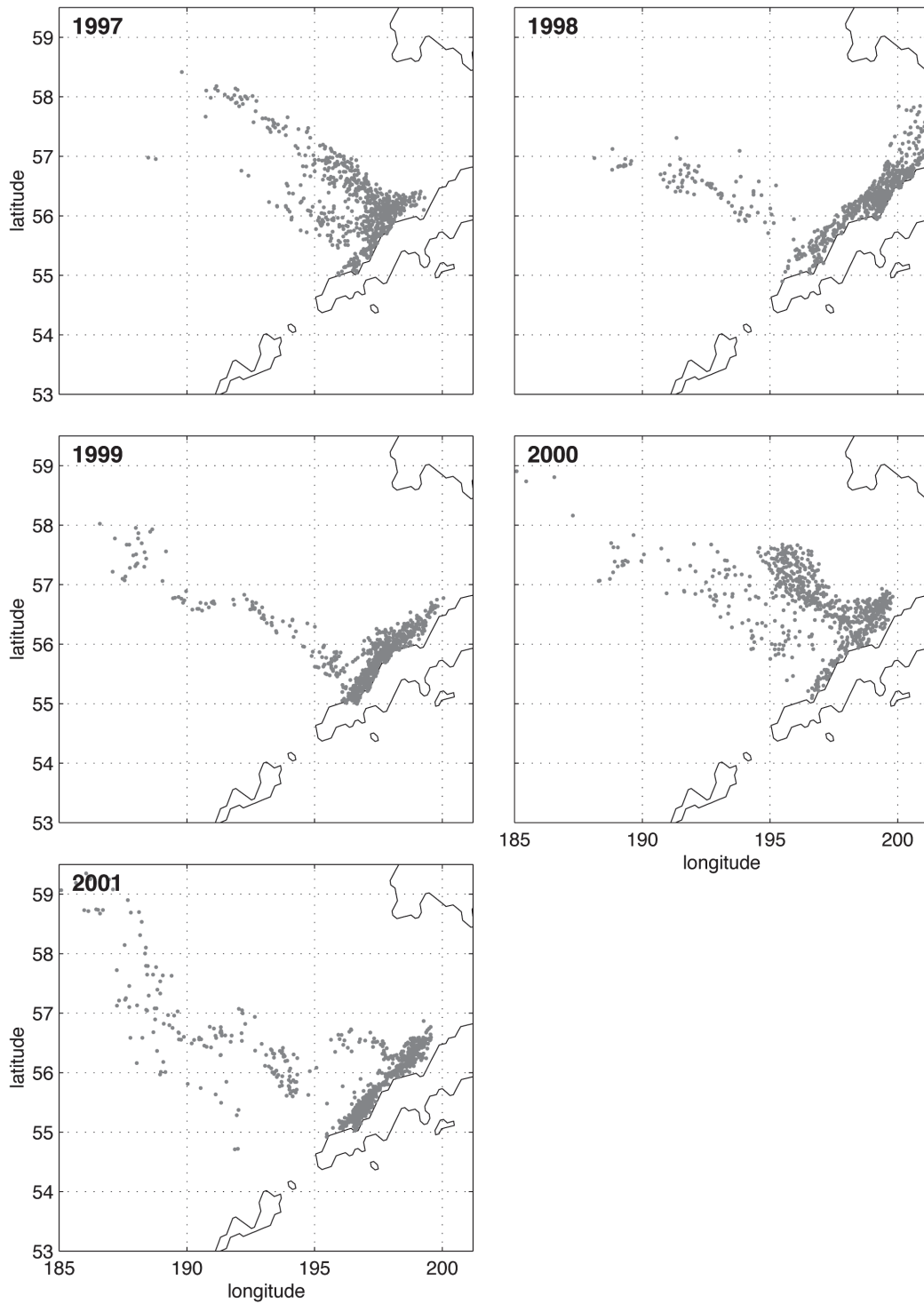


Figure 3.31: Endpoints for 90-day drifter trajectories for 1997–2001.

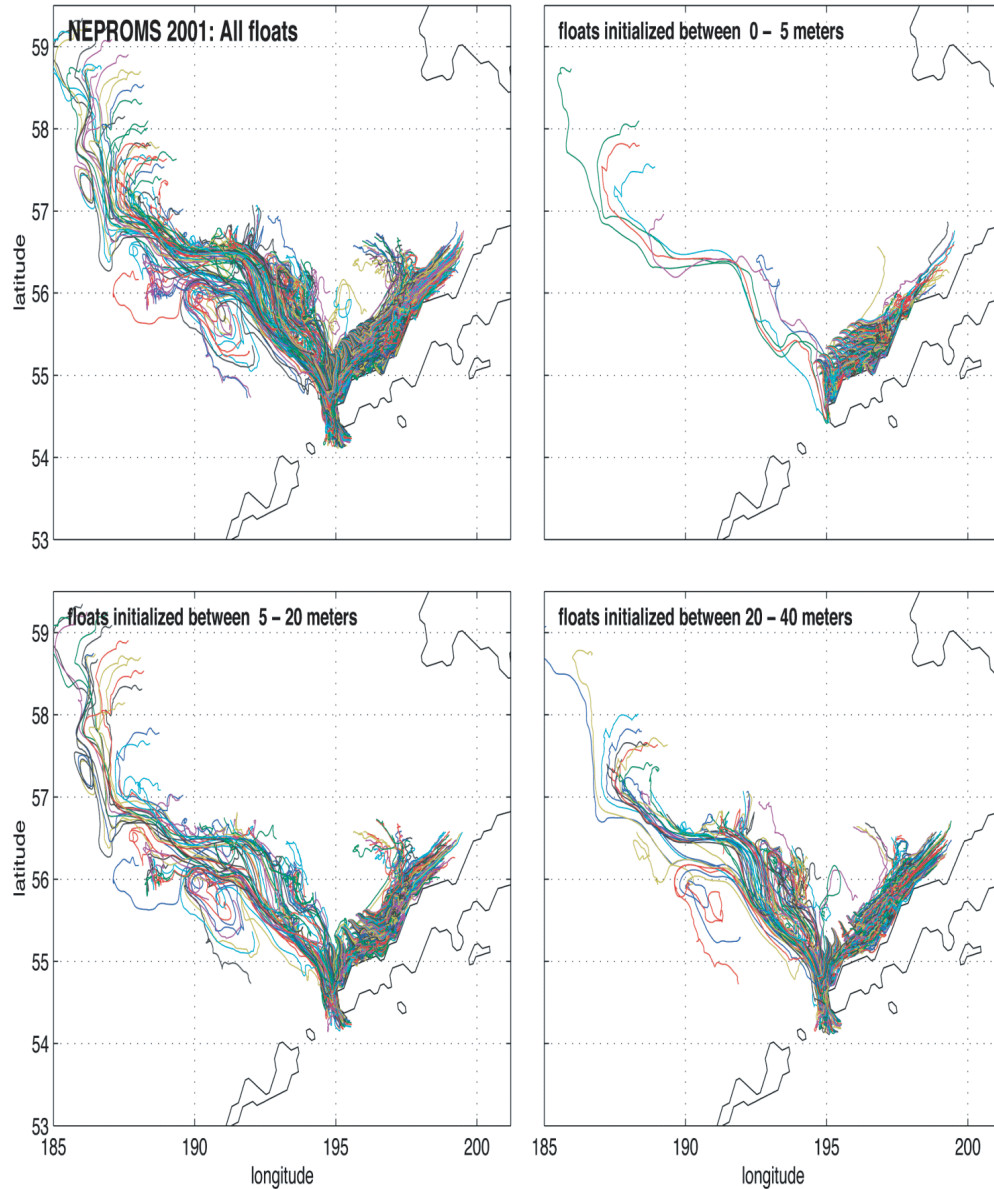


Figure 3.32: Full trajectories for the 2001 90-day simulated drifters. The upper left panel shows all drifters, while the other panels show drifters divided as a function of initial release depth.

in the matrix contain values for that index during that season of each year or links to data that provide values. Not all cells are occupied at this time.

At the bottom of Fig. 3.33 are labeled tabs that represent the spatial dimension of the matrix. The matrix encompasses the same geographic domains that are discussed elsewhere in this document (Section 3.3.4) and described by Hunt *et al.* (2002a). Clicking on a tab brings to the screen an identical grid of indices and years, but the cells are populated with values specific to the region selected.

Besides the indices matrix, there is also a matrix of data available for

Index	1997				1998			
	annual avg	spring bloom	summer	fall ovrtrn	annual avg	spring bloom	summer	fall ovrtrn
Age-0 cannibalism								
Ice retreat		Apr 2				Mar 7		
Last storm		May 15				May 15		
Stratification date		May 1				May 15		
Thermocline depth			20				30	
Thermocline ΔT			11				7	
SST maximum			14				12	
Depth-averaged T_{max}			4.5				6	
PWP stratification		0.7638				1.052		
PWP stratification date		ice				Jun 16		
PWP stratification temperature						2.87		
Slope current	6				2			
Fluorescence peak		Apr 15-30				May 10-?		
Early May nitrate		0 sfc 10 deep				12 sfc 11 deep		
Early May ammonium		8 sfc 10 deep				10 sfc 6 deep		
Copepod $^{*}N$	13.5				10			

Thermocline ΔT : stratification as measured by strength of thermocline ($^{\circ}C$) on Jul 1 (from Henrichs)

Inshore N. Middle Shelf S. Middle Shelf Peninsula N. Outer Shelf Pribilofs S. Outer Shelf Unimak

Figure 3.33: A portion of the SEBSCC indices matrix showing some indices for the South Outer Shelf region during 1997 and 1998.

the Pribilof Islands. This matrix, too, can be found by linking to “Phase III Working Groups” on the SEBSCC web site.

3.4 Application of a Transport and Predation Index to Recruitment for Stock Assessment Purposes (Jim Ianelli)

3.4.1 Background

Recruitment or year-class strength (the numbers of fish successfully surviving larval and post-larval stages, e.g., to age 1) is a fundamental part of the population model used for pollock stock assessments (e.g., Ianelli *et al.*, 1998). The recruitment estimates provide the basis for population numbers that are tracked over time and modified by various natural and fishing mortality sources. The statistical assessment models used in these analyses are similar to state-space models where unknown and unobservable quantities (e.g., numbers of fish) are modeled separately as “state” variables. “Observation” equations are then constructed to translate the state variables into model predictions. These predictions are then compared with actual data to tune the state variables (i.e., the fundamental parameters) using statistical methods such as maximum likelihood. Schnute (1994) provides a good description of this general approach.

Estimates of year-class strengths (e.g., Fig. 3.34) thus are derived from

a variety of information used in the assessment model. This information includes annual bottom-trawl surveys of the entire shelf area (within the U.S. EEZ), bi-annual echo-integration trawl (EIT) surveys of this region, annual fishery catch data from scientific observers aboard fishing vessels, and estimates of biological characteristics (age composition, growth, and maturation, etc.). These assessment analyses lead to recommendations on risk-averse harvest levels for the coming year. The recommendations are influenced by estimates of the underlying stock-recruitment relationship within the integrated assessment model (the so-called stock-recruitment sub-model; Fig. 3.35). Further, the stock-recruitment sub-model can be modified to incorporate environmental indices. Because the framework of the integrated model separates the state dynamics from the observations, it is relatively straightforward to test alternative hypotheses. We illustrate one such modification to evaluate the impact of progressively adding recruitment effects beginning with the simplest form (a mean and deviation) and then additional terms related to the stock size and any environmental terms and process errors. These can be written as recruitment state variables:

$$R = \text{Mean} + \xi, \quad (1)$$

$$R = f(S) + \xi, \quad (2)$$

$$R = f(S) + E, \quad (3)$$

$$R = f(S) + E + \xi, \text{ or} \quad (4)$$

$$R = f(S) + E' + \xi, \quad (5)$$

where R is an actual (unobserved) state variable (log-recruitment) for a given year, and the error term ξ can be thought of as one that encompasses all “natural” variability that is not described by other terms in the above sub-models. For example, sub-model (3) is written such that all recruitment variability is determined by the stock-recruitment function $f(S)$ and an environment term E . This simply means that there is no residual process error in recruitment specifications (i.e., the model terms determine all of the variability in recruitment). For sub-model (5), the conditions for the environment term E' (described below) are “smoothed” with respect to spatial correlation.

In searching for the appropriate environmental term(s), water temperature, turbulence, and transport have been related to success of recruitment for many marine species (e.g., Quinn and Niebauer, 1995). Here, we follow the construct that the transport of planktonic stages is important to establish separation of young pollock from their cannibalistic adults (Wespestad *et al.*, 2000). We used the Ocean Surface Current Simulations (OSCURS) numerical model (Ingraham and Miyahara, 1988) as a means to represent the effective interannual variability of advective egg and larval transport. The model simulates transport trajectories for passive, floating (or near-surface) objects that are propelled by ocean surface currents forced by wind.

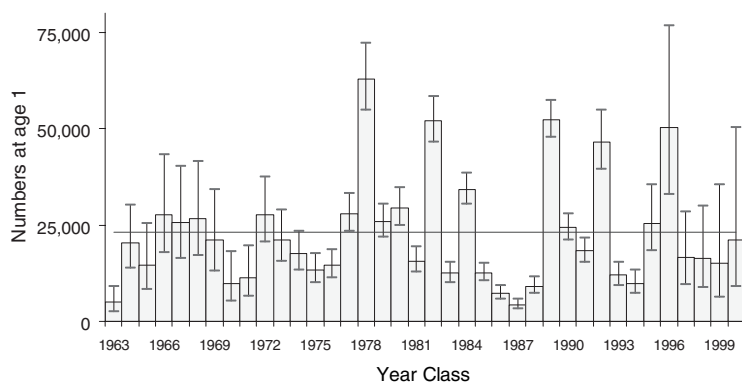


Figure 3.34: Time series of year-class abundance at age 1. Error bars represent approximate 95% univariate confidence bounds. Note that covariance estimates among adjacent year classes is typically highly negatively correlated. Source: Ianelli *et al.* (2001).

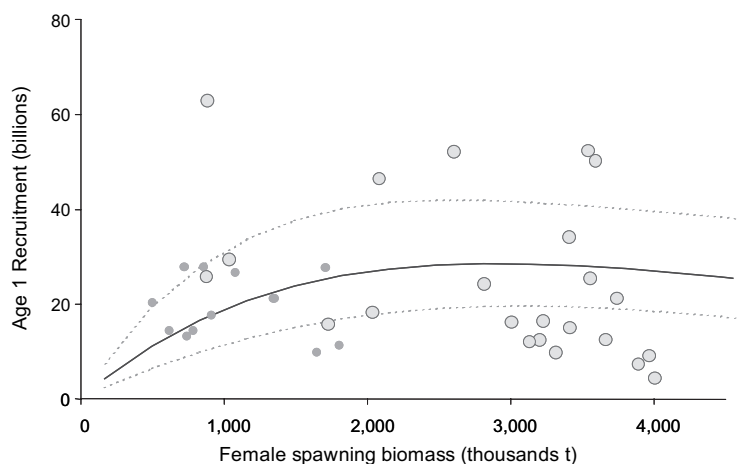


Figure 3.35: Stock-recruitment relationship showing the fitted effect due to spawning biomass (thick line) and estimates from the stock assessment model. Note that the large dots are used to tune the stock-recruitment sub-model while the smaller dots represent points from the regime prior to 1977. Dashed lines represent approximate 95% confidence bands about the curve. Source: Ianelli *et al.* (2001).

3.4.2 An application

The following serves to illustrate one method for incorporating environmental information within an integrated stock assessment approach such as that currently used for EBS pollock. Incorporation of any index can be done in a similar fashion. The integrated assessment model is a good way to evaluate candidate indices because consistency with all available data can be easily evaluated. In addition, compared to methods simply using recruitment residuals, the integrated model provides a more statistically defensible approach as fewer assumptions are required (e.g., analyses of residuals done separately

typically fail to account for the uncertainty of the estimates of the residuals themselves). A disadvantage of the integrated assessment approach is that a fair amount of specialization is required to run the models.

The OSCURS model was run using a single launch site (55.5°N, 165°W) for 90-d trajectories starting 1 April. This location and date were selected based on the distribution and timing of the main concentrations of spawning pollock. The variability of this location appears to be moderate based on the catch-distribution of the fishery for pre-spawning pollock (Fig. 3.36). However, this observed variability is partly attributed to fishing fleet behavior under variable ice conditions and management measures.

Simulations were generated for the years 1964 to 1998 (Fig. 3.37). The endpoints of these trajectories suggest that the young-of-year pollock are either just seaward of the inner front or in the coastal domain as defined in Kachel *et al.* (2002). To quantify the effect these trajectories may have on recruitment success, we chose to compute the average location of the 90-day drifter. The average location represents the characteristics of the advective forces better than the endpoints and reduces the impact of drift outliers (i.e., high-levels of drift over a few days). These average locations were then placed in the context of a grid (Fig. 3.38) in order to geo-reference the advection by year. Each year, therefore, was assigned to a grid-cell (but not all grid-cells had observations). The integrated assessment model was then used to estimate the “effect” a particular grid-cell has relative to recruitment success. In other words, each cell was estimated as being favorable, unfavorable, or neutral to pollock year-class strength.

To make the model well conditioned, two penalty weights were added to the (negative-log) likelihood function. First, a very small grid-cell penalty was added so that for cells with no observations, the estimated recruitment effect would be zero (yet still with the desired high variance). The second (more important) penalty effectively conditions the grid surface values to have a non-parametric surface such that there is some degree of spatial correlation. The value of this penalty weight affects the “smoothness” of the surface by way of multiplying the sums of squared third-differences between grid-cell values in both the lateral and longitudinal directions (Ianelli *et al.*, 1998). In the limit, as the value of this multiplier becomes large, the effect of the grid on explaining recruitment variability goes to zero (i.e., the two-dimensional surface is represented by a single mean value). As the smoothness penalty multiplier tends toward zero, the cells become independent from contiguous (and all other) cells. Alternative values of this multiplier have been explored and are shown in Figs. 3.39a and b. Note that in Fig. 3.39a, the “effect” of larval drift is more irregular compared to the model where smoothness in space is assumed (Fig. 3.39b). Root-mean squared errors of all five sub-models for this application are shown in Table 3.2.

3.4.3 Discussion

For the eastern Bering Sea, wind-driven advection of surface waters containing planktonic stages of pollock (Wespestad *et al.*, 2000) and Tanner crabs (Rosenkranz *et al.*, 2001) appears to account for some of the observed fluctu-

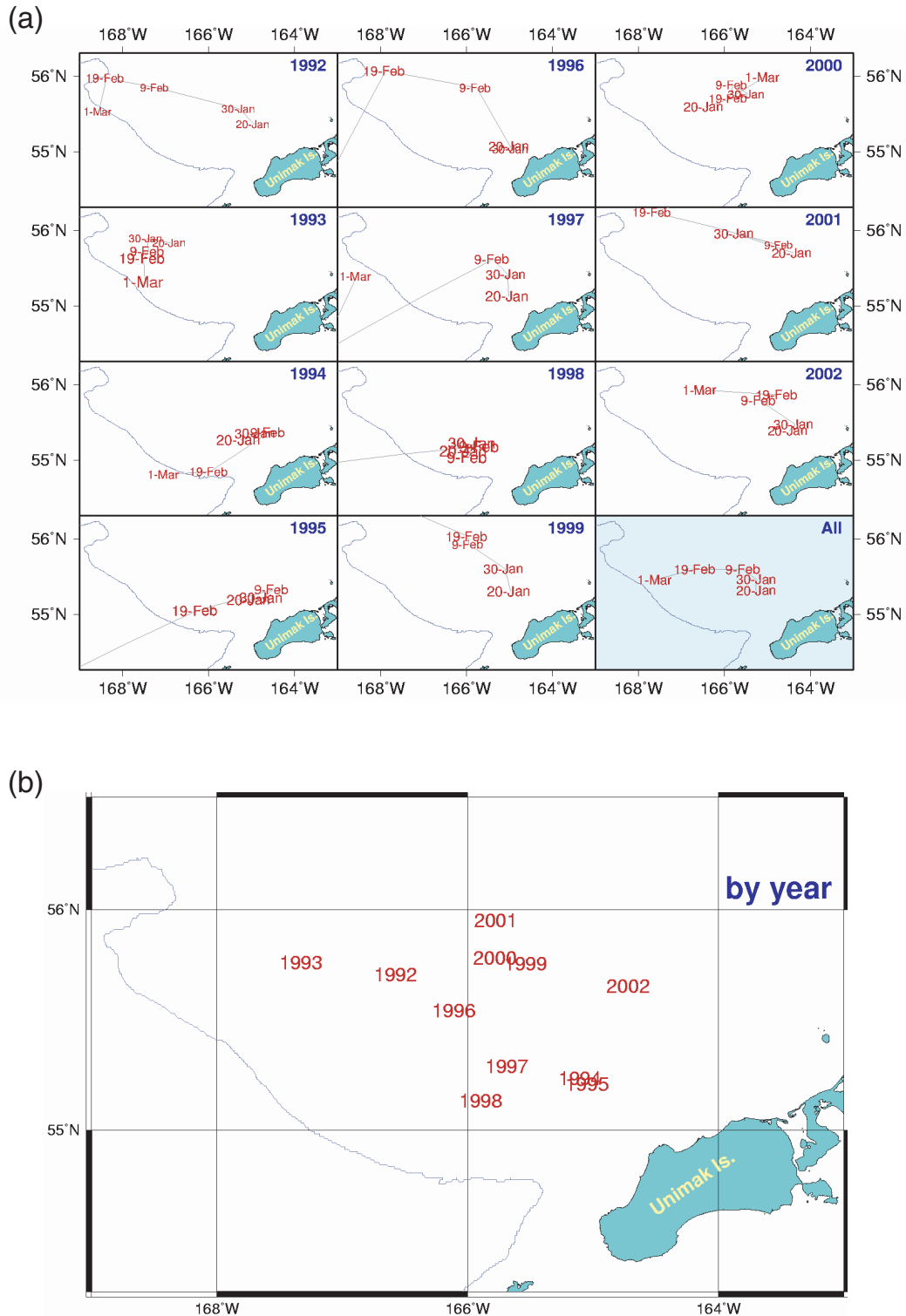


Figure 3.36: Top panel (a): Average catch distribution by 10-day periods, 1992–2002. Bottom right corner is average over all years combined. Bottom panel (b): Average catch distribution of the pollock fleet targeting pre-spawning pollock by year, 20 January–28 February.

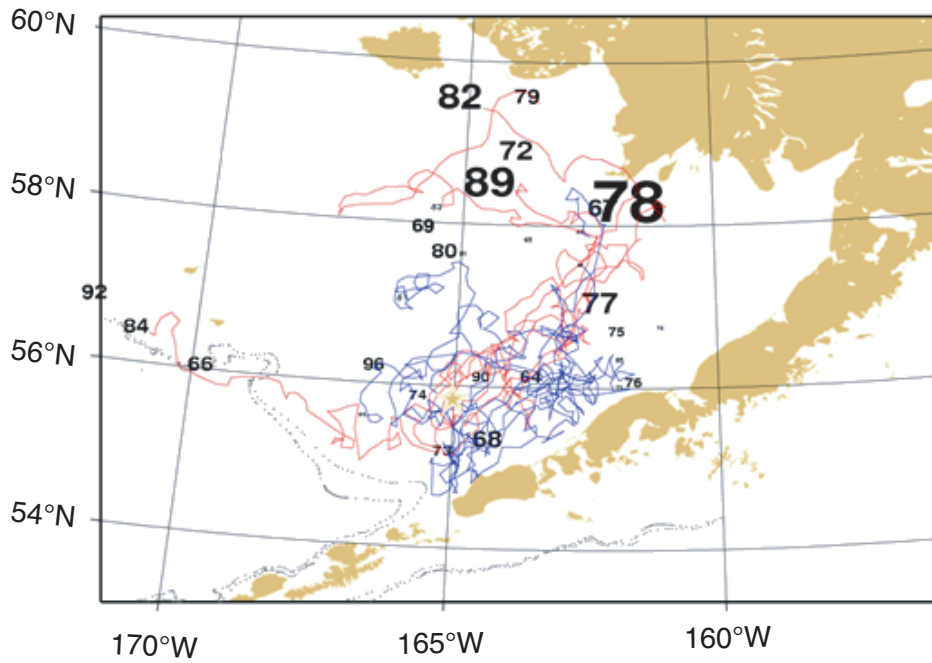


Figure 3.37: Trajectories resulting from 90-day simulated wind drift from the initial launch site (annotated with a star). The size of the labeled year indicates the relative strength of that year class.

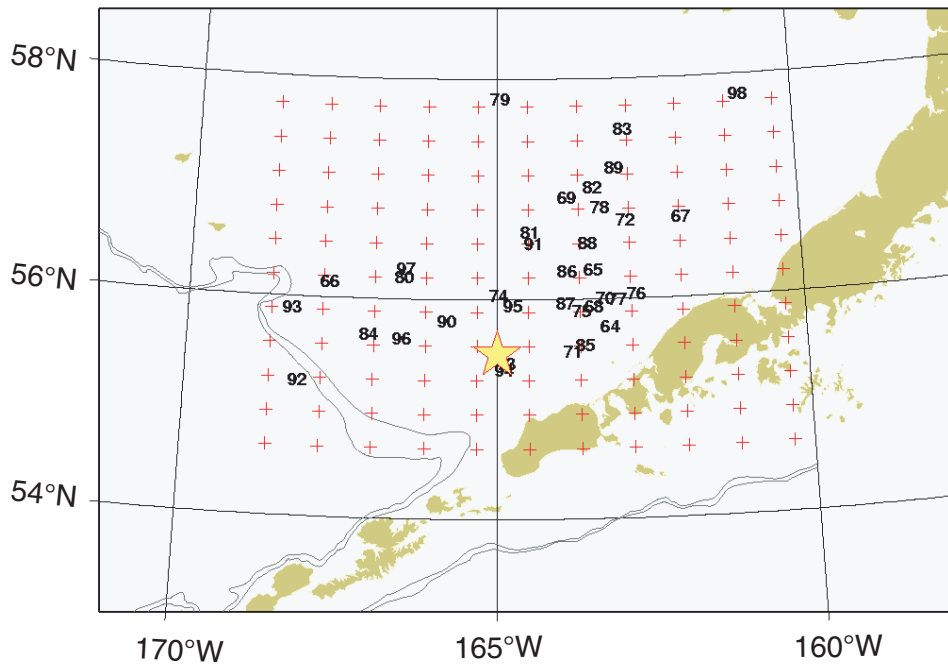


Figure 3.38: Arbitrary grid locations (crosses) and average location of 90-day simulated drifters (begun at the star from 1 April) indicated by two-digit year (number).

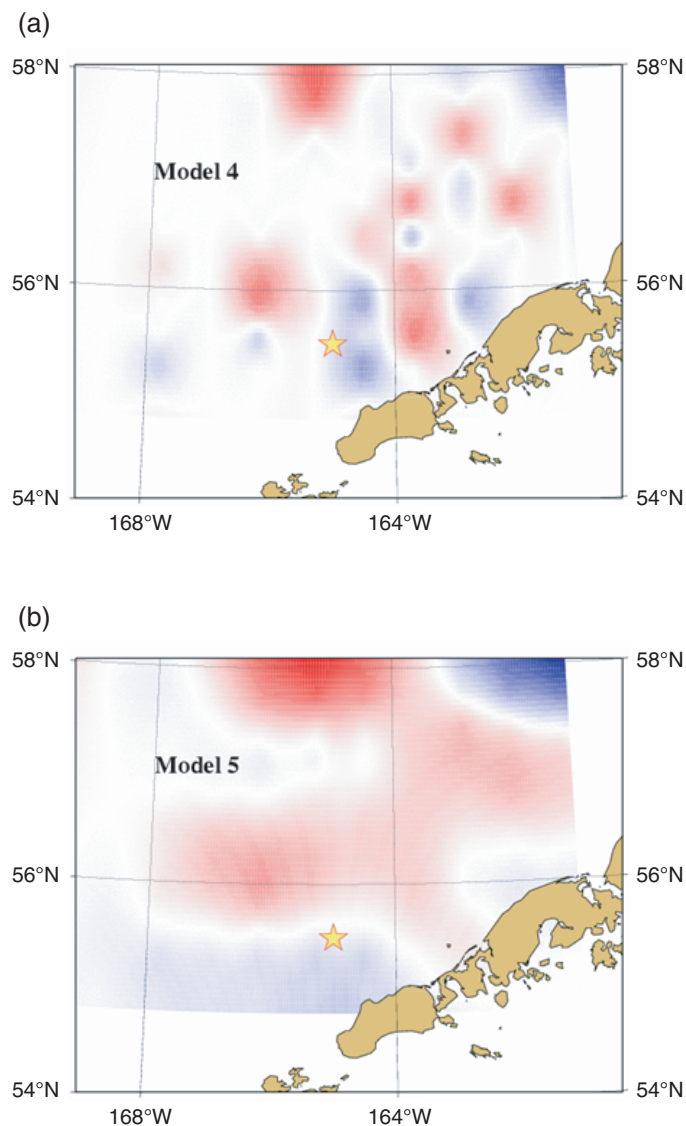


Figure 3.39: Graphical results of fitting a drift component within the integrated stock assessment model. Red areas indicate higher recruitment success while blue represents lower values. Panel (a) is the result for Model 4 (not smoothed) compared with Model 5 (where some degree of spatial correlation is specified).

tuations in year-class strength. In these studies, the biological process that links advection to year-class strength is differential survival.

The role of cannibalism in influencing population dynamics resulting from the strong year class has been examined (Livingston and Methot, 1998). For the age-0 pollock, predation by older pollock can have a strong influence on year-class strength.

A number of caveats exist in the above analysis. For example, the mechanistic model is one that deals with the negative effects of spatial overlap between age-1 juveniles with pollock that are generally older than age 2

Table 3.2: Root-mean squared errors of recruitment sub-model results.

Model component	Model				
	1	2	3	4	5
Mean	0.00	—	—	—	—
Stock-recruitment function, $f(S)$	—	0.04	0.08	0.09	0.09
OSCURS avg. drift	—	—	0.48	0.21	0.11
Residual (ξ)	0.75	0.72	—	0.21	0.28
Total	0.75	0.75	0.56	0.51	0.47

(Fig. 3.40). Analyses of an index of separation (Equation 6) may provide some insight on whether other data are consistent with this process.

$$I_i = \frac{\sum_{\text{all stations}_i}^{n_i} (p_{\text{age}2+} - p_{\text{age}1})^2}{\sqrt{n_i}} \quad (6)$$

where $p_{\text{age}1}$ and $p_{\text{age}2+}$ are the proportions at age 1 and ages 2 and older, respectively. These values were computed at each station sampled during a given survey (Wespestad *et al.*, 2000). Results compared with log-recruitment suggest a very weak relationship between separation index and year-class strength (Fig. 3.41).

Another caveat for this approach is that there are physical and biological assumptions imbedded in how accurately OSCURS simulates the actual transport of pollock eggs and larvae. From a purely physical perspective, we accept that OSCURS is a surface wind-drift model most applicable to approximately the upper 10 m of the water column and to regions where the ambient subtidal currents are weak. For much of the southeastern shelf, the climatological mean currents are weak, yet more active flow has been observed along the 100-m isobath and over the outer shelf/slope (Schumacher and Stabeno, 1998; Reed and Stabeno, 1996; Reed, 1999; Stabeno *et al.*, 2001). One solution is to compare the results from OSCURS to those from more sophisticated hydrodynamic models. Early indications suggest that there is good agreement, except in areas where depth dynamics are particularly acute, e.g., around the Pribilof Islands.

From a purely biological perspective, the question of location of planktonic stages in the water column, and selection of a single launch site must be examined. We show some indication of interannual variability of spawning location (Fig. 3.36) that may be useful to improve launch-site locations. Additionally, multiple launch sites in space and time may also better represent the effect of advection on pollock eggs and larvae. While extensive work has not been conducted on the vertical location of eggs and larvae, over the shelf, larvae do exist in the upper 10 m, but they are often found at greater depths (Napp *et al.*, 2000). This raises the question on what fraction of the planktonic life history stages would follow the wind-drift.

Spawning also occurs near Bogoslof Island and other locations over the

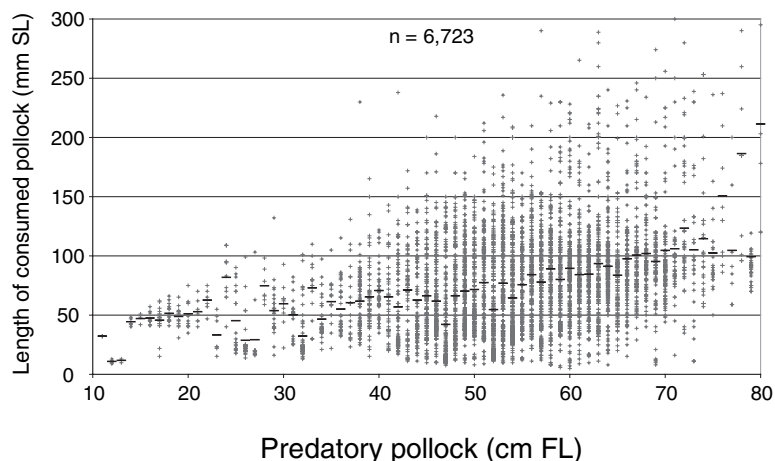


Figure 3.40: Length of pollock consumed compared to the length of the consuming pollock based on NMFS food-habits studies (Troy Buckley, NOAA/AFSC, personal communication).

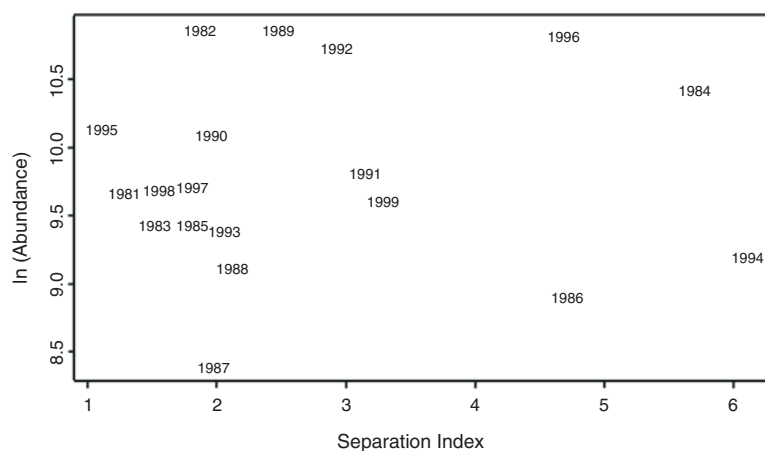


Figure 3.41: Separation index relative to estimates of the log-pollock abundance at age 1, 1982–1999. Numbers plotted represent year-class.

slope and basin of the eastern Bering Sea. These regions were hypothesized to be a source of larvae for the southeastern shelf (Francis and Bailey, 1983). If significant spawning occurs off the shelf where high concentrations of larvae have been observed (Schumacher and Stabeno, 1994), then the simple set of initial conditions for the drift-effect on recruitment are further complicated. It appears that larvae in these waters are likely to be deeper in the water column (Napp *et al.*, 2000) and the background currents are typically stronger than over the middle shelf (Stabeno *et al.*, 1999a). Alternative drift locations to represent the starting points of egg and larval stages may require further exploration, particularly if there is a significant amount of pollock egg production from the Aleutian basin region.

3.5 Changing Relationships between Climate and Biological Indices in the Eastern Bering Sea (Alan Springer)

3.5.1 Introduction

Climate change, whether considered at local or global spatial scales and annual or millennial time scales, is among the most controversial and intriguing environmental issues confronting us today. The obvious concerns over climate change are effects it has on ecosystem structure and function, food web productivity, the abundance of individual species, and the economies and livelihoods of people the world over.

Nowhere have the effects of climate change on marine ecosystems been better documented than in the North Pacific Ocean (e.g., McGowan, 1990; Ebbesmeyer *et al.*, 1991; Beamish, 1995; Mantua *et al.*, 1997; Francis *et al.*, 1998; Klyashtorin and Rukhlov, 1998; Springer, 1998; Welch *et al.*, 1998; Anderson and Piatt, 1999; Hare *et al.*, 1999; Hare and Mantua, 2000). The common approach in most analyses of climate and other ecosystem components has been to compare slopes of parameter values over time, slopes that change when the climate changes from one quasi-stable state, or regime, to another. Regime shifts are defined by abrupt, sustained polarity reversals of the Pacific Decadal Oscillation (PDO) (Trenberth and Hurrell, 1994; Mantua *et al.*, 1997).

In contrast, there have been comparatively few analyses of relationships between two variables when time was not one of them. In order to better understand ecosystem processes that respond to climate change and regime shifts, it would be helpful to have correlations between things that are, or might be, functionally related. For example, correlations between fluctuations in primary physical forcing parameters, such as the Aleutian Low pressure field, and some response variables, such as wind, mixing depth, and primary productivity, as was modeled for the Gulf of Alaska by Polovina *et al.* (1995); and temperature and zooplankton population dynamics in the Gulf of Alaska (Mackas *et al.*, 1998).

A small assortment of data sets for the Bering Sea can be grouped in ways that yield marginally miscellaneous and eclectic, but compelling, relationships. These relationships provide insight into time and space scales of interest and the sensitivity of ecosystem components and processes to climate change. This includes changes in the general climate state, e.g., PDO, and to interannual fluctuations in climate within and across regimes. Some of the relationships are between adjacent ecosystem elements that could be thought of as functional cause and effect relationships. Other relationships are separated by more than one element. Such ostensibly functional relationships are useful to know, even if the variables are separated by more than one trophic level, since they may give clues about where and how to look for processes responsible for biomass yield at any trophic level.

3.5.2 Observations

The time series used to develop and examine potential relationships are:

- a. North Pacific Index (NPI)—area averaged mean sea level pressure anomaly over the region 30° to 65°N, 160°E to 140°W (Trenberth and Hurrell, 1994; Minobe, 1999);
- b. Sea surface temperature (SST)—mean temperature of a 5° × 5° block centered on (55°N, 170°W) (Cayan, unpublished data);
- c. Bering Sea wind measured at St. Paul Island by the U.S. National Weather Service (Note, the wind speed has been cubed so that it provides an index of mixing.);
- d. Sea-ice coverage over the eastern Bering-Chukchi shelf (Niebauer, 1998 and unpublished data);
- e. Bering Strait transport—annual northward transport through Bering Strait (Roach *et al.*, 1995; T. Weingartner, unpublished data);
- f. Global ocean temperature (NCDC, 2004);
- g. Bowhead whale baleen stable carbon isotope ratios ($\delta^{13}\text{C}$) (Schell, 2000);
- h. Steller sea lion abundance (NMML, 1994 and unpublished data; Trites and Larkin, 1996);
- i. Age-1 pollock abundance and age-3+ pollock biomass (J. Ianelli, unpublished data);
- j. Red-legged kittiwake productivity at St. George Island, Pribilof Islands (Dragoo *et al.*, 2001);
- k. Seabird abundance at the Pribilof Islands and Aleutian Islands (Dragoo *et al.*, 2001);
- l. Fur seal pup production on St. Paul Island, Pribilof Islands (York and Hartley, 1981; York and Kozloff, 1987; A. York, unpublished data);
- m. Fur seal growth rates (A. Trites, unpublished data); and
- n. Common murre and thick-billed murres relative abundance at Walrus Island, Pribilof Islands (Peterson and Fisher, 1955).

3.5.3 *Physical-physical relationships*

Despite considerable uncertainty about the relative importance of processes governing community structure and the abundances of individual species, e.g., top-down versus bottom-up interactions, much which transpires in ecosystems begins with physics. Francis *et al.* (1998) have presented a conceptual model of the pathways by which changes in atmospheric features can influence biota, and Schumacher *et al.* (2003) have modified this model for the Bering Sea (Fig. 3.3). Both of these models show that physics can influence an ecosystem in either top down or bottom up modes. For the North Pacific and eastern Bering Sea, much of the physics begins with the Aleutian Low pressure system that can be scaled by the North Pacific Index (NPI).

Winter sea ice extent and duration in the Bering Sea are related at the decadal scale to mean atmospheric forcing (Niebauer, 1998; Wyllie-Echeverria and Wooster, 1998; Stabeno *et al.*, 2001). Sea ice influences the ecosystem through at least two pathways. First, the presence of sea over the southeastern shelf in March (when ambient light is adequate to sustain primary production) can result in an early phytoplankton bloom (Stabeno *et al.*, 1998). An early bloom may result in a greater energy flow to the benthic community, whereas a bloom later in spring likely favors pelagic pathways (Walsh and McRoy, 1986; Hunt *et al.*, 2002a). The extent of sea ice is also vital to the subsequent development of the middle shelf cold pool that appears to influence the distribution of pollock and Arctic cod. The timing and magnitude of the summer retreat of sea ice is related to summer climate, which can be indexed by the NPI (Fig. 3.42). Recent results indicate that regions of the Bering Sea have shifted toward an earlier spring transition (Stabeno and Overland, 2001). The retreat and melting of sea ice also have ecosystem effects as they alter the availability and distribution of essential habitat for symphagic food webs and pagophilic marine mammals. In addition, they are related to energy flow through the ecosystem as noted above.

One of the hallmark features of the Bering Sea is the transport of water north through Bering Strait into the Chukchi Sea. This transport occurs because of differential atmospheric pressure across the western Arctic that tilts sea level down toward the north (Coachman *et al.*, 1975). Not surprisingly, then, variability in annual transport is related to variability in atmospheric pressure, as reflected again by the NPI (Fig. 3.43). A long-term decline in the mean strength of the Aleutian Low may explain the decline in transport in the past five decades. This, in turn, would be expected to have a large effect on production budgets across the northern Bering-Chukchi shelf, because nutrients and biota carried in the current transform the region into one of the most highly productive regions in the world (Springer *et al.*, 1989; Springer and McRoy, 1993).

Wind measured at St. Paul Island is related to the atmospheric pressure field (Fig. 3.44). The dramatic drop in the mean winds during the mid-1970s to late 1980s corresponded to a similar change in the NPI and to a pronounced increase in average global ocean temperature (Fig. 3.45).

St. Paul wind is also related to ocean temperature in the Bering Sea (Fig. 3.46). However, the correlation is only apparent within a given regime and changes from one regime to the next. That is, wind and SST were generally out of phase prior to 1977, were generally in phase between 1977 and 1989, and then generally out of phase again after 1989. Interannual fluctuations in wind and SST are not always proportional, indicating, not surprisingly, that other factors are important in determining magnitudes of the two variables.

3.5.4 Physical-biological relationships

Carbon stable isotope ratios ($\delta^{13}\text{C}$) of baleen from bowhead whales exhibit considerable interannual variation since the late 1940s, including a

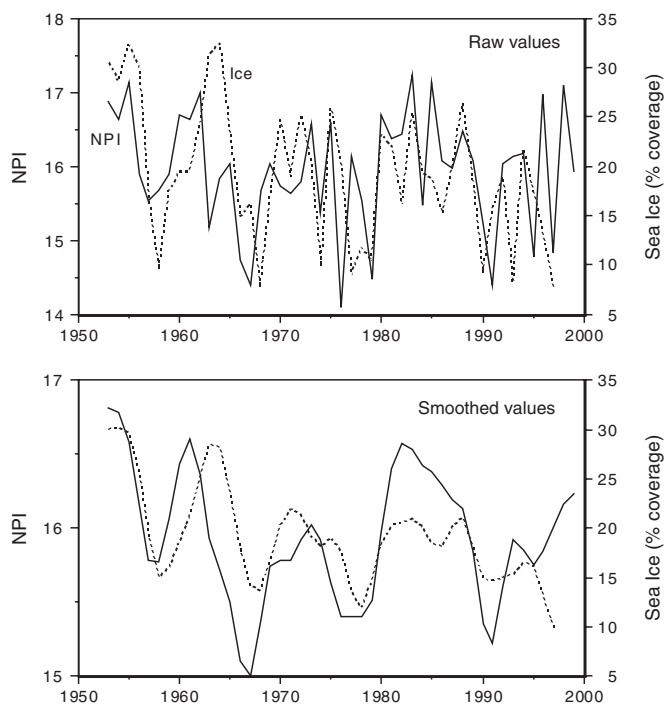


Figure 3.42: Summer extent of sea ice scaled as percent coverage of the Chukchi-Bering shelf (see Niebauer, 1998) and mean July–September NPI.

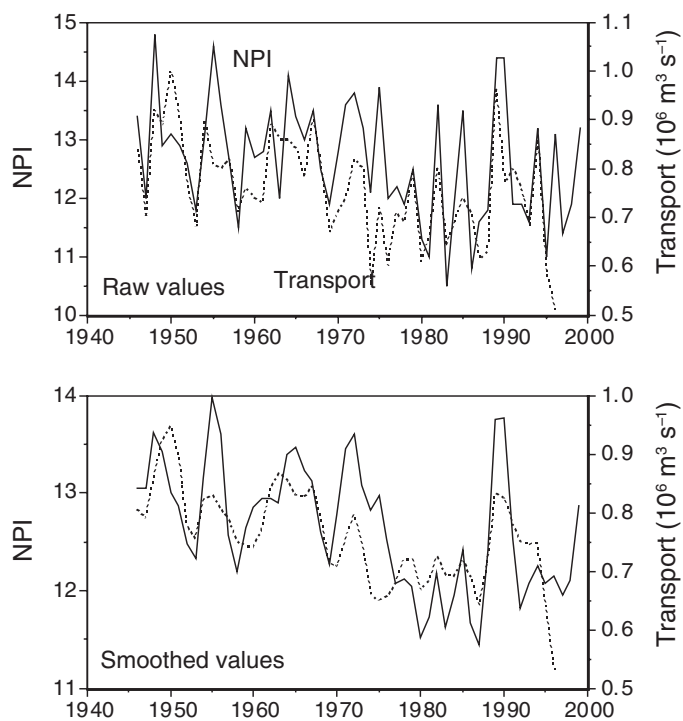


Figure 3.43: Annual northward transport through Bering Strait and the mean annual NPI.

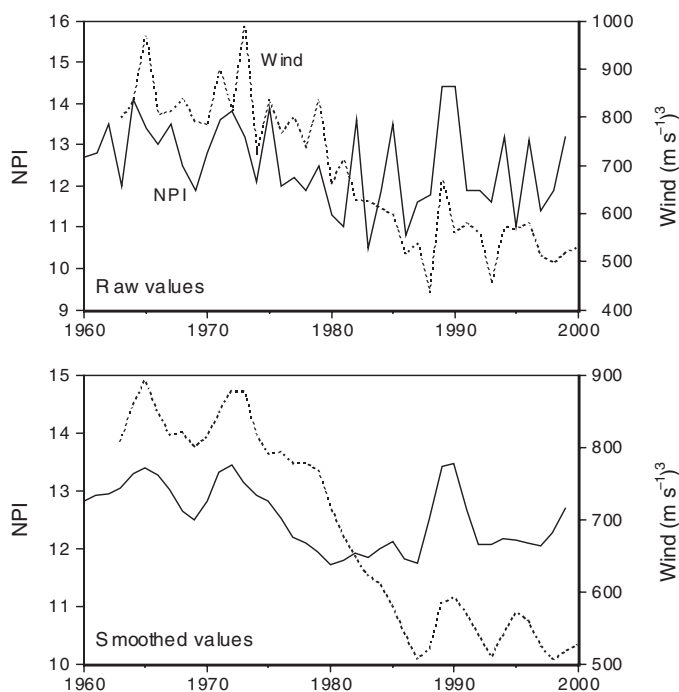


Figure 3.44: Mean annual wind at St. Paul and the NPI.

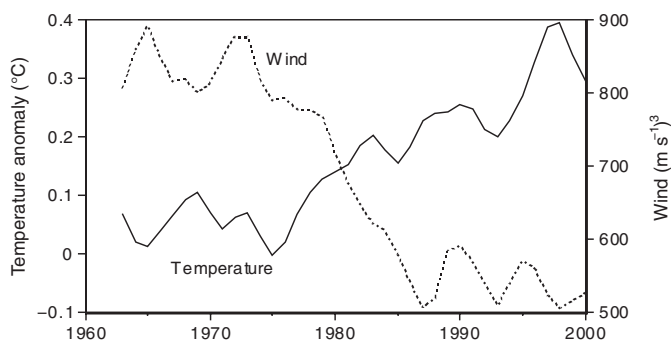


Figure 3.45: Mean annual wind at St. Paul and the global ocean temperature anomaly. Wind data smoothed.

pronounced overall shift that has been proposed as evidence of a decline in primary productivity of some 30% in the Bering Sea (Schell, 2000). The pattern in baleen $\delta^{13}\text{C}$ variability matches the pattern in winds over the same interval when baleen is lagged by 1 year to account for the ecological separation between whales and physical forcing (Fig. 3.47).

Wind also is correlated in a general way with sea lion abundance at several colonies in the Bering Sea range of the endangered western stock (Fig. 3.48). That is, sea lion abundance declined abruptly and precipitously at the same time that winds declined in a similar manner in the Bering Sea.

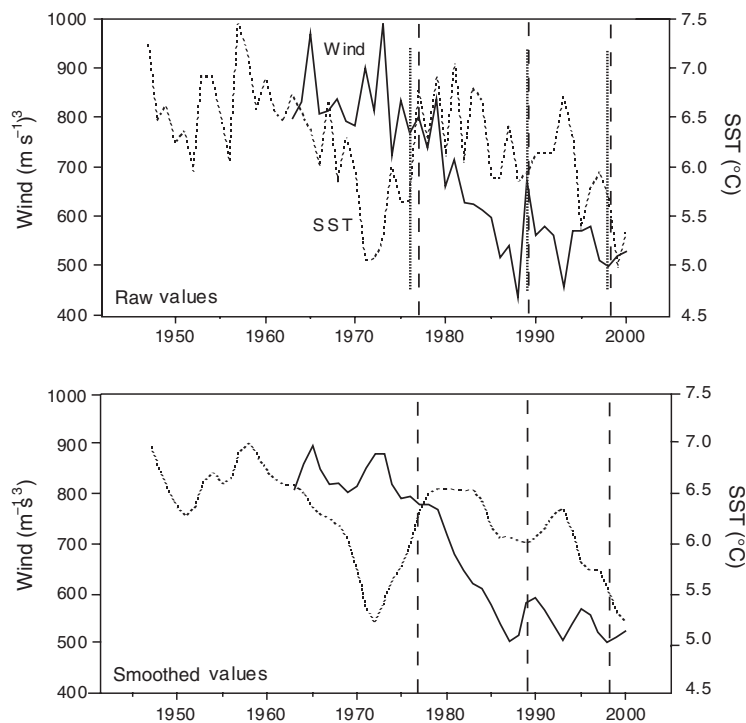


Figure 3.46: Mean annual wind at St. Paul and sea surface temperature (SST) in the eastern Bering Sea. Vertical lines show regime shifts in 1977, 1989, and 1998.

Sea surface temperature (SST) has varied since the late 1940s and is highly correlated with at least four biological variables in the Bering Sea: the abundance of age-1 pollock, the biomass of age-3+ pollock, and the productivity of black-legged and red-legged kittiwakes on the Pribilof Islands. However, except for age-3+ pollock biomass, the correlations exist only within regimes as defined by the PDO, where they are very strong but have alternating signs from regime to regime (Figs. 3.49, 3.50). Pollock biomass was positively correlated with spring SST for 25 years when SST is lagged by four years to account for separation between given SST years and the integrated effect expressed in the pollock age classes where most biomass resides (Fig. 3.51). Does the 4-year lag also suggest that most of the impact of SST (or for whatever it is surrogate) on pollock populations occurs between egg and age-0 fish? If so, one could infer many possible pathways from the correlation.

3.5.5 Biological-biological relationships

The most conspicuous correlations between biological variables in the Bering Sea are trends in abundances of piscivorous seabirds and fur seals on St. Paul Island and St. George Island (Pribilof Islands) and Bogoslof Island and Buldir Island in the Aleutian Islands (Table 3.3). Trends are uniformly negative on St. Paul and uniformly positive on Bogoslof and Buldir. On St. George, both species of kittiwake and fur seals are declining as at St.

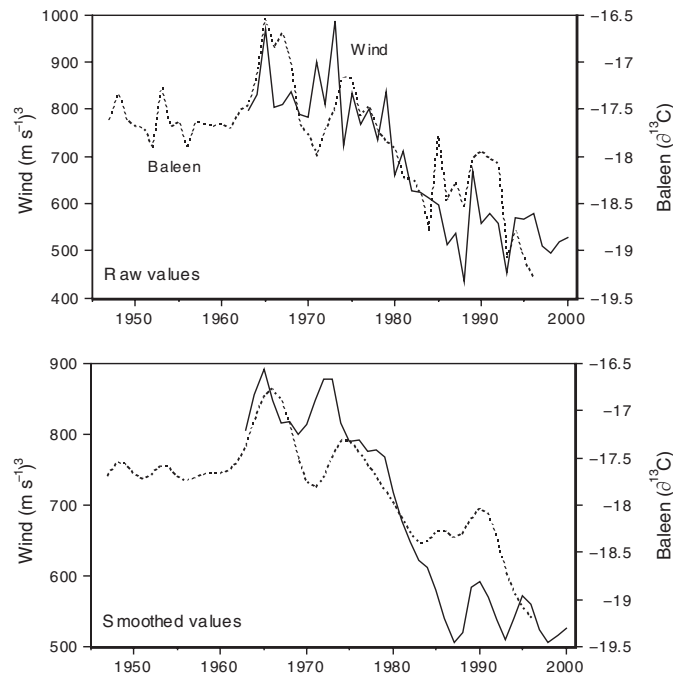


Figure 3.47: Bowhead whale baleen $\delta^{13}\text{C}$ (lagged 1 year) and mean annual wind at St. Paul.

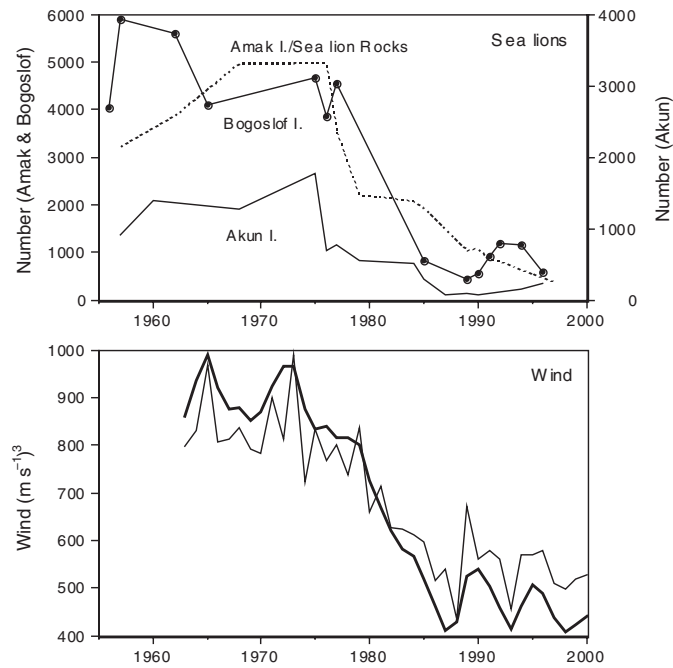


Figure 3.48: Sea lion abundance at rookeries in the eastern Aleutian Islands and wind at St. Paul Island. Heavy line in wind panel is the smoothed trend.

Table 3.3: Trends in populations of seabirds and fur seals at four locations in the Bering Sea.

Location	Species	Interval	n	% Change	r ²
St. Paul I. (<i>Pribilofs</i>)	Black-legged Kittiwake	1976–1999	12	–73	0.79
	Red-legged Kittiwake	1976–1999	12	–70	0.72
	Common Murre	1976–1999	12	–62	0.62
	Thick-billed Murre	1976–1999	12	–44	0.72
	Northern Fur Seal	1975–2000	24	–37	0.6
	Mean (SE)				–57 (7.1)
St. George I. (<i>Pribilofs</i>)	Black-legged Kittiwake	1976–1999	11	–47	0.45
	Red-legged Kittiwake	1976–1999	11	–52	0.63
	Common Murre	1976–1999	11	+55	0.56
	Thick-billed Murre	1976–1999	11	0	—
	Northern Fur Seal	1975–2000	24	–70	0.84
	Mean (SE)				–23 (23)
Bogoslof I. (<i>E Aleutians</i>)	Black-legged Kittiwake	1973–2000	3	+150	0.8
	Red-legged Kittiwake	1973–2000	3	+550	0.95
	Tufted Puffin	1973–2000	5	+130	0.98
	Northern Fur Seal	1980–1997	12	+2500	0.98
	Mean (SE)				+832 (564)
Buldir I. (<i>W Aleutians</i>)	Black-legged Kittiwake	1974–1996	10	+450	0.84
	Red-legged Kittiwake	1974–1996	10	+200	0.81
	Thick-billed Murre	1974–1996	10	+320	0.91
	Mean (SE)				+323 (72)

Paul. Thick-billed murres declined through the 1980s but have increased since then, whereas common murres increased throughout this period. All of these species are supported by a common suite of pelagic forage fishes and squids that includes prominently juvenile pollock at the Pribilof Islands.

There is an obvious similarity between the pattern of change in fur seal numbers at St. Paul—a prolonged decline punctuated by intervals of increase—and the pattern of change in $\delta^{13}\text{C}$ of bowhead whale baleen (Fig. 3.52). Were it not for the overriding effect of the female harvest on population stability in the period 1956–1968 (York and Hartley, 1981), the response of fur seals to an apparent environmental signal might have been stronger. That is, the increasing trend in numbers in the mid-1960s may have been attenuated by pressure on the population from excessive female harvests. Otherwise, fur seal pup production and bowhead baleen seem to be recording events that originate with fluctuations in climate and propagate through the system.

Additional evidence of the sensitivity of fur seals to ecosystem state is found in patterns of growth in body size over time. In the past century, fur seals on St. Paul experienced periods of faster and slower growth (A. Trites, unpublished data), with each period lasting about as long as a climate regime

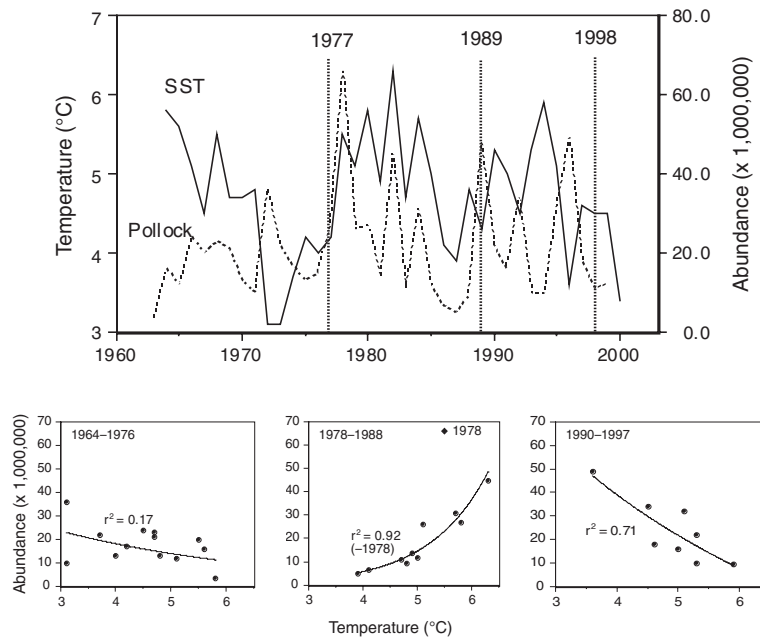


Figure 3.49: Abundance of age-1+ pollock and mean April–June sea surface temperature (SST: lagged 1 year) on the eastern Bering Sea shelf. The transition years (1977, 1989, and 1998) are not included in the regression, nor is 1978, as it was an extreme in recruitment.

(Fig. 3.53). Faster growth occurred in regimes when common murre apparently predominated at Walrus Island, a small island in the Pribilof group where murre once nested in immense numbers: murre were eliminated by foxes that gained access to the island over winter ice in the early 1970s. Conversely, slow growth occurred in regimes when thick-billed murre apparently predominated. The well-documented alternation between murre species on Walrus Island (Peterson and Fisher, 1955) also corresponded to shifts in climate regime (Springer, 1998).

Fur seals are ecologically more similar to common murre than to thick-billed murre. That is, fur seals and common murre are more dependent on pelagic prey, whereas thick-billed murre incorporate a significant amount of benthic prey in their diets (Springer, 1991; Sinclair *et al.*, 1994; Springer *et al.*, 1996). Therefore, the correspondence of positive responses of fur seals and common murre during periods when thick-billed murre apparently responded negatively is theoretically tractable.

3.5.6 Discussion

Functional relationships should typically have just one sign—positive or negative. Among the examples presented here, it is reasonable to believe that the common pattern of variability in meteorological conditions, as indexed by the NPI, and regional wind (observed at St. Paul) represents a positive functional forcing-response relationship over the Bering Sea. It further can be

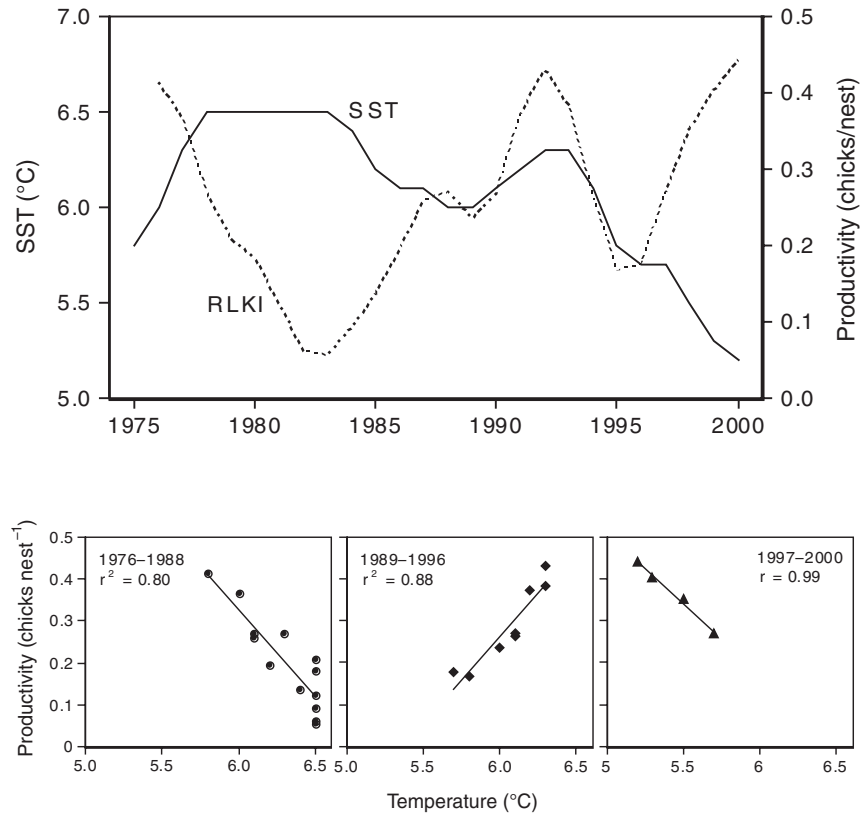


Figure 3.50: Red-legged kittiwake productivity at St. George Island and mean annual sea surface temperature (SST) in the eastern Bering Sea. Smoothed trends. A similar relationship exists for black-legged kittiwakes.

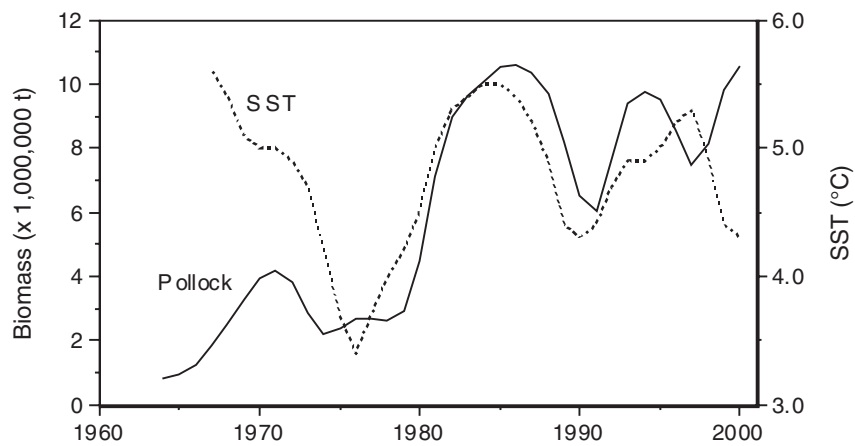


Figure 3.51: Biomass of age 3+ pollock in the eastern Bering Sea and mean April–June sea surface temperature (SST: lagged 4 years). Smoothed trends.

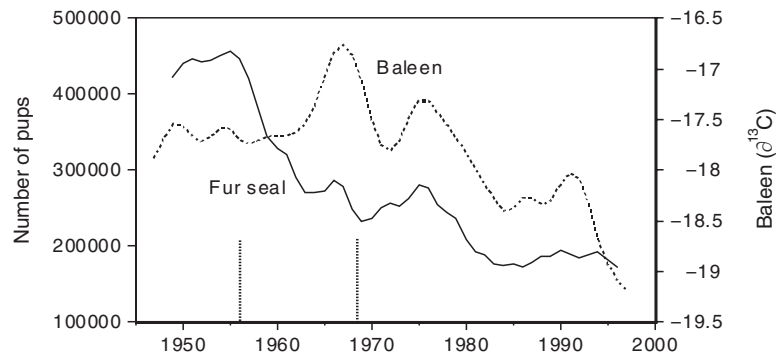


Figure 3.52: Fur seal pup production on St. Paul Island and isotope ratios in bowhead whale baleen. Smoothed trends. Dotted vertical lines at 1956 and 1968 mark interval of experimental female harvest.

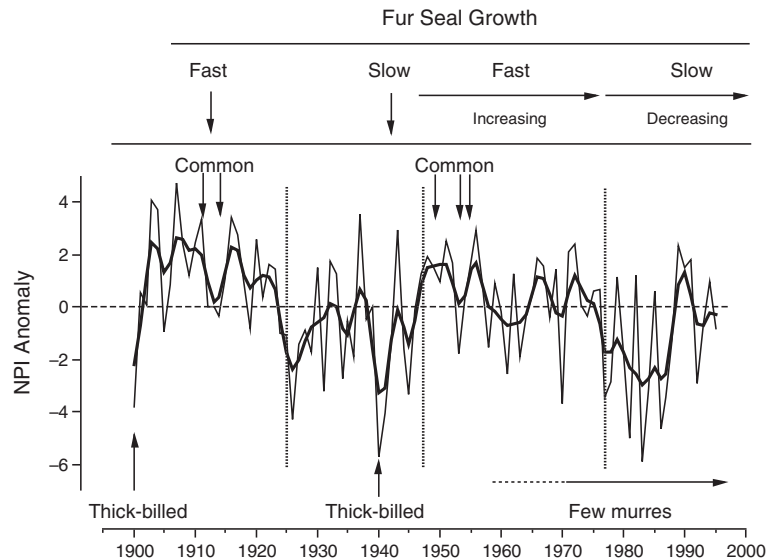


Figure 3.53: Fur seal growth at St. Paul Island and the relative abundance of common and thick-billed murre on Walrus Island. Dotted vertical lines mark regime shifts in 1925, 1947, and 1977 (Mantua *et al.*, 1997). Adapted from Springer (1998). Heavy line is smoothed trend.

argued that basin-scale meteorology and thus regional winds are influenced by changes in mean characteristics of the global-scale ocean-atmosphere interactions. Variability in the Aleutian Low and elements of physical oceanography, such as transport through Bering Strait and the summer retreat of sea ice in the Chukchi Sea, must represent positive functional forcing-response relationships across the atmosphere-ocean interface.

In contrast to these single sign relationships, the sign of the relationship between wind and SST in the Bering Sea has alternated between generally negative and generally positive depending upon regime. A negative relation-

ship might always be expected, since during much of the year wind mixes the upper layers of the ocean, countering effects of stratification and surface heating from the sun. Thus, it appears that while wind and SST in the Bering Sea may be adjacent ecosystem elements under certain conditions, under other conditions they may be separated by one or more other elements. Alternatively, it may be that under certain conditions, another element overrides the likely role of wind on SST, or perhaps wind and SST are responding independently to some other feature(s) of the physical system.

Similarly, it appears that the relationship between summer atmospheric forcing and summer retreat of sea ice was generally in phase during the 1950s through 1980s, but has been out of phase since. This may also represent the influence of another element dominating sea ice extent, e.g., an interaction with the Arctic Oscillation. Even during the long interval of positive correlation, the pattern of the NPI did not always exactly match that of summer sea ice extent, further implicating other factors in the full equation.

Biological variability should reflect physical variability. In the Bering Sea, the 50-y time series of $\delta^{13}\text{C}$ in bowhead whale baleen, an ostensible proxy of primary productivity, is well correlated with the NPI and wind. At least two processes could explain these relationships, both of which begin with meteorology. One is that baleen $\delta^{13}\text{C}$ is mediated by wind, which plays major roles in primary and secondary production by creating turbulence that affects mixed layer and nutrient dynamics and feeding efficiencies of planktonic organisms and micronekton. Wind is clearly important to primary production in the Bering Sea (Sambrotto and Goering, 1983; Sambrotto *et al.*, 1986). Another possibility is the effect of atmospheric pressure on transport across the northern Bering-Chukchi shelf, where bowheads obtain the bulk of their annual nutrition (Lee, 2000). Variability in northward transport leads to variability in primary production and the rate of advective supply of zooplankton (Springer *et al.*, 1989; Springer and McRoy, 1993) that might be reflected in the $\delta^{13}\text{C}$ of bowhead baleen.

Members of two contrasting food webs—deep basin pelagic (red-legged kittiwakes) and continental shelf pelagic (black-legged kittiwakes and juvenile pollock)—are extremely influenced by whatever it is that SST indexes. The most intriguing aspect of this is that the sign of the relationship between SST and juvenile pollock and kittiwakes changes between regimes, just as it does with SST and wind. These correlations probably should not be considered functional relationships in the strict sense, since there are potentially several ecological levels that are a bridge between them. It is more likely that SST serves as a proxy for one or more other features of the ecosystem (that change in fundamental ways between regimes relative to SST) that are responsible for the variability in abundance and productivity of the birds and pollock. Still, in a predictive sense, SST is a powerful index provided one knows when a regime shifts.

SST was strongly predictive of age-3+ pollock biomass on the eastern shelf for over two decades, and the sign was always positive regardless of regime, i.e., it did not change after 1989. The significance of the apparently negative relationship in the 1960s is unclear because of the uncertain effect of the rapidly developing commercial fishery on the relatively small virgin

stock. However, the relationship may have again become negative since the mid 1990s. The reason for differences between trends in abundance of juvenile pollock and biomass of adult pollock in relation to trends in SST and regime are not readily apparent.

Just as signs of several relationships change over time as regimes shift, signs of trends in the abundance of seabirds and fur seals vary between habitats within regimes (Pribilof and continental shelf regions vs. Bogoslof and oceanic regions), and ratios of congeneric murre on Walrus Island and growth rates of fur seals vary within habitat between regimes. In the case of fur seal growth rates, the effect is apparently manifested in the Gulf of Alaska as the seals return to the Bering Sea in spring (Trites and Bigg, 1996). The geographic distance between locations where fur seal annual growth is determined and where various parameters are measured in the Bering and Chukchi seas illustrates the spatial scale of influence of an overriding physical forcing factor, which is most likely the Aleutian Low pressure system.

In aggregate, there are numerous correlations among a variety of ecosystem components from fundamental meteorological forcing (the Aleutian Low pressure system) to primary physical response factors (winds, currents, and SST), to secondary physical and biological response parameters (sea ice extent, surrogate primary productivity, and the abundances and productivity of planktivorous fish and piscivorous marine birds and mammals). None of the physical-physical or physical-biological correlations proves cause and effect, but a considerable weight of evidence indicates that climate and climate change are extremely important in regulating production regimes in the Bering Sea. Routes through the ecosystem taken by these supposed chains of cause and effect are conjectural still, but several plausible scenarios come to mind. For example, fluctuating atmospheric pressure affects winds and currents that alter sea ice extent and primary productivity (as indexed by isotope ratios in bowhead baleen). Variable food web productivity, arising from the effect of wind on primary productivity or on transfer efficiencies at low trophic levels, would be important at high trophic levels and could be expressed in fur seal growth, sea lion abundance, and alternating dominance of one or the other species of murre at Walrus Island. The biological-biological correlations presented here demonstrate common responses to signals propagating through the ecosystem, rather than functional cause and effect relationships.

The emphasis of most recent analyses of effects of climate change has been on comparisons of mean parameter values or slopes, e.g., relatively higher or lower atmospheric pressure or increasing or decreasing abundance of a species, between regimes. That is, a given parameter in a given regime is reduced to a single value or sign (positive or negative). The data sets presented here show, in addition, a considerable amount of interannual coherence within and across regimes, supporting the notion that several may involve functional forcing-response relationships. Still, none of the supposed independent forcing variables, e.g., the summer atmospheric pressure field, explains all of the variability in the dependent response variables, e.g., summer sea ice retreat. In all cases, multiple forcing factors are at play.

Many things can affect any parameter's value within a given year, such

as measurement error and random events in the ecosystem. These can be important, for example as when a severe summer storm with high wind and heavy rain blows and washes away seabird chicks from nests, radically lowering productivity from a level that otherwise could have been supported by the system. Such random events are commonly unrelated to fundamental trends in forcing factors and can blur the picture of fundamental form. Thus, for example, the fundamental waveform of the longer-term oscillation of summer NPI and sea ice, irrespective of regimes, can be more clearly seen when the data are smoothed as in Fig. 3.42.

The relationships presented here implicate bottom-up control of various processes linking the Aleutian Low to seabirds and marine mammals. However, this should not be construed to mean that all demographic changes at high trophic levels represent responses to changing food web production and the availability of prey to responding species. In the case of fur seals, for example, variable growth rates likely do reflect changing prey abundance: declining pup production could be caused by declining carrying capacity affecting the ability of females to produce pups, or by the loss of females brought on by starvation (a prey issue) or by predation. That species are sensitive to fluctuations in productivity of supporting food webs is not surprising, nor is it surprising that they are sensitive to changes in predation that might result from, or be exacerbated by, the same bottom-up pathways.

The tendency for the Bering Sea ecosystem to behave in particular ways depending upon seasonal, annual, and mean decadal physical forcing also is not surprising and is evident in numerous time series. What is less intuitive are explanations of the changing signs of relationships between elements of the ecosystem from one climate regime to another, such as between wind and SST and between SST and the productivity of pollock and kittiwakes. In all of these examples, other ecosystem elements must be involved in the actual functional relationships. Nevertheless, it is puzzling how the signs of these relationships change between positive and negative as climate regimes change. Whatever the explanation may prove to be, in the meantime it is important to be mindful of the potential for inconstant polarity, relative not only to time but to other ecosystem attributes. It is especially important when attempting to develop ways to predict an outcome, such as pollock production, based on one or a combination of indices. Ecosystems apparently do have memory, or inertia, but the path taken by ecosystem processes is steered in different directions under different climate situations, thus changing outcomes in ways that are surprising and unpredictable.

3.6 Summary

3.6.1 *Progress accomplished in the development of indices*

The goal of the IWG was to identify potential single- or multi-parameter constructs or indices that lead to development of survival indices for pollock in the early life history stages, and that this information would provide input to the National Marine Fisheries Service (NMFS) in stock assessment of juvenile pollock for use by fisheries scientists at the Alaska Fisheries Sci-

ence Center (AFSC)/NMFS. Toward attaining this goal, extensive progress was made in the development of indices (Table 3.1). The conceptual switch model (Fig. 3.2) developed during SEBSCC Phase I was expanded to include timing of prey production (that, in turn, is related to the presence of sea ice) for first feeding survival, thereby becoming a more complete mirror of the natural ecosystem. The development of an index of mixed-layer characteristics (see Section 3.3.1) provided input to the development of the Oscillating Control Hypothesis (Hunt *et al.*, 2002a). This index of the physical environment, however, does not account for the observed variability in age-1 pollock year-class strength. An index of wind turbulence versus larval feeding success was developed (see Section 3.3.2). The project ended, however, prior to developing a time history of this index to compare with recruitment estimates. For the first time in Bering Sea studies, variations in net short wave radiation were considered as an index (Section 3.3.3). The importance of such variations is only now being recognized world wide as a crucial aspect of time varying forcing for climate and ecosystem change (e.g., Foukal, 2003). A new index of sea ice was developed that led to new insight regarding changes in timing of spring in the region (Stabeno and Overland, 2001). The compilation of water temperature data from the annual trawl survey (Section 3.3.5) now permits further development of indices related to thermal conditions. The model simulations (Section 3.3.6) show that surface wind drift is not sufficient for simulating pollock egg and larval drift. The use of NEPROMS to generate annual drift trajectories requires further funding. A technique was developed that combines early life history transport and predation by adult pollock (Section 3.4). This technique has been transferred to NMFS and is an operational element of the annual stock assessment. Further application of this technique awaits the use of more realistic transport simulations. An examination of a large set of biological and physical indices showed that potential relationships could change sign with regime shifts (Section 3.5), providing a clear warning that a simple linear solution does not exist. The IWG concluded its deliberations by generating a set of indices-related topics that need to be examined (Section 3.6.2), and tools that need to be developed (Section 3.6.3).

The vast quantity of information collected during SEBSCC has led to new understanding and hypotheses of how the southeastern Bering Sea ecosystem functions. This information is providing input to the National Marine Fisheries Service's stock assessment of juvenile pollock. At present, the pathway to providing input is through a "grass-roots" approach; the integrative research method employed during SEBSCC included fisheries scientists at the Alaska Fisheries Science Center whose tasks are directed toward status of stocks. Some of these scientists were SEBSCC Principal Investigators and/or members of the Indices and Pribilof Island Working Groups. They were the ones who helped to develop both indices of potential survival of early life histories of pollock and a formal technique to use such indices in stock assessment models. The quantitative use of annual metrics of the physical and biological environment is the next logical step in the progression toward improved forecasts of age-1 recruitment. As the management of fisheries matures toward an ecosystem-based approach, the integrated biophysical

knowledge attained by fisheries scientists during SEBSCC will prove to be an invaluable foundation.

3.6.2 Further development of indices

Based on the results from four workshops, the members of the IWG believe that the following are logical next steps in the development and refinement of indices. These suggestions have been grouped into two categories: indices that are related to changes in strength of a given year class of pollock and an index that may provide guidance regarding interpretation of the annual stock assessment from trawl results. While this later category was not in the original charge to the IWG or a focus of SEBSCC, it is a vital component of fishery management.

Indices for Estimating Recruitment of Age-1 Pollock

- Continue comparisons with other model simulations and observations to provide verification of the Bering Sea model (NEPRIMS).
- Develop a wind index of nutrient supply to the shelf from Bering Canyon.
- Develop a user interface and/or other techniques so the NEPRIMS is more accessible as a tool.
- Examine various indices versus occurrence of northwest and southeast centers of the adult pollock population.
- Extract an index of zooplankton abundance from ECOSYM.
- Develop a history of the time/space occurrence of the roe fishery to help define time/space limits for pollock eggs as initial points for trajectory simulations.
- Develop a similar product for spawning that occurs near Bogoslof Island.
- Use temperature observations from annual trawl surveys to develop an index of the presence of the cold pool and the locations of the inner and middle fronts (i.e., the boundaries of the middle shelf domain) in given years.
- Use temperature observations to create annual distributions of temperature that, in turn, can be used to simulate zooplankton production.

An Index for Interpretation of the Annual Stock Assessment

- Examine the influence of changes in the physical environment (e.g., water temperature, location of fronts) on preferred habitat for pollock, and how variations in these features affect estimates from trawl results.

3.6.3 Concluding remarks

Simulations from the NEPROMS are vital to further development of indices for the Bering Sea ecosystem. Continued verification of simulations (both velocity and water property fields) from this model and improvements to its physics (i.e., inclusion of northward flow through Bering Strait) has the highest priority. The development of a wind-related index of potential nutrient transport shoreward along the Alaskan Peninsula from Bering Canyon can be accomplished independently of the NEPROMS. Comparisons between OSCURS and NEPROMS (Section 3.3.6.2) demonstrate that dynamics other than direct wind forcing are critical throughout most of the water column. Thus, model simulations of the integrated flux through appropriate cross sections would provide a more complete measure of nutrient flux. Model simulations can also be used to establish temperature distributions for a time perhaps more appropriate for making estimates of zooplankton production (May–June) than the July–August data from the trawl survey.

Given the overall importance of NEPROMS simulations to help us understand physical mechanisms and their impact on biota, the utility of this model must be improved. In addition, as techniques and understanding of dynamics improve, this model should be updated to include as much physics as is possible. How can the NEPROMS become a user-friendlier tool? This may take the form of having made and stored average (e.g., daily) water property and velocity field distributions. If these simulations were then coupled with an interactive interface that would allow a naive user to choose particular simulations and then access them in selected time and space domains, then the NEPROMS would permit far more research into indices and questions of how the ecosystem functions than is possible today.

Part 4—Pribilof Islands: A Microcosm for the Southeast Bering Sea

RESULTS FROM THE PRIBILOFS WORKING GROUP ON THE ECOSYSTEM OF THE PRIBILOF ISLANDS WITH RESPECT TO HABITAT FOR, AND SURVIVAL OF, WALLEYE POLLOCK

Principal Author: Gordie Swartzman

With participation and contributions from:

Ric Brodeur, Troy Buckley, Lorenzo Ciannelli, Ken Coyle, George Hunt, Jim Ianelli, Allen Macklin, Jeff Napp, Rolf Ream, Bruce Robson, Sigrid Salo, Beth Sinclair, Phyllis Stabeno, Gordie Swartzman, Lucy Vlietstra, and Andreas Winter

4.1 Overview of the Pribilof Island Ecosystem

The Pribilof Island ecosystem has been a major focus for the Southeast Bering Sea Carrying Capacity Program (SEBSCC) and the Bering Sea Fisheries-Oceanography Coordinated Investigations (BS FOCI) projects sponsored by NOAA Coastal Ocean Program. The region was chosen, in part, because it is thought to be a major nursery area for age-0 walleye pollock (*Theragra chalcogramma*), the target species for these projects. Early hydroacoustic studies suggested higher than background abundance of juvenile pollock (Traynor and Smith, 1996). Satellite-tracked drifters released in a pollock spawning area (Unimak Island) slowly drifted northwest toward the Pribilof Islands, arriving in late summer and fall (Stabeno *et al.*, 1999b), suggesting that young-of-the-year pollock spawned in the southeastern Bering Sea might be transported preferentially to the Pribilofs.

The oceanographic region around the Pribilofs contains, in miniature, all of the domains (coastal, inner front, middle shelf, middle transition zone, outer shelf, outer front, slope, and basin; Section 2.1.3) present in the greater southeastern Bering Sea. For this reason, scientific focus on the Pribilofs should yield understanding of dynamics and processes affecting the greater region. The Pribilofs, then, are a microcosm and natural laboratory for investigation of the southeastern Bering Sea ecosystem. Under the auspices of BS FOCI and SEBSCC, the area has undergone extensive survey during late summer for 6 years, from 1994 through 1999. Acoustic surveys, with concomitant physical and biological sampling, occurred along four transects (Fig. 4.1). These transects were chosen to be representative of different habitats around the Pribilof Islands.

This report section is a synthesis of our best understanding at present of the relationship between juvenile walleye pollock of the Pribilofs and juvenile pollock in the remainder of the southeastern Bering Sea. Such an index will prove valuable in helping to forecast future year classes in the important pollock fishery. Work leading to this report was discussed at a series of three workshops by a working group consisting of the editor, participants, and contributors to this report listed on the preceding page. The first workshop was held at the Pacific Marine Environmental Laboratory (PMEL) in Seattle,

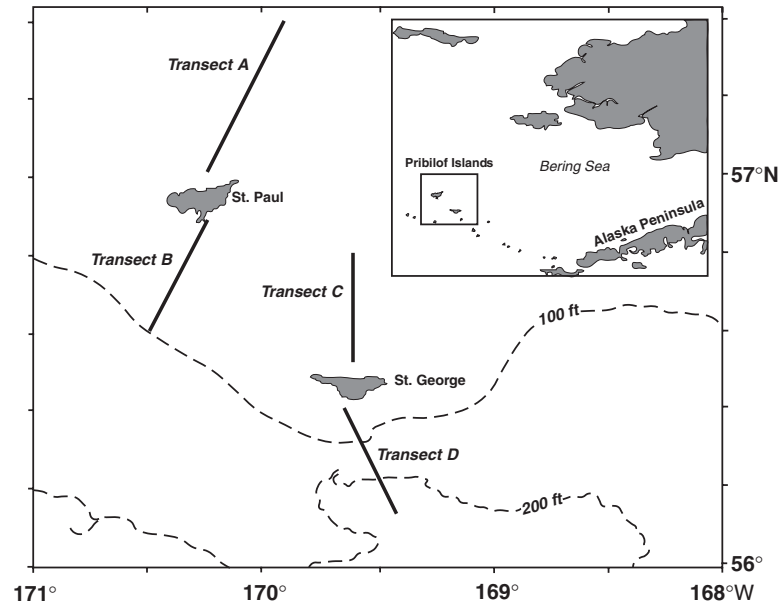


Figure 4.1: Pribilof Island study region showing transects A-D repeatedly sampled both day and night during September 1994–1999.

Washington, 20–21 September 2001, the second in Victoria, BC, Canada, on 12 October 2001, and the third at PMEL on 22–23 April 2002.

4.2 Working Group Products

The working group focused on a synthesis of available information concerning the Pribilof Island ecosystem. To this end, we developed a web site containing a table of links to available data sets and to relevant supporting and summarizing literature. The web site link is http://www.pmel.noaa.gov/sebscc/PWG_data_matrix.html.

Issues addressed by the working group and used to structure this section of the report are:

1. How large an area is the Pribilof region? How much area around the islands is necessary to support local populations of seabirds and mammals?
2. How much transport is there to this area from major pollock spawning regions?
3. How does the abundance of juvenile pollock near the Pribilof Islands compare with abundance along the Bering Sea shelf?
4. Is there a relationship between the abundance of age-0 pollock near the Pribilof Islands and the diet breadth, feeding energetics, survival, or recruitment of apex predators (seabirds, fish, and mammals)?

5. How important is predation to pollock abundance near the Pribilof Islands?

4.2.1 *How large an area is the Pribilof region?*

The Pribilof Island region is oceanographically complex, with several habitats in a small area. Large numbers of species inhabit the region, at least for part of the year. To define a region of influence of the Pribilof Islands, we used a biological assessment that relates the species composition at different distances from the islands with the energetic balances of those biota in circular areas, centered on the islands, defined by radii equal to the different distances. The working region is then the one with the greatest self-containment; i.e., having the largest percentage of the energetics demand satisfied within the region of interest. An energy balance model, ECOPATH (Polovina, 1984; Ciannelli, 2002), was used to compute the percentage of annual energetic demand for each species or functional group in the model satisfied by feeding within the region around the Pribilofs. ECOPATH is a linear, non-dynamic compartment model framework in which flow rates between the compartments are obtained as parameter values by searching the literature and available data for diet compositions for the groups in each compartment. Biomass estimates for each compartment are made by multiplying population estimates by average weight. There are 41 compartments in the Pribilof Island region model, including phytoplankton, small and large jellyfish, fur seals, crabs, small and large flatfish, common and thick-billed murre, juvenile gadids (over 95% of which are age-0 pollock) and macrozooplankton. The model produces a steady-state computation of how much of each prey item is eaten by each predator. The ratio of output (amount removed by predation or fishing) to input (amount eaten or synthesized), the ecological efficiency, is computed for each compartment. An ecological efficiency greater than 1.0 implies that some source of input outside the defined area must be available to maintain energetic balance. The model was run for circular regions around the Pribilof Islands with radii of 50, 100, and 150 nautical miles (nm; 1 nm = 1.85 km). The resulting computations suggested that at a radius of 100 nm, the ecological efficiency is closest to 1.0 for the most groups, implying that this region is the most energetically self contained. While we recognize that there is significant migration into and out of the Pribilof region, we decided to define the region as that area within 100 nm of the midpoint between the Pribilof Islands. We use the 100-nm boundary loosely, since a circle of radius this size around the Pribilof Islands (Fig. 4.1) encloses basin, shelf, and frontal habitats, and the basin habit is quite different from the shelf and frontal habitats. Thus, the Pribilof habitat should not extend as far into the basin region. A 100-nm radius region is supported by oceanographic and phytoplankton production considerations (Flint *et al.*, 2002), which suggest that the outer front regions around the Pribilofs occur at about this distance. Also, this is close to the dimensions of the expanded, slow circulation that frequently appears around the Pribilof Islands during the summer (Stabeno *et al.*, 1999b). As such, we will use this region in considerations concerning biomass, production, and distribution

of biota and in comparing these quantities to other areas (i.e., how relatively productive is the Pribilof Island region compared to other areas of the eastern Bering Sea, and how similar is the standing stock of dominant species?).

4.2.2 How much transport is there to this area from major pollock spawning regions?

The Pribilof Islands are not permanent habitat for young-of-the-year pollock. Larvae likely are transported to the region from pollock spawning grounds to the south. These pollock are transients, and probably benefit from higher food density, local water circulation patterns that concentrate food, and lower predation. Later in their juvenile stage, they migrate to the northwest.

An indication of how many pollock larvae ended up near the Pribilof Islands is available for most years from 1994–2000 based on drifters released near the two major known pollock spawning areas in the eastern Bering Sea—Bogoslof Island and the Unimak Pass area (Napp *et al.*, 2000). Plots of the paths of these drifters are available online at <http://www.pmel.noaa.gov/foci/visualizations/drifter>. There is also a third large spawning area near the mouth of the Pribilof Canyon, smaller than the other two (Napp *et al.*, 2000). Most drifters were drogued at 45-m depth during April or early May. This depth appears to be somewhat deeper than the average depth of pollock larvae (Napp *et al.*, 2000 report an April 1992 study showing highest aggregations of pollock larvae at a depth of 30 m with few larvae below 50 m). A significant fraction of these eventually drifted near the Pribilofs and some were entrained in currents around the islands. Stabeno (NOAA/PMEL, personal communication) estimated, for the years 1994–2000, the relative fraction of drifters that passed the Pribilof Islands. The classes were low (less than 20%), medium (20–40%) and high (>40%). All the years were classified as medium, except 1995 and 2000 (high) and 1998 (no data). In all cases, drifters released in April or May did not arrive near the Pribilofs until late August or September, at the earliest. Since the Unimak Pass spawning generally occurs in April (Napp *et al.*, 2000), it is unlikely that the age-0 pollock observed in the Pribilof region in June and July (see above) came from Unimak Pass. Bogoslof Island spawning is generally earlier (March), and thus, it is feasible, if drifter data are representative of larval drift, that larvae could be advected toward the Pribilofs and arrive there in June or July. However, this and other evidence on the distribution of adult pollock to be presented later in this section (Fig. 4.6 and Section 4.2.5), suggest that the primary source for pollock observed in June and July may be the Pribilof Canyon and other smaller spawning areas closer to the Pribilof Islands. There may also be some genetic differences between pollock found northwest and southeast of the Pribilof Islands (Kevin Bailey, NOAA/AFSC, personal communication), which may make possible identification of the age-0 pollock spawning location.

4.2.3 *How does the abundance of juvenile pollock near the Pribilof Islands compare with abundance along the Bering Sea Shelf?*

The region around the Pribilof Islands has been suggested as a region of unusually high production in the eastern Bering Sea, and it has been termed a green belt (Springer *et al.*, 1996a). This hypothesis is supported by evidence from Sambrotto *et al.* (1986) and Flint *et al.* (2002). These studies showed higher primary and secondary production in the Pribilof Island frontal regions. Flint *et al.* (2002) argue that current and mixing processes around fronts bring higher nutrient concentrations to the euphotic zone, enhancing production.

This section relates the importance of the Pribilof Island stock to the total pollock abundance, and to how typical year-to-year changes in age-0 pollock abundance in the Pribilof region compare to changes in other areas along the Bering Sea shelf. To establish a baseline for comparison with the abundance of pollock in the Pribilof Island region, we found data sets that either spanned the Pribilof Islands and neighboring areas or used similar sampling methods to assess pollock abundance in other shelf areas of the Bering Sea. The relative abundance of age-0 pollock in the Pribilof Island area to other shelf and front areas throughout the eastern Bering Sea was considered using:

1. Net samples for age-0 pollock taken at selected stations both near the Pribilof Islands and beyond during July aboard the Japanese T/S *Oshoro Maru* (Jeff Napp);
2. Net trawls for age-0 pollock taken aboard the R/V *Miller Freeman* during MACE acoustic surveys (Jim Ianelli and Neil Williamson);
3. Comparison of acoustic abundance near the Pribilof Islands with abundance on transects in the Inner Front, the Bering Sea shelf, and shelf-break region running along the Alaska continental shelf (Andreas Winter and Ken Coyle).

Net samples from *Oshoro Maru*. Surveys of the southeastern Bering Sea shelf for juvenile (age-0) walleye pollock have been conducted in collaboration with scientists from the Faculty of Fisheries, Hokkaido University, Japan every summer since 1995 (1995–2001), using the Fisheries Training Vessel *Oshoro Maru*. The survey grid is fixed (approximately 30 nm between stations), although not all stations are sampled every year. The time of the cruise has not varied from late July. Double oblique tows of a rectangular, midwater, framed trawl (5-m² mount opening, 3 × 2-mm mesh in the body of the net, and 1-mm mesh in the cod end) were used each year. A flow meter mounted in the mouth of the net recorded distance traveled. A “rough count” of age-0 pollock was taken immediately after the tow using either a sub-sample or the entire catch. The catch was then preserved and sent to Poland for processing at the Polish Plankton Sorting and Identification Center. Rough counts were standardized to 100-m² area surveyed.

To test the hypothesis that catches of juvenile pollock were higher around the Pribilof Islands than over other parts of the shelf, the survey area was

divided into two strata (Fig. 4.2). The size of the Pribilof stratum took into account recent research (Ciannelli, 2002) that concluded that the influence of the Pribilof Islands extended 100 nm around the islands (excluding the basin region south of the Pribilof Islands). A fourth-root transformation was applied to the age-0 pollock rough count data to eliminate heteroscedasticity. We then used an ANOVA to test for differences among years, between the two strata, and interactions between strata and years. There were no significant interactions between year and stratum ($P = 0.101$), but there were significant differences among years ($P = 0.011$), and between the two strata ($P \ll 0.001$), with the mean value for abundance around the Pribilof Islands significantly higher than abundance in the other stratum.

The ratio of abundance within the Pribilof region to that outside it, which can be used as a rough index of the relative abundance, by year for juvenile pollock in the Pribilof region to that in the surrounding eastern Bering Sea shelf region, is given in Table 4.1. On average, the ratio of per-area abundance in the Pribilof vs. surrounding area was 2.95.

Net trawl data from the NMFS MACE survey group. Initial analysis of oblique tow Methot data collected during summer MACE surveys in 1982, 1984, and 1985 (Traynor and Smith, 1996) provided estimates of age-0 pollock abundance in the eastern Bering Sea. Additional Methot samples taken during summer 1999 were summarized by Honkalehto *et al.* (2002). All these results show the Pribilof region to be highly variable in age-0 pollock in July or late June, with abundance of age-0 pollock in 1984 and 1985 being higher than other regions, while in 1999 they were lower. Additional data, not yet analyzed, are available from surveys in 1996, 1997, and 2000 using Methot trawls and in earlier years (e.g., 1991, 1994, and others) using Marinovich and/or Methot trawls.

Traynor and Smith (1996) wrote that the center of abundance (based on surveys in 1982, 1984, and 1985) was near the Pribilof Islands, but there were also other areas of high abundance (Figs. 4.3 and 4.4). However, these distributions may not be consistent from one year to the next. For example, Honkalehto *et al.* (2002) showed that from limited 1999 sampling, the abundance of age-0 gadids (presumably primarily pollock) were distributed in areas generally outside of the Pribilof Islands (Fig. 4.5). Note that this appears somewhat inconsistent with the 1999 age-0 abundance presented in Table 4.1. However, the two samples were taken at different times of the summer, and, considering the likely transport of age-0 pollock from spawning areas near Bogoslof Island and Unimak Pass, high densities along the shelf may end up by September near the Pribilof Islands. Continued sampling of age-0 pollock in the greater shelf region over the July–September

Table 4.1: Ratio of abundance per 10 m² for the Pribilof Region to that in the surrounding area based on *Oshoro Maru* surveys from 1995–2002.

Year	1995	1996	1997	1998	1999	2000	2001	2002
Abundance ratio	0.808	5.168	1.035	7.975	3.782	1.487	1.281	2.035

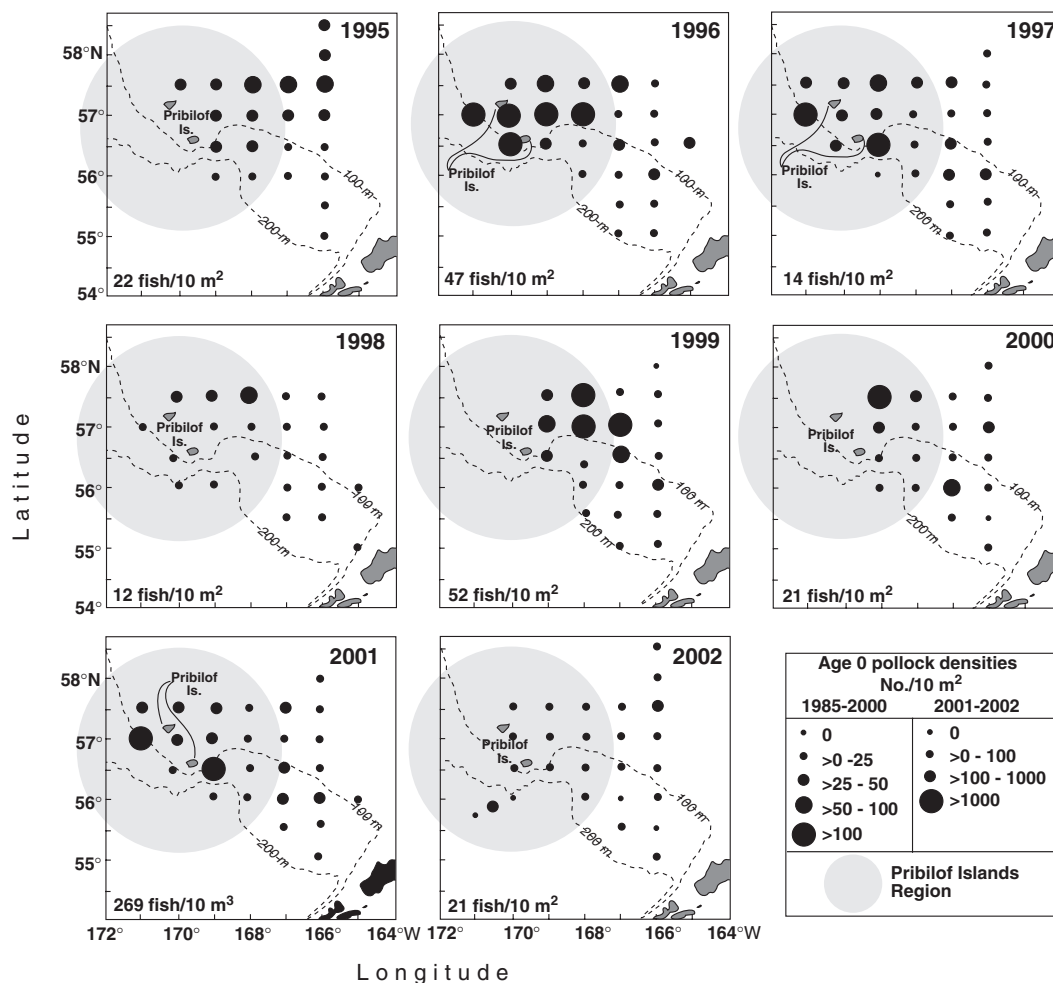


Figure 4.2: Distribution of age-0 pollock from net hauls taken in July 1995–2001 from the T/S *Oshoro Maru*.

period would help provide a better indication of interannual spatial variability, as well as within-season temporal variability—apparently essential for constructing an accurate picture of the factors that contribute to pollock year-class success in their first year of life. The timing of the samples is important since there now appears to be some evidence of different spatial distributions of adult pollock in years leading to strong year-classes (Buckley *et al.*, 2001; Fig. 4.5), which may influence the dominance of different spawning habitats, which in turn would affect the timing of arrival of different cohorts of age-0 pollock to the Pribilof region. That there is significant change in the spatial distribution of age-0 pollock over the summer is supported by a comparison of the distribution of age-0 pollock in early July 1999 from the MACE survey (Fig. 4.5) with the same distribution from the *Oshoro Maru* in late July 1999 (Fig. 4.2). Clearly, more pollock were close to the Pribilof Islands later in the summer. The pattern may have been different, however, in 1984 and 1985, when age-0 pollock abundance was highest near the Pribilof Islands in early July (Fig. 4.3), and in 1987, when

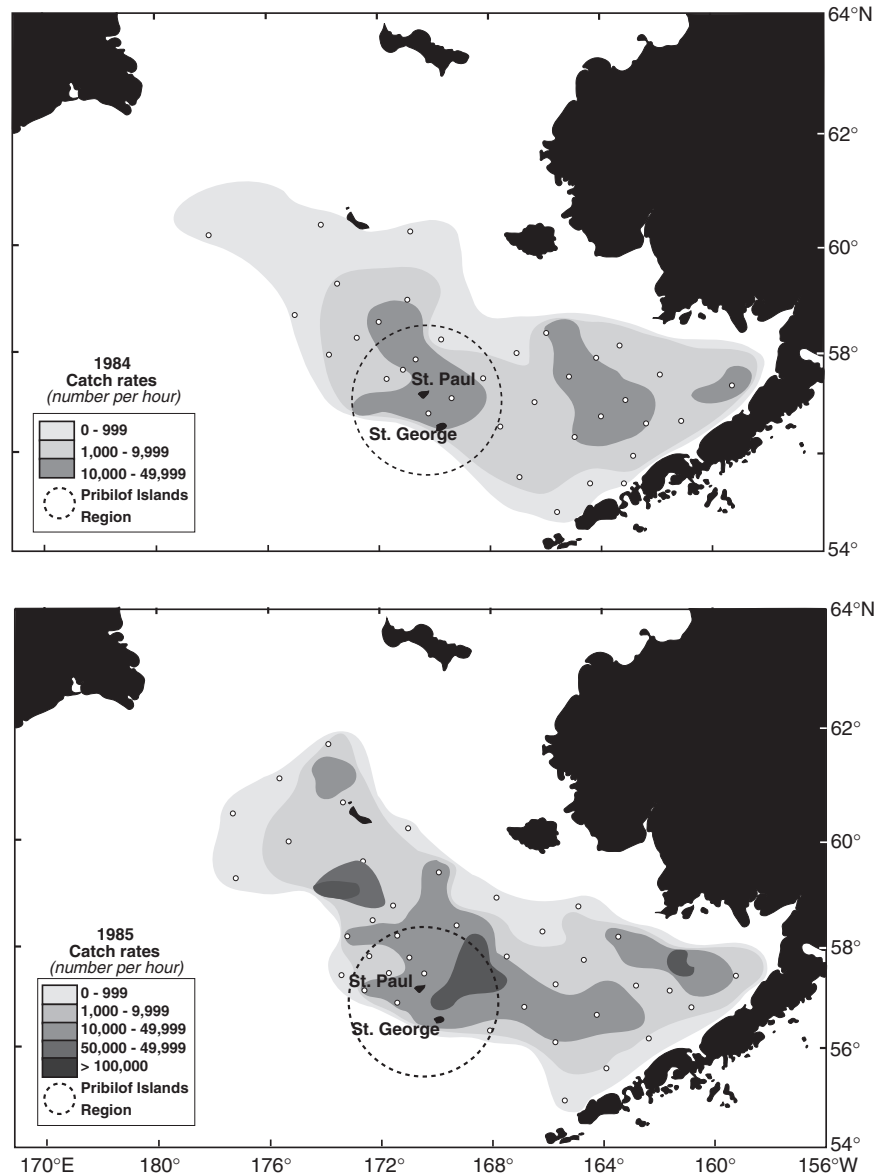


Figure 4.3: Catch-rate distributions for age-0 walleye pollock in the EBS during 1984 (upper panel) and 1985 (lower panel). Reproduced from Traynor and Smith (1996). A 100-nm radius region is shown around the Pribilof Islands.

abundance was high near the Pribilof Islands, but higher still near Unimak Pass (Fig. 4.4). Changes in spatial patterns of age-0 pollock in early summer could result from changes in the spawning distribution of different cohorts (Fig. 4.6).

Acoustic survey comparisons between Pribilof and Inner Front surveys. A comparison of acoustic data between the Pribilof region and several acoustic transects in the Inner Front region of the eastern Bering Sea was conducted by Andreas Winter and Ken Coyle (Section 4.3). Direct comparisons of pollock and zooplankton abundance were made for 1997, 1998,

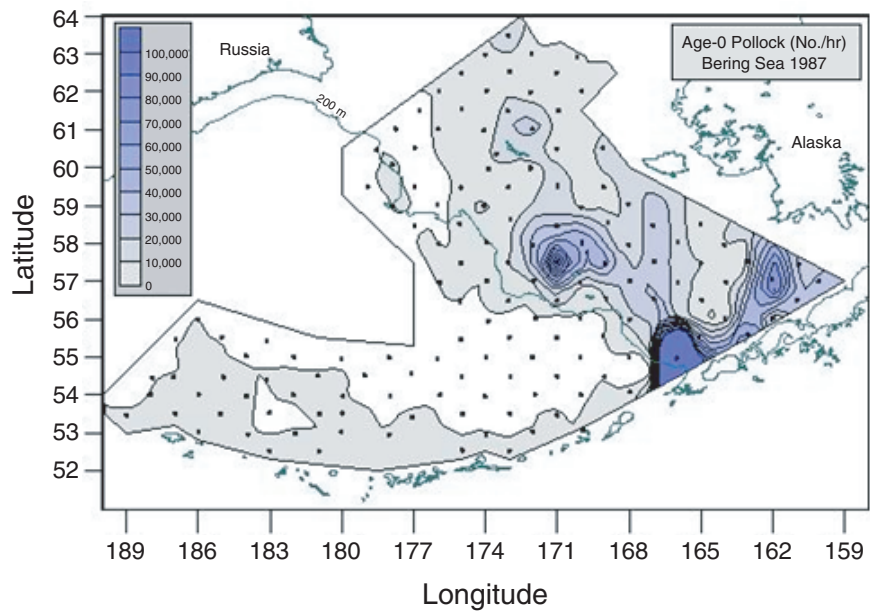


Figure 4.4: Distribution for age-0 walleye pollock in the EBS during summer 1987 taken from the Russian survey aboard the MV *Darwin*.

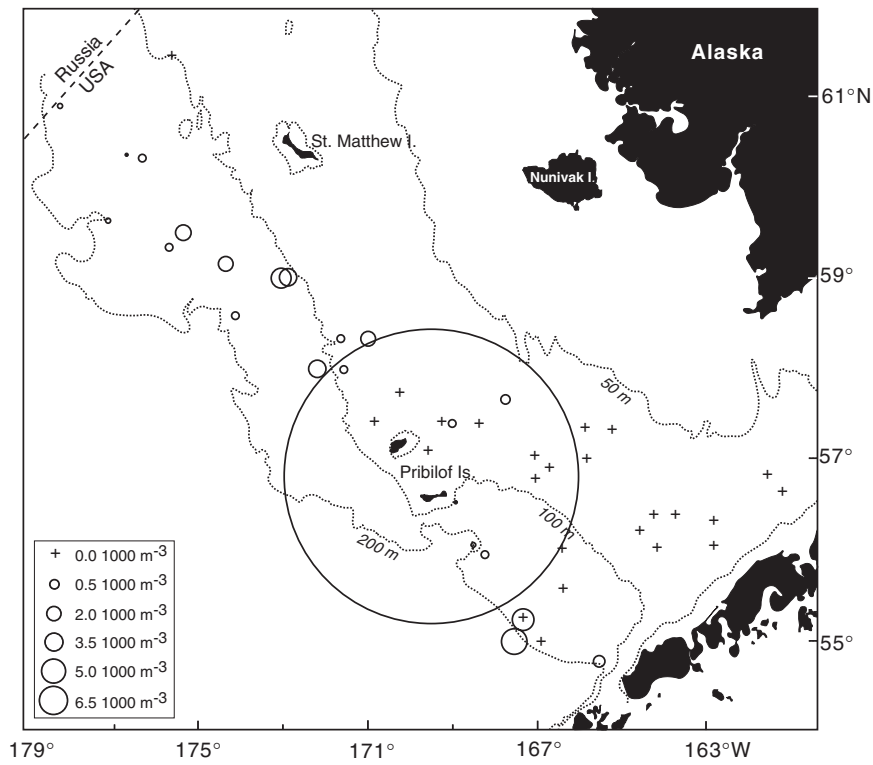


Figure 4.5: Distribution of age-0 gadids observed from the 1999 summer (June–July) EIT survey (from Honkalehto *et al.*, 2002).

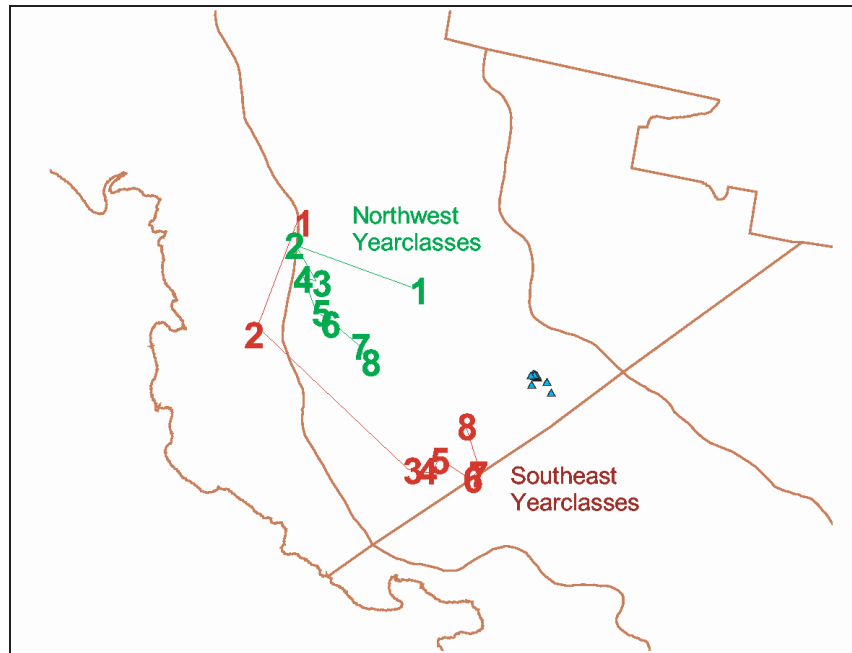


Figure 4.6: The average locations (centroids), ages 1–8 for pollock year classes that remain concentrated in the NW area of the EBS shelf and those that shift southeastward as they age. Triangles represent the centers of survey operations in each year. The average is computed from the period 1975–2001 with 1975–1978, 1989, and 1990 representing the “southeast” year-classes and all other (since 1975) representing “northwest” year-classes.

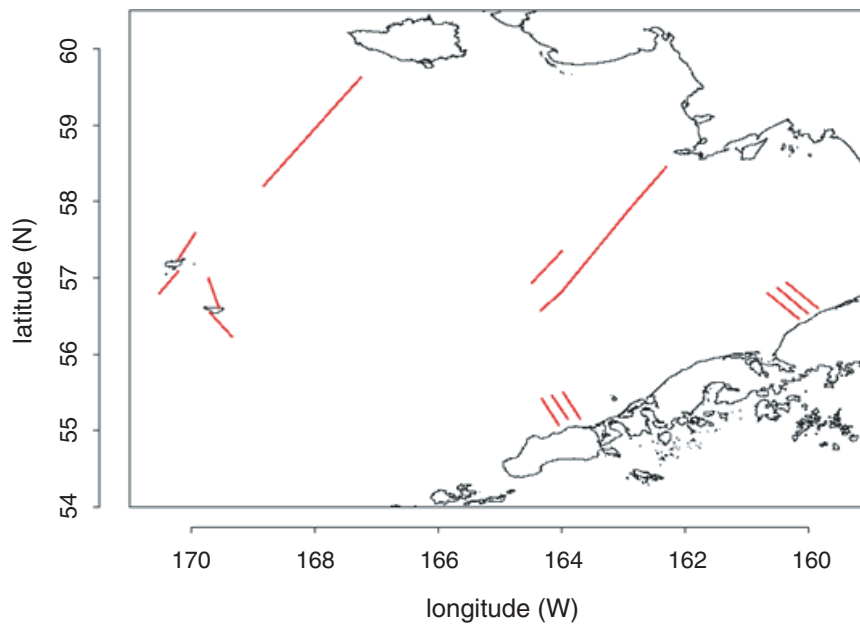


Figure 4.7: Acoustic survey areas used in comparing the Pribilof Island with other shelf areas in the Bering Sea. Surveys were conducted from 1997 to 1999. Red lines indicate transects.

and 1999 survey years, when data were available in both areas. Acoustic data were collected across the Inner Front at four locations: Slime Bank near Unimak Pass, Port Moller along the Aleutian inner front, and Nunivak and Newenham transects off the Yukon-Kuskokwim river delta (Fig. 4.7). Net sample data collected by Coyle and Pinchuk (2002a) suggested that the abundance of age-0 pollock and zooplankton was about the same order of magnitude as in the Pribilof region. This was corroborated by the acoustic data comparison. In each region, data were subdivided into nearshore, offshore stratified, and transition regions.

For the Pribilof region, we selected transect A, as it was found to be representative of conditions. For transects A, B, C, and D (Fig. 4.1), age-0 pollock mortality estimates between August and September were calculated from the average differences in fish/m³ derived from acoustic biomasses recorded during the (August) EIT and (September) FOCI survey cruises in the vicinity of the Pribilof Islands. Mortality estimates were made separately for each transect line, but not for regions within transects. The identical transect lines were not run during the EIT surveys, and therefore nearest-matching segments of the EIT survey tracks were used instead to approximate lines A, B, C, and D. Only daytime transects were used in all surveys. Acoustic backscatter was quantified as age-0 pollock according to the algorithms of Swartzman *et al.* (2002). Length-frequency distributions of age-0 pollock in each survey were obtained from Methot trawl samples collected during the cruises. Length averages were converted to measures of individual target strength (TS) using an extrapolated Kirchhoff ray-mode model as explained in Section 4.3, and numbers of fish per m³ on each transect were calculated as the ratio of pollock acoustic backscatter energy/TS applicable to that transect.

Each transect area received 1–2 daytime passes in the August surveys and 2–3 daytime passes in the September surveys. Fish densities and time stamps (normalized date + hour) of the ~1–3 passes per area per survey were averaged. Mortality rates (z ; day⁻¹) were calculated as

$$z = \frac{\ln(\text{fish m}^{-3}\text{August}/\text{fish m}^{-3}\text{September})}{\text{norm.day}_{\text{September}} - \text{norm.day}_{\text{August}}} \quad (7)$$

Results are summarized in Table 4.2.

Given the representativeness of transect A for the Pribilof region, comparison was made with data collected along transects of the four Inner Front locations. Winter and Coyle found that the nearshore domains in all transects and years generally had the lowest abundance of both fish and zooplankton, while the stratified region generally had the highest abundance for both groups (Fig. 4.8; details in Section 4.3). Also, there was general agreement in year-to-year changes in age-0 pollock abundance between all Inner Front and Pribilof transects, with 1997 having the lowest and 1999 generally having the highest abundance. A comparison of the depth distribution of young-of-the-year pollock and zooplankton showed no apparent differences between regions and no consistent patterns (Section 4.3). It is likely that the daytime depth distribution of fish and zooplankton depends

Table 4.2: Comparison of age-0 pollock density and mortality for transect lines A, B, C, and D from August and September surveys during 1996 and 1997 (“norm.day”: cumulative days where 1 = August 1, 0000 hours).

Year	Transect	August		September		Mortality (day ⁻¹)
		Norm. Day	Density (fish/m ³)	Norm. Day	Density (fish/m ³)	
1996	A	2.96	0.400	43.14	0.122	0.030
	B	3.12	0.336	41.26	0.083	0.037
	C	2.15	0.223	41.18	0.116	0.017
	D	1.75	0.139	37.46	0.038	0.036
1997	A	2.76	0.173	47.15	0.005	0.081
	B	2.67	0.074	44.83	0.005	0.065
	C	1.63	0.142	42.90	0.002	0.106
	D	1.98	0.045	41.39	0.0006	0.110

on the size and abundance of the fish as well as the depth and strength of the thermocline (Swartzman *et al.*, 2002).

Comparison of the abundance of zooplankton and fish around the Pribilof Islands with other front areas (work by Winter and Coyle reported here) suggest that abundance in the Pribilof region is no higher than in other eastern Bering Sea frontal regions. While standing stocks are higher in the front region than nearshore, they appear to be generally higher in stratified waters offshore of the coastal front (Fig. 4.8). However, T/S *Oshoro Maru* data (Fig. 4.2) suggest that abundance of age-0 pollock around the Pribilof Islands is consistently higher than in adjacent shelf and offshore stations.

Thus, we hypothesize that abundance of age-0 pollock and macro-zooplankton around the Pribilof Islands and in other frontal regions in the eastern Bering Sea is generally elevated compared with shelf and basin abundance. That the Pribilof area supports elevated densities of seabirds and marine mammals compared with other Bering Sea frontal areas without increased age-0 pollock abundance may be due to its isolation and the closeness of the front regions to land more than its elevated production. We hypothesize that, although front regions may have elevated primary production relative to adjacent stratified areas, the abundance of macro-zooplankton and juvenile fish may be consistently higher in the stratified than in front areas. The greater depths of the stratified regions may provide some protection from predation for zooplankton and age-0 pollock through diel migration (Swartzman *et al.*, 2002). Finally, stratified areas adjacent to frontal regions may have enhanced production due to transport from the front regions. The stratified regions at the extremities of transect A (away from the islands) did not show any reduction in age-0 pollock abundance (Swartzman *et al.*, 2002), while the *Oshoro Maru* data did show reduced age-0 pollock abundance in shelf regions more remote from the Pribilof Islands. This suggests that a longer transect than transect A might have been necessary to detect a lessening in pollock abundance away from the Pribilof Islands.

Given data, as discussed above, on age-0 pollock abundance near the

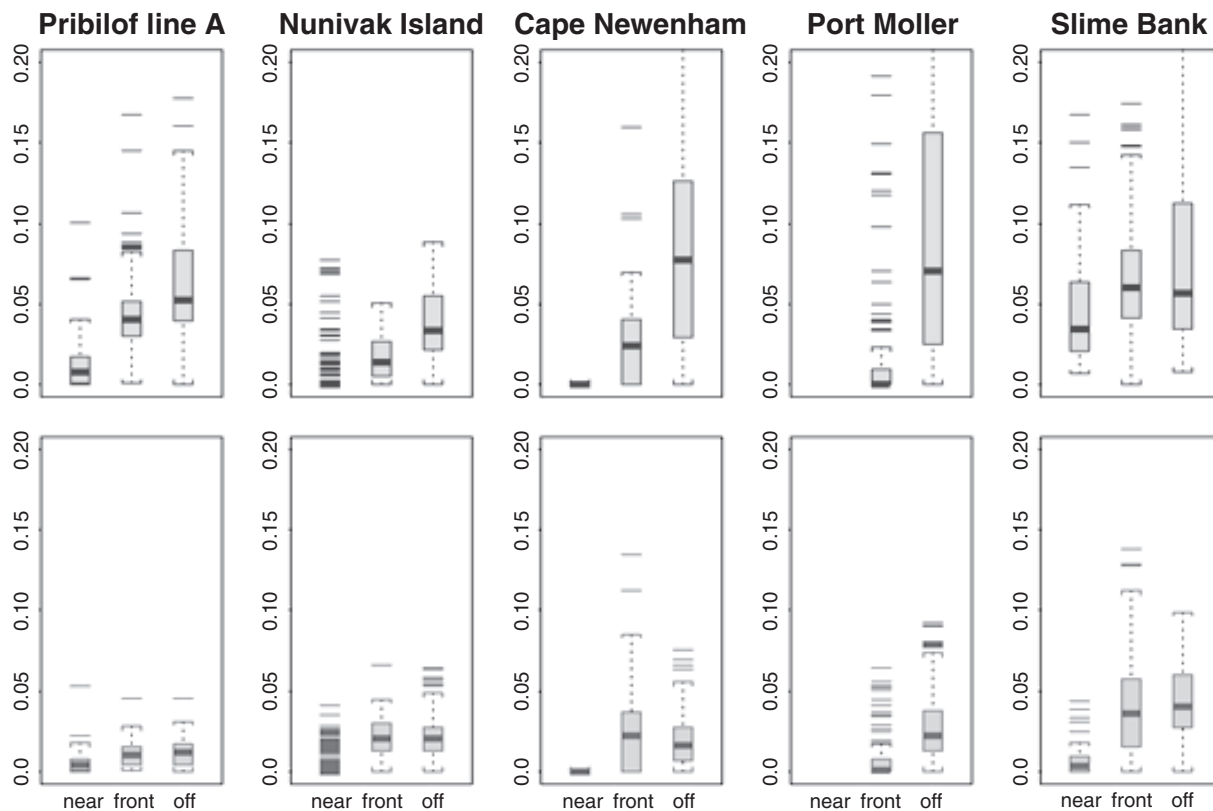


Figure 4.8: Comparison of age-0 pollock (upper panels) and zooplankton (lower panels) abundance per 250-m horizontal bin in the nearshore tidally mixed, transition front, and offshore stratified zones in four surveyed areas along the Bering Sea shelf in 1999.

Pribilof Islands, near other Inner Front regions, along the MACE survey route and in shelf areas farther from the Pribilof Islands (*Oshoro Maru* data), it is possible to compute the fraction of the entire eastern Bering Sea age-0 pollock abundance near the Pribilof region by computing the total area in five habitats: nearshore, front and shelf adjacent to fronts, other shelf and basin, and then multiplying these areas by the density of pollock per unit area. However, this was not done. It was difficult to relate the abundance from data taken at different times of the summer (late June, late July, and early September), because (1) these distributions appear to change over time, and (2) substantial mortality accrues between the early and later periods. Thus, we provide only the rough abundance ratios in Table 4.1.

The dominance of particular year classes and differences in their spatial distribution may explain why in some years early July surveys showed high abundance of age-0 pollock around the Pribilofs (e.g., 1984 and 1985), while in others (e.g., 1999) their abundance was lower than in other survey areas. From 1994–2000, the abundance of age-0 pollock, sampled in late July by the T/S *Oshoro Maru*, was consistently higher near the Pribilof Islands than in surrounding areas. Perhaps as the age-0 pollock become larger and better able to maintain position, they tend to congregate near the Pribilof Islands,

whereas earlier in the year, happenstance of birth location determines how abundant they are near the Pribilof Islands.

4.2.4 How does the abundance of age-0 pollock near the Pribilof Islands relate to diet, survival, and energetics of higher predators?

Bird survival and energetics (George Hunt, Beth Sinclair, and Lucy Vlietstra). It has been difficult to establish a relationship between pollock abundance near the Pribilof Islands and bird populations or their energetics parameters. Fledging success on St. George and St. Paul islands were highly correlated for black and red-legged kittiwakes and common murres, but not for thick-billed murres (Fig. 4.9). This would suggest that some environmental conditions around the islands are affecting all the breeding colonies on the islands in the same way, except not thick-billed murres. However, no relationship to age-0 pollock abundance and fledging success of any of these species was found. The only significant relationship was with black-legged kittiwake fledging success and age 3+ pollock abundance, and it was a negative relationship (Fig. 4.10). This may possibly indicate competition for age-0 pollock food resources. Current efforts on diets of these bird species may shed some light on the importance of age-0 pollock to these birds. Hunt and Vlietstra did find that diets of black-legged kittiwakes in the 1970s changed through the summer, from primarily age-1 pollock in July–August to primarily age-0 pollock in September. Since these birds are near-surface feeders, this suggests that the age-1 pollock became deeper and unavailable sometime in later summer, while age-0 pollock became large enough to provide some energetic resources for the kittiwakes (Fig. 4.11).

Studies of pollock otoliths in fur seal scat collected on the Pribilof Islands 1994–1999 (Rolf Ream). Scat samples from female foraging fur seals have been collected for many years on the Pribilof Islands. It is possible that the abundance of age-0 pollock otoliths in the scat can be used as a surrogate for pollock abundance to extend the data base to previous years and perhaps use scat for prediction of age-0 pollock abundance. Although they feed over a wide area, it has been suggested that female fur seals resident for the summer on the Pribilof Islands may top up their stomachs with age-0 pollock just before returning to land. This is supported by scat data, which show a consistently high presence (and percentage) of age-0 pollock in the scats (Fig. 4.12) and diving behavior from tagged seals (data from Mike Goebel, University of California, Santa Cruz). As such, it was felt that age-0 pollock otoliths in fur seal scat might be indicative of their near-Pribilof abundance.

Trajectories of tagged, feeding fur seals (Robson, 2002; Jeremy Sterling, NOAA/NMML, personal communication) suggest that the feeding areas of fur seals depend on the location of their rookery. We examined the percent occurrence of age-0 pollock otoliths in fur seal scat collected on rookeries adjacent to the four Pribilof Island acoustic transects (Fig. 4.1) for 1994–1999 with an eye to the relationship of this percentage to the acoustic abundance of age-0 pollock on each of these transects and years.

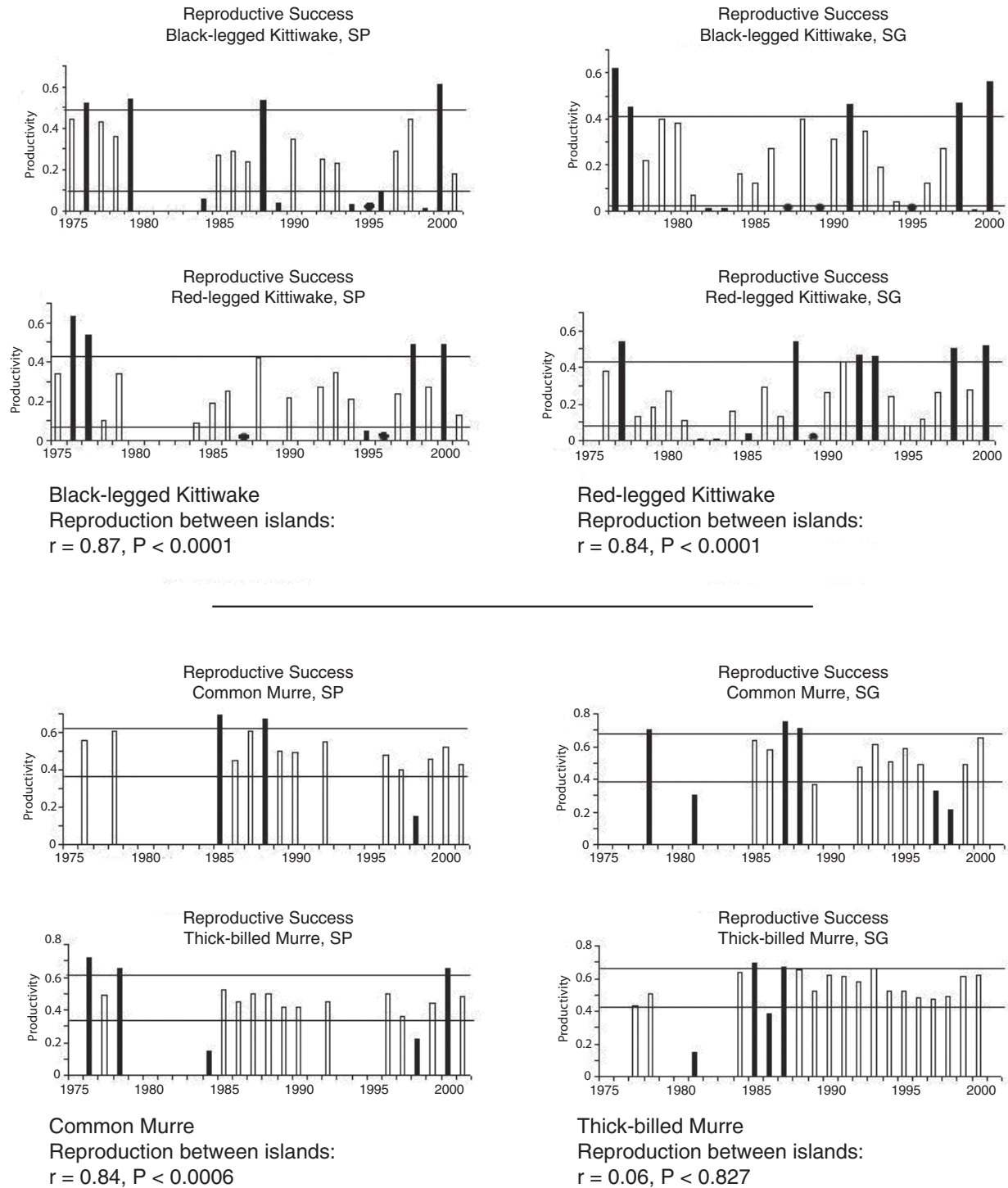


Figure 4.9: Reproductive success in murre and kittiwakes on the Pribilof Islands, AK. Horizontal bars show range of mean (\pm SD). Solid bars indicate years in which reproductive success exceeds or falls below this range. (Figure courtesy of Vlietstra and Hunt.)

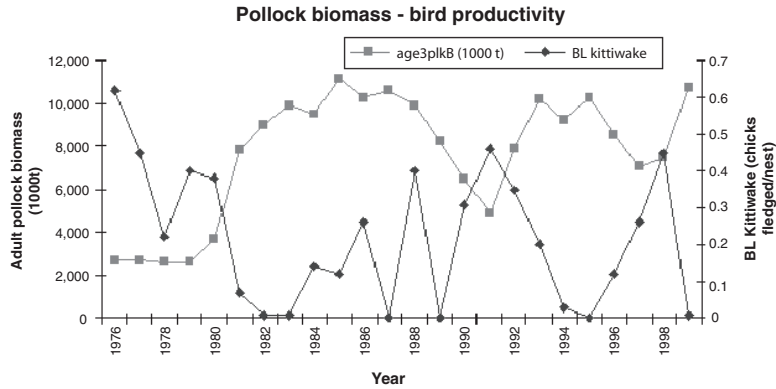


Figure 4.10: Relationship between black-legged kittiwakes on the Pribilof Islands, AK and shelf-wide, age-3 pollock abundance.

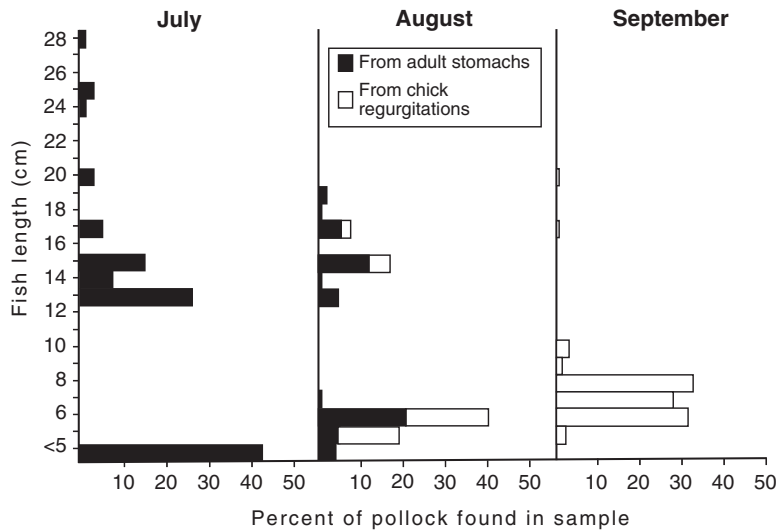


Figure 4.11: Seasonal length distribution of walleye pollock taken by black-legged kittiwakes on the Pribilof Islands, AK.

Scats were collected from rookeries at the end of August. Adult, post-parturient females are the main group of feeding northern fur seals present and the rookery and thus the scat data primarily represent their diet. Based on preliminary telemetry data (Jeremy Sterling, NOAA/NMML, personal communication), females forage closer to the island than juvenile males, so their scats may better represent the food base, and availability of pollock, closer to the Pribilofs. The data may be biased toward the last meal on the return leg of the foraging trip, which is desirable for this study because this percentage is more indicative of pollock abundance on the study transects rather than farther afield where fur seals usually feed before returning to the Islands.

Otoliths were used to identify and age pollock. Percent occurrence (PO

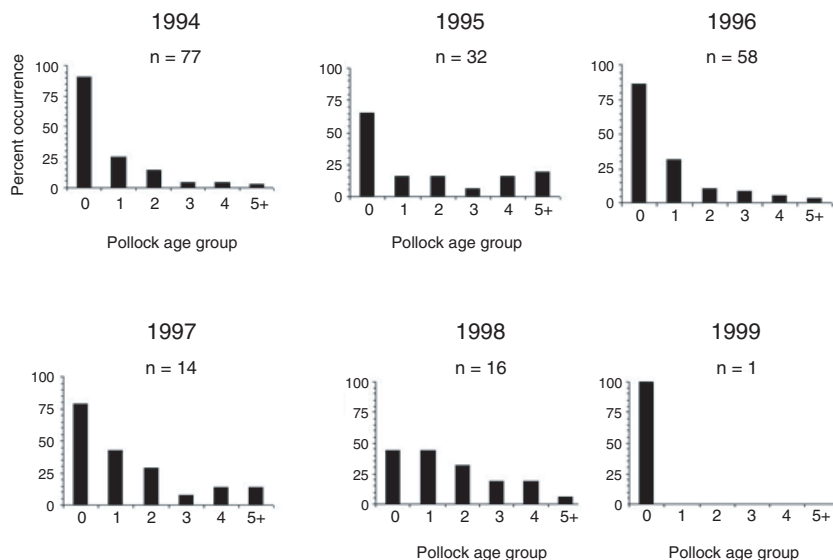


Figure 4.12: Percent occurrence of different age classes of pollock in fur seal scat collected on St. Paul Island rookeries adjacent to transect A.

or FO) was calculated as the number of samples with a given age class of pollock, divided by the number of samples with pollock otoliths that could be aged.

Data were examined first for all rookeries combined on St. Paul in 1994–1999 (1994, 1996 highest for age 0 pollock, 1998 lowest). The lowest age-0 pollock abundance occurred in 1997. There appears to be an increased percent occurrence in scat of older rather than age-0 pollock in 1997.

Data from individual rookeries on St. Paul were then assigned to acoustic transects A, B, and C (G. Swartzman, UW/APL, personal communication) based on the overlap of the female foraging locations and the location of the transects. Note that some rookeries were assigned to two transects. For transect A (NE St. Paul) the percent occurrence of age-0 pollock was highest in 1994 and lowest in 1998 and 1995). Transect B (SW St. Paul) had a similar percent occurrence of age-0 pollock for most years, with the exception of 1998 when it was much lower. On transect C (SE St. Paul) the percent occurrence of age-0 pollock was highest in 1994 and 1996, lowest in 1998 (Fig. 4.12). Data from 1999 is included only for completeness because the sample size is too small.

Finally, data for all rookeries on St. George were combined to correspond to transect D. The percent occurrence of age-0 pollock was highest in 1995 and 1996, lowest in 1998 and 1997. In general, it appears that the percent occurrence of older pollock is greater on St. George (Rolf Ream, unpublished data), though 1996 had very few older pollock.

These results (Fig. 4.12) suggest that frequency of occurrence of age-0 pollock in fur seal scat cannot be used to distinguish large year classes because the percentages of age-0 pollock in the scats are so high in most cases. It would be preferable to explore the relationship between age-0 pollock

otoliths in scat and pollock abundance using the percentage of otoliths in the scat rather than percent occurrence (percent of the samples that have any age-0 pollock otoliths). Nonetheless, the data suggest that low abundance year classes may be distinguishable using percent occurrence of age-0 pollock otoliths in fur seal scat.

4.2.5 How important is predation to pollock abundance near the Pribilof Islands?

Several approaches were adopted to look at the importance of predation to the abundance and distribution of age-0 pollock near the Pribilof Islands:

1. Comparison of pollock abundance and distribution along transect A (Fig. 4.1) to the abundance of groundfish predators (see Lang *et al.*, 2000).
2. Comparison of the relative abundance of age 1+ pollock and other age-0 pollock fish predators by year in the Pribilof Island region to their abundance in other shelf regions including the Inner Front region and to the abundance of age-0 pollock (from acoustic surveys) in the Pribilof Island region. This comparison will be based on data collected in the annual groundfish survey in July–August (1978–2001).
3. Review of the Pribilof Island acoustic surveys and the Inner Front surveys (by Andreas Winter) to assess where fish schools having large target strength (for individual targets) were encountered along the transects and to relate this to the distribution of age-0 pollock (i.e., are they proximate or divergent from the predator locations?).
4. Use of the ECOPATH model (Ciannelli) for the Pribilof Island region to estimate the amount of consumption during September of each study year (1994–1999) of age-0 pollock by fur seals, fish predators, jellyfish, and birds, and compare this to standing stock and production. Diet information will be updated with input from Troy Buckley (groundfish), Rolf Ream and Beth Sinclair (fur seals), and George Hunt and Lucy Vlietstra (birds).

Predation by fish on age-0 pollock near the Pribilof Islands compared with other areas in the eastern Bering Sea (Troy Buckley). Predation by fishes on age-0 walleye pollock has been described as part of a larger, ongoing study examining the trophic relationships in the eastern Bering Sea (Livingston, 1991; Livingston *et al.*, 1993; Livingston and deReynier, 1996; Lang *et al.*, 2003). In these documents the length composition, the relationship to predator size, and the geographic distribution of predation of walleye pollock are described. From these documents, it appears that signals from strong year classes can be seen in the prey-length composition of various fish predators. Currently these data are being compiled and analyzed with regard to the spatial distribution of the prey, including age-0 walleye pollock. The diet of predatory fish in the Pribilof region will be examined to see whether these diets include more age-0 walleye

pollock than the diet in other areas and whether this changes from year to year. If the diets of Pribilof Island region groundfish are higher in age-0 pollock, this could suggest higher densities of age-0 pollock and/or that there is higher vulnerability to predation in that area. A majority of these data are collected during the spring and summer when piscivory tends to be lower because of the abundance of zooplankton. Lang *et al.* (2000) conducted a study directed toward examining predation on age-0 walleye pollock in the vicinity of the Pribilof Islands in late summer and found very high rates of predation. Ciannelli (2002) reviewed data from Lang *et al.*, (2000) and suggested that predation pressure may vary considerably from year to year.

Information on the distribution of walleye pollock year classes ages 1 through 8 suggested that some year classes predominated in the northwestern part of the eastern Bering Sea, while others appeared to predominate in the southeastern part of the EBS (Fig. 4.6; Buckley *et al.*, 2001; <http://www.afsc.noaa.gov/refm/reem/Default.htm>). Northwest year classes, which appear to remain from year to year in the northwestern region during the summer, may not be contributing to the Bogoslof and Unimak spawning stocks. Spawning has been observed northwest of the Pribilof Islands from June through August (Hinckley, 1987).

Results of ECOPATH analysis for 1996–1997 (Lorenzo Ciannelli). The ECOPATH model (Polovina, 1984), which was discussed earlier on the basis of an average year, was run for the Pribilof Island region for 1996 and 1997 separately. These years were chosen because the age-0 pollock abundance was extreme for the study period, being highest in 1996 and lowest in 1997. Figure 4.13 compares the percentage of total consumption of several groups, including juvenile gadids (over 90% age-0 pollock) for 1996 with that in 1997. While the model runs in Fig. 4.13 include differences in age-0 pollock abundance for the two years, they assume the same diet selectivity for all their predators does not account for possible differences in abundance between these predators.

As can be seen (Fig. 4.13), there is little to choose from between the two years. In both years, flatfish and large jellyfish dominate predation on juvenile gadids, with adult pollock also contributing a significant amount of mortality through cannibalism. The results are almost identical despite the large difference in abundance. These results, which are admittedly speculative, reflect the linear nature of the model as well as the model parameters chosen. There was not enough time to analyze the groundfish stomach contents in those two years to distinguish any major change in diet composition. As such, only the biomass estimate of age-0 pollock changed, which apparently did not affect mortality sources as much as the diet compositions did. Future work, with diet information, as outlined the previous section of this report, may remedy this situation. The extremely high predation by jellyfish on juvenile gadids is surprising. Although large jellyfish and age-0 pollock are seen in close association, the two being forced together in the cod end of nets may bias the consumption of pollock by jellyfish. On the other hand, jellyfish showed extremely large increases in abundance near the Pribilof Islands during the 1990s and in theory could have eaten many age-0 pollock in 1996 and 1997.

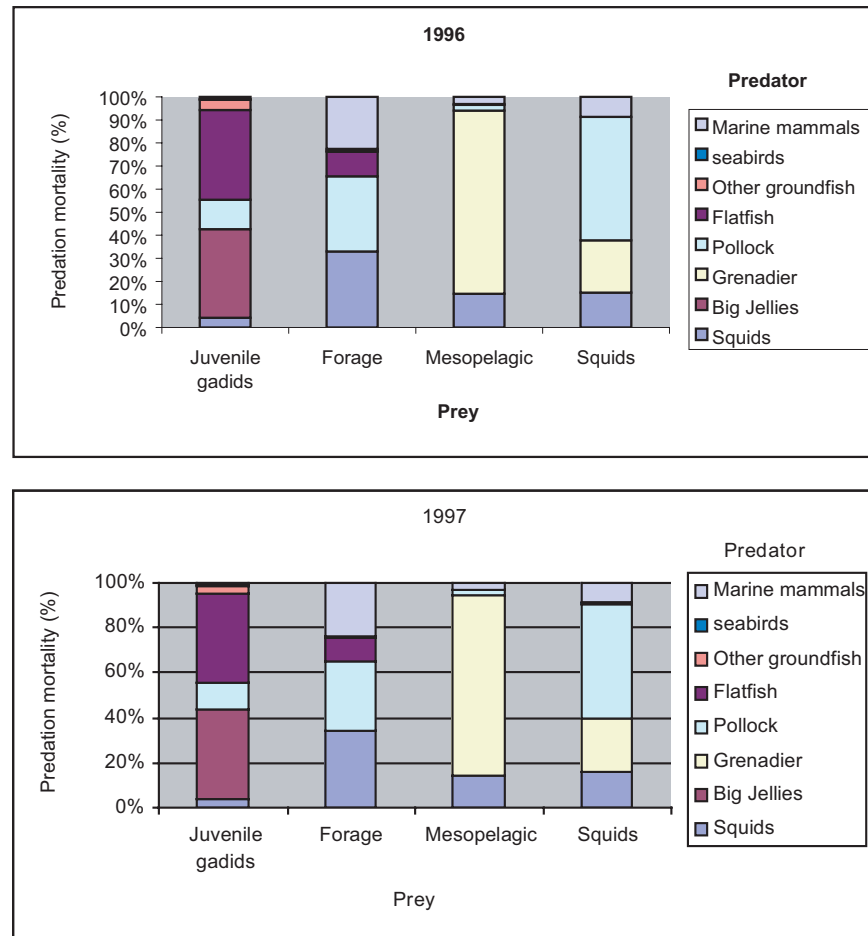


Figure 4.13: Partition of predation mortality of key forage species, 1996 and 1997.

Although we have not attempted the calculation because of our concerns about model parameter estimates, it is possible to compute, for each year, the total consumption of age-0 pollock by various predators and its percentage of the standing stock. To do so, however, considerable effort will be needed to improve our estimates of year-to-year changes in predator abundance as well as diets in the neighborhood of the Pribilof Islands—work that is proceeding apace, but not yet finished. Given the predicted large impact of jellyfish predation on age-0 pollock, further effort is needed on substantiating the consumption rates, abundance, and diet composition of jellyfish—a project not yet attempted.

4.3 Comparison of abundance of juvenile pollock and zooplankton between the Pribilof Islands and other shelf areas in the eastern Bering Sea based on acoustic surveys in 1997, 1998, and 1999 (Andreas Winter and Kenneth Coyle)

The waters around the Pribilof Islands have been identified as an important nursery area for juvenile walleye pollock (Swartzman *et al.*, 2002). Hydrographic fronts surrounding these islands (Stabeno *et al.*, 1999a) are believed to play an important role in structuring the habitat and concentrating food resources for the juvenile fish (Ciannelli *et al.*, 2002), as likewise do fronts occurring in other regions of the eastern Bering Sea (Coyle and Pinchuk, 2002a).

It has been suggested that conditions for juvenile pollock in the Pribilof Islands area may be representative of rearing conditions throughout the Bering Sea (Brodeur and Wilson, 1999; Swartzman *et al.*, 2002) and serve as an indicator for Bering Sea pollock production. Thus, a question of current interest is how the Pribilof Islands area compares to other frontal regions with respect to the population of juvenile pollock it supports from year to year. In this section, we address the question by examining echo-integration data from three recent years (1997, 1998, 1999) in which acoustic fishery surveys were conducted, at approximately the same times, around the Pribilof Islands and four other locations of the eastern Bering Sea.

4.3.1 Methods

The Pribilof surveys were carried out in September of each year under the Bering Sea FOCI (Macklin, 1999a) and SEBSCC programs (Macklin, 1999b), and occupied four transects radiating north and south from St. Paul and St. George Islands (Fig. 4.1). Acoustic data on these surveys were collected using a hull-mounted SIMRAD EK-500 split-beam echo-sounder system operating at 38 and 120 kHz, and integrated to horizontal \times vertical resolutions of ~ 9 m \times 0.5 m in 1997 and 1999, and ~ 9 m \times 1 m in 1998.

Nunivak Island, Cape Newenham, Port Moller, and Slime Bank were surveyed between late July and early September as part of the Inner Fronts project (Coyle and Pinchuk, 2002a). Each sampling location comprised up to three parallel transect lines running orthogonal to the bathymetry (Fig. 4.6). Acoustic data were collected with an HTI model split-beam system operating at 43 and 120 kHz. Sampling was conducted during the day only. The transducers were towed beside the vessel about 4 m from the hull and 2 m below the surface. Echo data were integrated to (horizontal \times vertical) ~ 180 m \times 2 m in 1997, and ~ 45 m \times 1 m in 1998 and 1999.

The acoustic data were processed to delineate shoals of fish and patches of zooplankton. In order to derive comparable biomass indices, a common algorithm was applied to the data of both sets of surveys. This algorithm is described in Swartzman *et al.* (1999, 2002). Briefly, the spatial echo-integration units (i.e., pixels) are thresholded to the ranges of backscatter expected for fish or zooplankton aggregations at the appropriate frequency,

and morphologically filtered to retain only contiguous areas (patches) greater than a given minimum size. Fish shoals only are expected to have backscatter within threshold range at the low frequency, and having higher backscatter (above a minimum value) at the high frequency than at the low frequency identifies zooplankton patches.

Because this algorithm was designed for the Pribilof Islands surveys (38 and 120 kHz; ~ 9 m horizontal resolution), adjustments had to be taken into consideration for using it on the Inner Fronts surveys (43 and 120 kHz; ~ 45 –180 m horizontal resolution). The difference between 38 and 43 kHz as the low frequency turned out to be negligible for juvenile pollock, as evidenced by target strength vs. length plots calculated from the Kirchhoff ray mode model (Hazen and Horne, University of Washington, personal communication).

However, the large discrepancies in echo-integration resolution (9 m vs. 45–180 m horizontally) required calibration of the backscatter-difference value used to identify zooplankton patches. Since each pixel averages the echo return over its area, a larger pixel size (lower resolution) requires a lower backscatter-difference value to represent the same level of discrimination between the two frequencies. Through empirical testing, we found an appropriate calibration factor to be given by dividing the backscatter-difference value by the square root of the ratio of the spatial resolutions that need to be normalized with each other. For example, 5 dB is used as the standard backscatter-difference value for spatial resolutions averaging $9 \text{ m} \times 0.5 \text{ m}$ (Swartzman *et al.*, 1999). A spatial resolution of $45 \text{ m} \times 1 \text{ m}$ would thus be set to a backscatter difference of:

$$5 \text{ dB} / \sqrt{\frac{45 \text{ m} \times 1 \text{ m}}{9 \text{ m} \times 0.5 \text{ m}}} = 1.58 \text{ dB} \quad (8)$$

After processing of the echo-integration data, acoustic biomass indices for fish and zooplankton were calculated as the sums of backscatter (s_A) per pixel \times pixel area. Acoustic biomass totals were calculated separately for sampling locations and for habitat regions at each location; i.e., nearshore (mixed), front, and offshore (stratified) habitats. Boundaries between habitat regions follow the definition of Stabeno *et al.* (1999a), and are described in Ciannelli *et al.* (2002), Kachel *et al.* (2002), and Swartzman *et al.* (2002).

Acoustic biomass totals of pollock and zooplankton per area and habitat are summarized as box plots in Figs. 4.14–4.16 for each year of the study. Following the convention used by Swartzman *et al.* (1999), the data were binned by 250 m of horizontal distance. The acoustic biomass totals per bin were then modeled as a function of distance using generalized additive models (GAM; Hastie and Tibshirani, 1990). In order to standardize transects and highlight the effect of fronts, distances were scaled to an index such that the front region of each transect goes from 0 (nearshore boundary) to 1 (offshore boundary). These GAMs are plotted in Figs. 4.17–4.19. The relative distributions by depth of the acoustic biomass are plotted in Fig. 4.20 for each study area and year. Only transect lines “A” of the Pribilof Islands surveys have been included in the analysis.

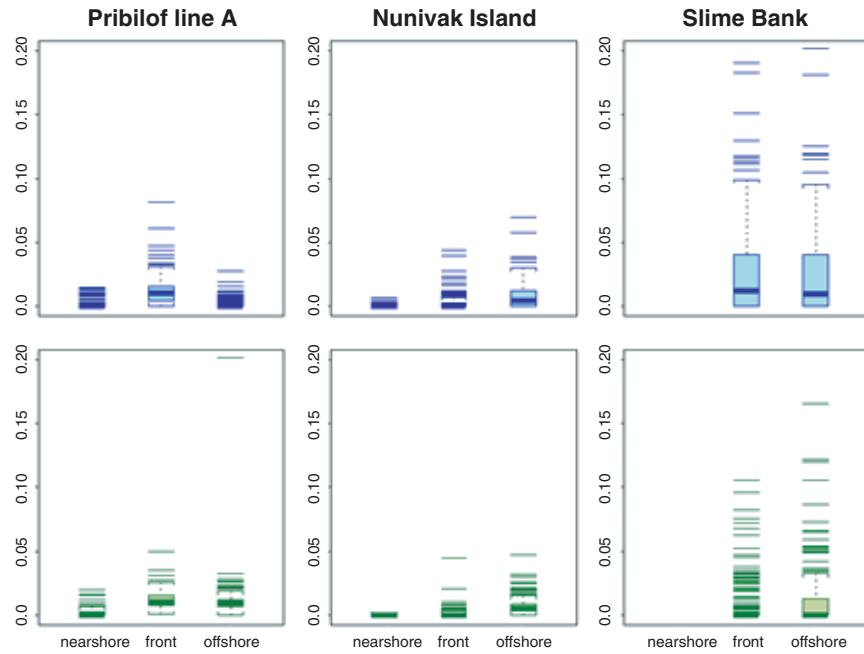


Figure 4.14: Box plots of acoustic biomass per 250-m bin, by habitat region, in each survey area, 1997. Top panels (blue): pollock. Bottom panels (green): zooplankton.

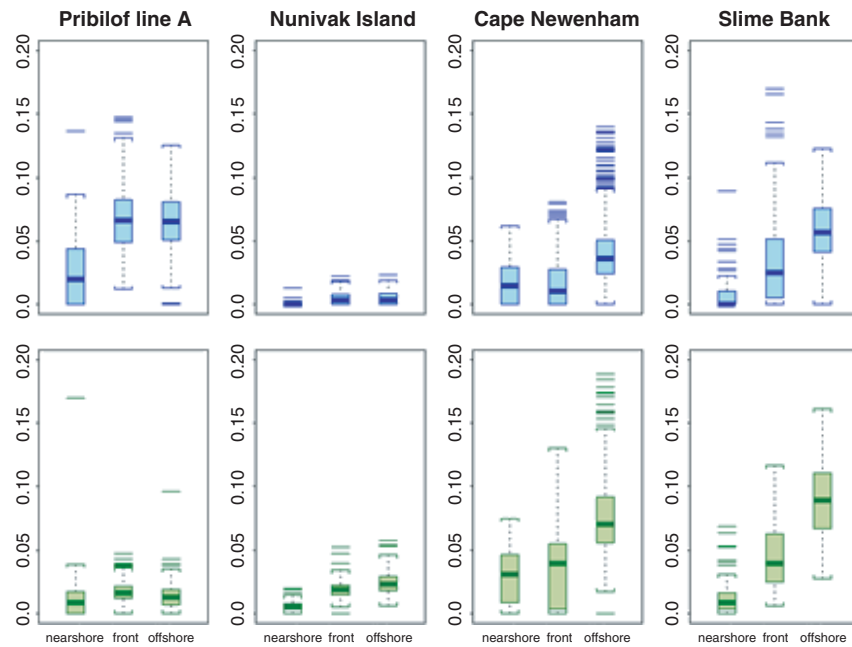


Figure 4.15: Box plots of acoustic biomass per 250-m bin, by habitat region, in each survey area, 1998. Top panels (blue): pollock. Bottom panels (green): zooplankton.

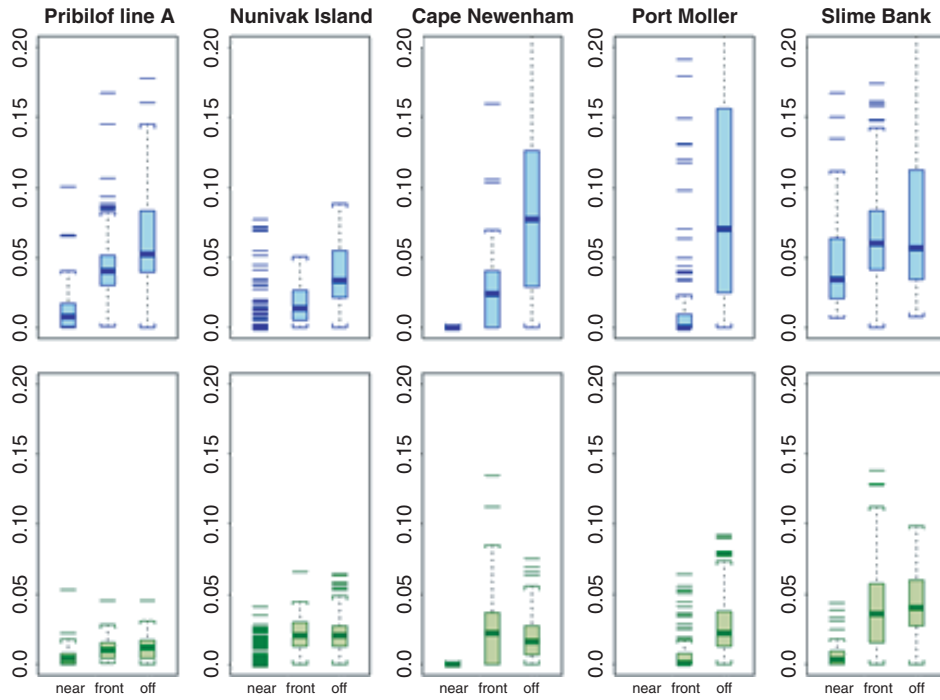


Figure 4.16: Box plots of acoustic biomass per 250-m bin, by habitat region, in each survey area, 1999. Top panels (blue): pollock. Bottom panels (green): zooplankton.

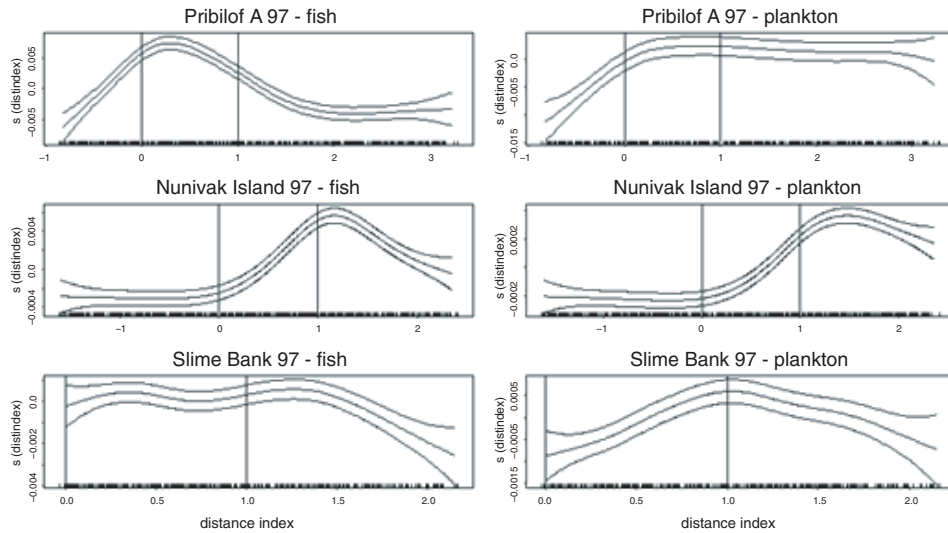


Figure 4.17: GAM smoothed plots of acoustic density as a function of distance index per survey area in 1997. Vertical lines on the plots mark the inner and outer boundaries of the hydrographic fronts.

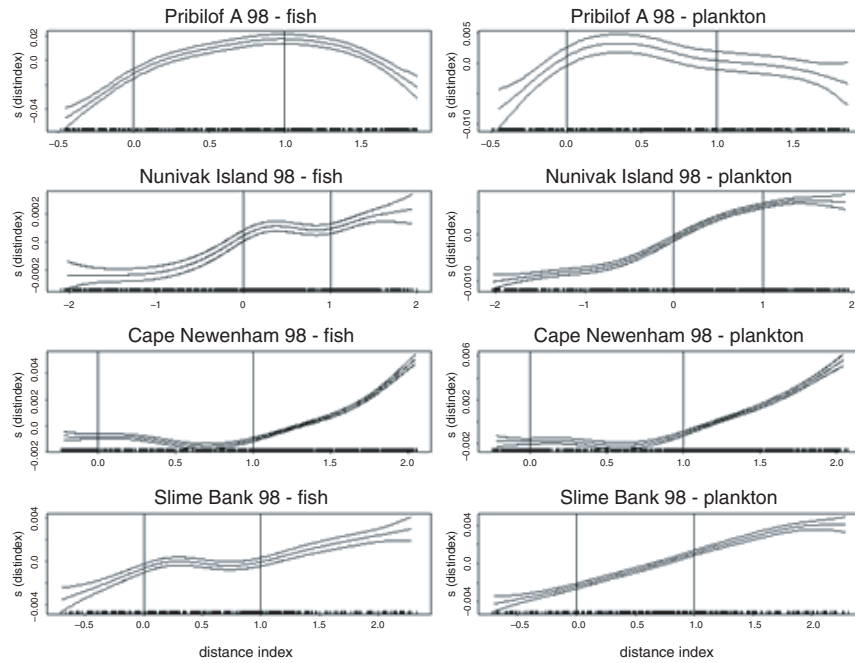


Figure 4.18: GAM smoothed plots of acoustic density as a function of distance index per survey area in 1998. Vertical lines on the plots mark the inner and outer boundaries of the hydrographic fronts.

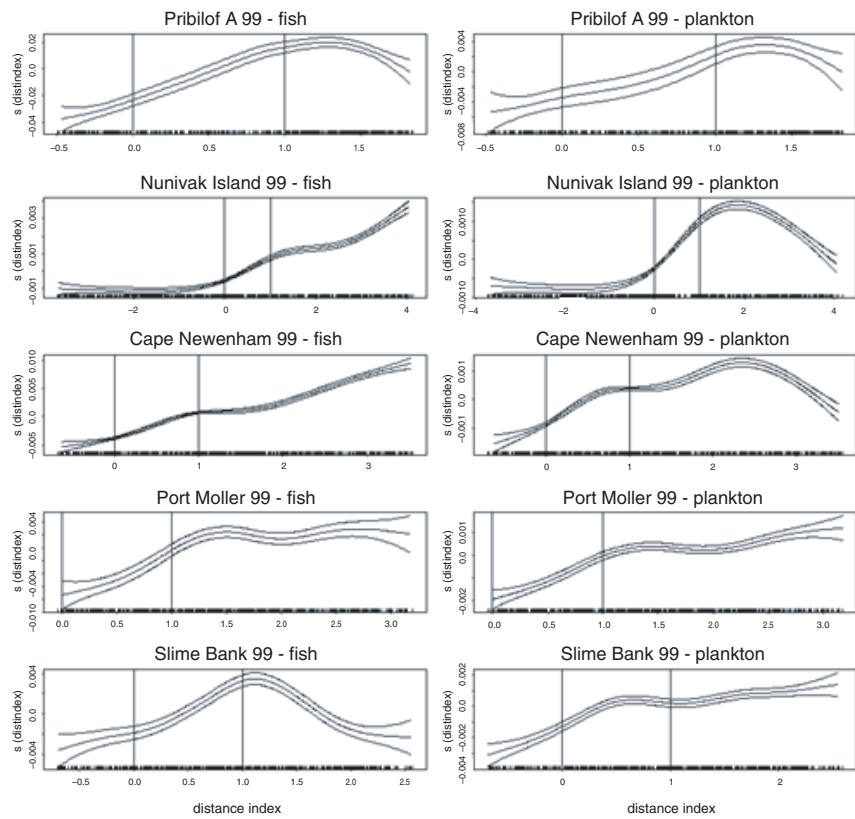


Figure 4.19: GAM smoothed plots of acoustic density as a function of distance index per survey area in 1999. Vertical lines on the plots mark the inner and outer boundaries of the hydrographic fronts.

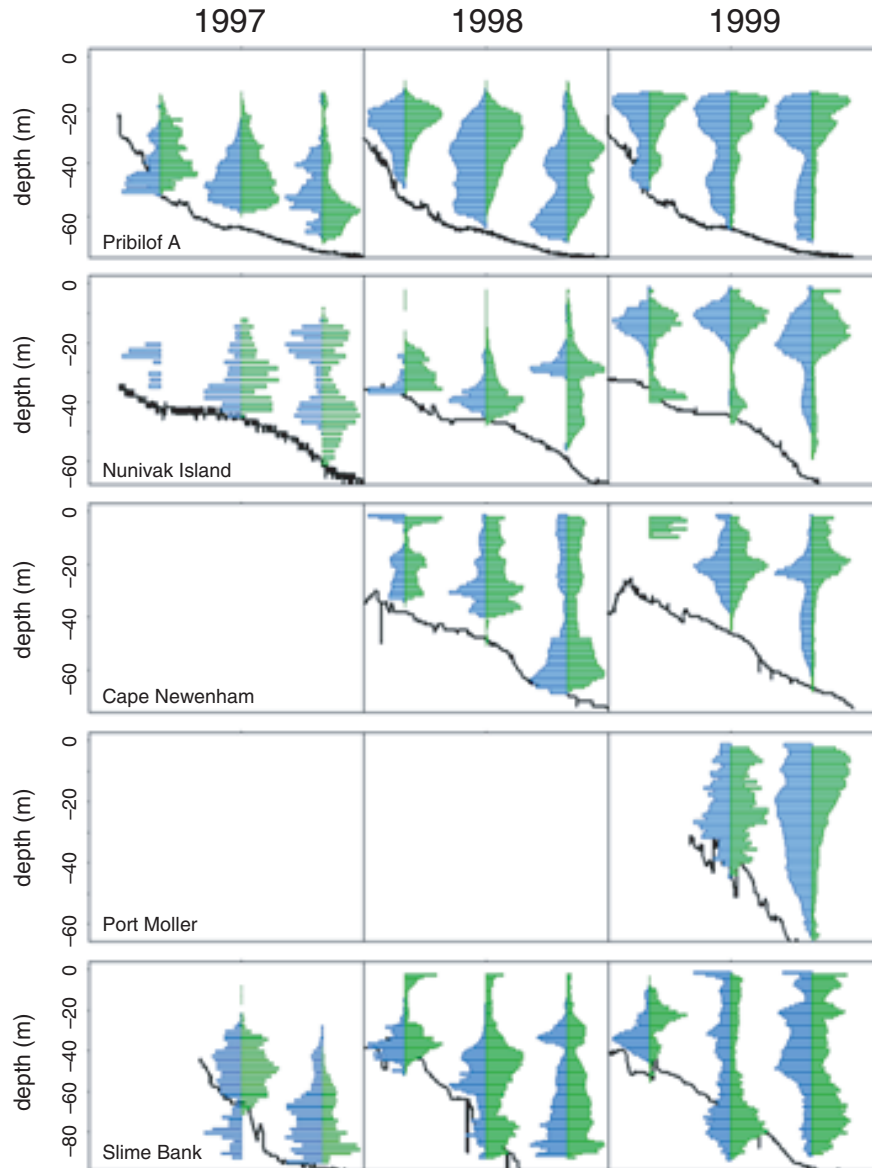


Figure 4.20: Bar plots of the relative depth distributions in 1 m decrements of acoustic pollock (blue) and zooplankton (green) biomass in each survey area by year and habitat region. Each panel represents from left to right the nearshore, front, and offshore regions.

4.3.2 Results

Three of the five study areas were surveyed in all three years. Pribilof line A had its lowest average pollock biomass density in 1997, and the acoustic pollock sign tended to be clustered near the inner boundary of the front. In 1998 and 1999, the pollock sign was denser and more evenly distributed among habitats, with maximum concentration near the outer boundary of the front. Both pollock and zooplankton average acoustic biomass were concentrated closest to the bottom in 1997 and highest in the water in 1999.

Among individual transects within each year the depth distribution was variable.

In the Nunivak Island area, average pollock biomass was lowest in 1997 over the nearshore and front habitats and lowest offshore in 1998. One acoustic transect was recorded in 1997, and showed pollock sign to be maximal near the outer boundary of the front, with vertical distribution throughout the water column. Offshore, the heaviest pollock sign occurred high in the water, with a second mode at intermediate depth, and near shore small schools were present mid-water and near bottom. In 1998, density increased from nearshore outwards, leveled through the front, and increased again offshore. The nearshore pollock sign occurred on the bottom, and from the front toward offshore formed a narrow mid-water band. In 1999, very little pollock sign was detected nearshore; the acoustic density increased through the front, leveled off around the outer boundary of the front, and then increased again offshore.

The Slime Bank area also had its overall lowest pollock densities in 1997 (although the near-shore was not surveyed that year). Pollock density decreased beyond the outer boundary of the front and predominantly moved to deeper water. In 1998, average pollock densities increased from shore to the front, leveled off across the front, then increased again offshore. In 1999, densities increased through the outer boundary of the front, then decreased. In both 1998 and 1999, acoustic pollock sign occurred mostly near-bottom in the shallows and slope of the transects, and throughout the water column in the deep part. In 1998, the offshore depth distribution spread toward distinct modes in deep- and mid-water. In 1999, a dense, narrow band of pollock sign was also detected just below the surface.

Cape Newenham was surveyed in 1998 and 1999. In 1998, pollock density increased from the outer part of the front toward offshore. Separate aggregations high and low in the water column were evident across the length of the transects. The smaller, upper bands of acoustic sign appeared distinctly restricted by the thermocline below. In 1999, pollock density increased near-monotonically from nearshore to offshore, with a slight plateau at the outer boundary of the front. No pollock sign at all was detected in the nearshore region. Horizontally stratified biomass distributions, similar to 1998, occurred throughout the front and offshore.

Port Moller was surveyed only in 1999, from the front to offshore. Average pollock density increased in the offshore direction until just beyond the outer boundary of the front, and then leveled off. The average vertical distributions were the most uniform of any of the surveys, although some evidence of stratification did appear on the transects.

4.3.3 Discussion

The 2001 eastern Bering Sea pollock stock assessment (Ianelli *et al.*, 2001) estimated 1-year-old stock sizes of 16482, 16233, and 14994 millions from the 1997, 1998, and 1999 year classes, respectively. The relative sizes of those stock assessments are not supported by the acoustic survey data presented here. Rather, 1997 appeared to be substantially the weakest year-class

throughout the eastern Bering Sea. The temporal variability of the Inner Fronts surveys prohibits definite conclusions about the absolute quantities of biomass, but the data are sufficiently consistent to indicate larger numbers of age-0 fish in 1998 and 1999 than in 1997. The average offshore densities were highest in 1999 in all areas surveyed (non-significantly different from 1998 in the Pribilof area), and lowest in 1997 in all areas except Nunivak Island. The three easternmost areas (Cape Newenham, Port Moller, and Slime Bank) had very consistent average offshore densities in 1999, the year that all three were surveyed. Cape Newenham and Slime Bank were similar also in 1998, suggesting that the juvenile pollock populations in those areas might be closely related. Pribilof and Nunivak Islands varied independently of the other three areas, but their acoustic biomass were always within the same order of magnitude.

Average acoustic plankton biomass was lowest in all habitat regions in 1997 for Nunivak Island and Slime Bank areas, and lowest on Pribilof line A everywhere except the front region. All areas except the Nunivak Island front region had higher average plankton biomass in 1998 than in 1999, although the differences were generally not very great. By contrast, Coyle and Pinchuk (2002a) found no evidence of significant interannual differences in euphausiid biomass. The relative density distributions of acoustic plankton sign, as a function of distance index, closely matched the distributions of fish sign in most areas and years (Figs. 4.17–4.19). Two visible exceptions are Pribilof line A in 1997, where plankton densities remained near maximum in the offshore, while fish densities strongly decreased; and Slime Bank in 1997 where fish densities were high throughout the front, while plankton densities increased from the inner to the outer boundary of the front.

Frontal structures had an evident impact on the horizontal distributions of fish biomass. In five of the twelve survey areas, the maximum of the smoothed GAM density occurred within 30% of the frontal width from the outer boundary (i.e., distance index 0.97–1.30). In three further surveys, either the absolute or a local maximum density occurred inside the front. Overall, maximum fish density, and maximum plankton density, was offshore of the fronts in all surveys except Pribilof line A during 1997 and 1998.

The relative depth distributions of pollock and zooplankton substantially correlated over most of the surveys. Exceptions occurred primarily in areas of high pollock density, e.g., Slime Bank and Port Moller offshore in 1999; and Pribilof line A front and offshore in 1998 (Fig. 4.20). Those observations may indicate consumption or avoidance, but are possibly due to masking of the acoustic zooplankton sign by pollock. As the transects in this study were recorded by day, the patterns cannot be directly interpreted as feeding interactions, which are known to take place primarily at dusk (Schabetsberger *et al.*, 2000). A common overall trend among the surveys appears to be that pollock were deepest in the water in 1997, intermediate in 1998, and nearest to the surface in 1999. Further data analyses will be needed to examine possible causes for this outcome, e.g., predation pressure from above or below, or the water temperature gradients.

4.4 Summary and Conclusions

In this section, we addressed the importance of age-0 pollock in the Pribilof Island region as possible indicators of eastern Bering Sea pollock recruitment, and we discussed relationships of age-0 pollock to their prey and predators. To this end, we defined how large an area to include as the Pribilof region, and how age-0 pollock abundance in the Pribilof Island region relates to their abundance in other parts of the eastern Bering Sea.

We defined the Pribilof Island region as an area extending along the shelf and shelf-break 100 nm from the center of the islands, based on runs of the energetic-trophic web-based ECOPATH model that suggested that this region had the highest ecological efficiency—that is, the largest percentage of the energetic demand of region biota was met by food sources within the region.

Of all the drogued buoys released near Unimak Pass during the pollock spawning season, a significant percentage ended up near the Pribilof Islands, suggesting that the pollock found near the Pribilofs during summer are likely coming from these spawning areas. There were year-to-year changes in the percentage of released buoys reaching the Pribilof Islands. Based on the timing of these results, pollock found near the Pribilof Islands during June and July, on which some of our comparisons are based, could not have come from the Bogoslof and Unimak spawning areas and were spawned closer to the islands.

There may be an interaction among the spatial distribution of adults (that appears to have two modes over the years: a northwest and southeast mode), the relative importance of different pollock spawning areas and the summer wind patterns that can influence changes in the distribution of age-0 pollock over the summer. To wit, the abundance of age-0 pollock near the Pribilof Islands may change drastically throughout the summer.

We examined the abundance density (abundance per unit area) of age-0 pollock near the Pribilof Islands relative to abundance in surrounding shelf areas and areas along the Inner Front. Findings show that, while pollock abundance was generally higher than in the surrounding area, it was about the same as abundance in the Inner Front region.

It is difficult to establish a relationship between bird and mammal diets and abundance of age-0 pollock near the Pribilof Islands. No such relationships were found for murrelets or kittiwakes. Percent occurrence of age-0 pollock otoliths in fur seal scat was high throughout most summers, which suggests that large year classes cannot be distinguished from moderate sized year class by scat samples. However, small pollock year classes may be distinguishable using scat data.

When autumn age-0 pollock abundance near the Pribilof Islands, assessed using acoustic surveys from 1994–1999, was compared to pollock recruitment from the AFSC pollock model, the root mean square error was about the same as similar comparisons of the pollock model to age-1 estimates from the annual bottom trawl survey and age-3 estimates from the EIS survey. This suggests that age-0 pollock may provide an acceptable early predictor for pollock year-class strength (Section 3.3.6).

Part 5—SEBSCC Administration and Management

From the outset, the University of Alaska Fairbanks, the NOAA Alaska Fisheries Science Center, and the NOAA Pacific Marine Environmental Laboratory managed SEBSCC jointly. NOAA Coastal Ocean Program was the funding agency.

The project's management goals were to

- Conduct a first-quality scientific program that supported a specific goal to provide critical knowledge needed for formulating policy and management of resources of the southeastern Bering Sea ecosystem.
- Build partnerships and encourage multidisciplinary cooperative efforts among research scientists within the academic community, NOAA, and other agencies interested in the southeastern Bering Sea.
- Provide an open process in establishing research objectives and proposal selection to ensure quality and diversity.

The project management structure consisted of a Project Management Team, a Technical Advisory Committee, a Research Council, and Office of Coordination. This structure built on successful structures of the Coastal Ocean Program, i.e., NECOP, SABRE, and Bering Sea FOCI. In addition, it provided a coordinated forum for marine ecological research in the southeastern Bering Sea.

5.1 Project Management Team

The Project Management Team (PMT) actively led the scientific conduct of SEBSCC, maintained financial and project accountability, and directed project administration. A primary function of the PMT was to assemble a multidisciplinary research team for multi-year investigations of the southeastern Bering Sea ecosystem during each of the three research phases of SEBSCC. The PMT conducted a workshop early in 1996 to define specific 2-year and 5-year research objectives for investigations into biophysical domains, juvenile pollock productivity, and modeling. The SEBSCC workshop attracted a substantial group of potential PIs. A recently completed National Research Council review of the Bering Sea ecosystem and a PICES Workshop on the Bering Sea helped establish a foundation for discussion. Shortly after the workshop, and at two other intervals in the life of the project, the PMT conducted a competitive, peer-reviewed proposal process. SEBSCC's Technical Advisory Committee (section 5.2) ranked the proposals based on peer-review scores and scientific merit, making a recommendation for subproject funding to the Coastal Ocean Program.

During all research phases of SEBSCC, the PMT assured that balance and integration was maintained among subprojects, and that academic, NOAA, and resource manager viewpoints were included. The PMT, with guidance from the TAC and RC, prioritized research, and adjusted the mix

of investigators during the progress of the study to reflect the evolving needs for observation, modeling, and synthesis. The PMT was responsible for ensuring that integrated results were passed to management organizations such as the North Pacific Fishery Management Council.

The primary way that the PMT achieved the SEBSCC research and management goals was through clear guidelines of accountability. The PMT acted as COTRs (monitors) on the accepted proposals. The expertise within the PMT included integrative approaches to modeling fisheries stock structure; lower-trophic, process-oriented research; and a regional oceanographic approach. The PMT also balanced a research orientation with a NOAA perspective of providing scientific products to the North Pacific Fishery Management Council. The PMT members did not compete for funds from the program. The composition of the team was as follows:

Vera Alexander, University of Alaska Fairbanks: Dr. Alexander is Dean of the School of Fisheries and Ocean Sciences. She has a long career of studying the Bering Sea, specializing in physical influences on lower trophic level processes. She is one of two U.S. delegates to PICES and serves on numerous research and review boards. The North Pacific Marine Science Organization (PICES) was established to promote scientific coordination among Pacific Rim nations. Dr. Alexander is a Fellow of the American Association for the Advancement of Science, the Arctic Institute of North America, and the Explorers Club.

Anne Hollowed, Alaska Fisheries Science Center: Dr. Hollowed provides scientific advice to the North Pacific Fishery Management Council for the Gulf of Alaska fisheries. She works with population models and publishes on the connectivity between strong year classes throughout the North Pacific. She serves on the steering committee for U.S. GLOBEC and is leading PICES-GLOBEC planning to address the issue of carrying capacity and climate change in the North Pacific and Bering Sea.

Jim Overland, Pacific Marine Environmental Laboratory: Dr. Overland has published research on the Bering Sea for 20 years. He was co-director of the Bering Sea FOCI project for the previous 5 years and conducted two proposal solicitations. He served a 5-year term as an editor for the Journal of Geophysical Research-Oceans and served on the National Research Council Committee for the Coastal Ocean and the PICES Bering Sea Working Group. Dr. Overland provided the primary contact with the Coastal Ocean Program office.

All members of the PMT agreed to undertake the following:

- Actively manage the scientific conduct of this research.
- Participate in meetings for planning and coordination of the program.
- Evaluate and report on interim progress and steps required to meet the project objectives.
- Prepare annual implementation plans.
- Ensure that quality-controlled data are made available to other investigators in a timely manner.

- Participate in synthesis and interpretation of research results and the development of products of value to environmental and scientific communities.
- Participate in selected fora to encourage communication between the resource management and scientific communities.
- Encourage the publication of research results in the peer-reviewed literature for the benefit of the marine scientific community.
- Prepare a data management plan and schedule.

5.2 Technical Advisory Committee

The Technical Advisory Committee (TAC) provided independent oversight to the PMT. Members reviewed the science implementation plan and suggested how to better coordinate the program to meet its goal and objectives. They provided peer-review of proposals and recommended subprojects for funding. TAC members participated in annual meetings, helping to guide the project to meet changing research challenges during the life of the project. The following members served:

Dr. Michael J. Dagg is Professor, Louisiana Universities Marine Consortium, Chauvin, Louisiana. He was Interim Director during 1990–1991. Dr. Dagg was a participant in PROBES and NECOP. His specialty is secondary production.

Mr. D. Bart Eaton is Vice President of Alaska Operations with Trident Seafoods Corporation. He has been active in the commercial fishing industry for 30 years and is currently partner in two state-of-the-art catcher/processors operating in the Bering Sea and Gulf of Alaska. Mr. Eaton is a past member of the North Pacific Fishery Management Council and was a Technical Advisor to Bering Sea FOCI. Mr. Eaton resigned from the TAC during phase II.

Dr. Eileen E. Hofmann is Associate Professor at the Center for Coastal Physical Oceanography, Old Dominion University, in Norfolk, Virginia. Her primary interest is marine ecosystem models.

Dr. Thomas C. Royer was Professor of Marine Science at the University of Alaska Fairbanks before moving to Old Dominion University. His specialties are coastal boundary currents and mesoscale ocean circulation with emphasis on the sub-polar gyre. He is a member of the National Academy of Science Ocean Studies Board and Committee on the Bering Sea Ecosystem. Dr. Royer has served as an Associate Editor of the *Journal of Geophysical Research*.

Dr. Albert V. Tyler, now retired, was Associate Dean and Professor of Fisheries at the School of Fisheries and Ocean Sciences, University of Alaska Fairbanks. Dr. Tyler has served as a Research Scientist with the Fisheries Research Board of Canada, Professor at Oregon State University, and Research Scientist with the Canada Department of Fisheries and Oceans. Dr. Tyler is active in developing models of stock assessment in multi-species

fisheries and at-sea surveys of groundfish assemblages. Dr. Tyler was chair of the PICES Bering Sea Working Group.

Dr. Warren S. Wooster is Professor Emeritus of the School of Marine Affairs, University of Washington, Seattle, Washington. He has held positions as Research Oceanographer and Professor at the Scripps Institution of Oceanography, Director of UNESCO's Office of Oceanography, and Dean of the Rosenstiel School of Marine and Atmospheric Sciences at the University of Miami. A Technical Advisor to the Bering Sea FOCI, Dr. Wooster also was Chairman of PICES and a member of the National Research Council Committee on the Bering Sea Ecosystem. He is a Fellow of the American Geophysical Union and a Fellow of the American Meteorological Society. His main area of scientific interest is the relationship between climate and large marine ecosystems.

Dr. Jerald S. Ault is Associate Professor of Marine Biology and Fisheries at the Rosenstiel School of Marine and Atmospheric Science, University of Miami. He replaced Dr. Wooster on the TAC during phase II. Dr. Ault's expertise is in ecosystem dynamics synthesis, specifically theoretical and applied population and community dynamics for fishery assessment and management in marine ecosystems.

5.3 Research Council

The Research Council was a loosely knit, informal collective of project-funded principal investigators and associate PIs from other projects, notably the NSF Inner Front Study and the NMFS resource survey team. The Council provided a forum for exchange of information on the multidisciplinary aspects of the southeastern Bering Sea. Several smaller interdisciplinary scientific working groups evolved from the Research Council, as needed. The continuity of the Council promoted extensive cross-disciplinary cooperation.

5.4 Project Coordination and Communication

SEBSCC supported a small office to coordinate communication among project investigators, other agencies, and researchers studying the SE Bering Sea ecosystem, and NOAA's Coastal Ocean Program and National Marine Fisheries Service. The Project Coordinator was Mr. Allen Macklin, Pacific Marine Environmental Laboratory, Seattle, Washington. Products provided were data management, personnel directories, seminar series and announcements, publication and presentation lists, reports and documents, minutes of meetings, production of conferences and workshops, a graphic archive, and cruise plans and schedules. The primary method was by a World Wide Web SEBSCC home page at <http://www.pmel.noaa.gov/sebscc>. This office maintained a catalog of investigators and encouraged interdisciplinary contact among investigators.

The SEBSCC Office of Coordination also managed a Bering Sea and North Pacific Ocean theme page on the World Wide Web (<http://www.pmel.noaa.gov/bering>). This site exploits existing home page developments to create a single, hyper-linked resource that enables any user to browse the

most recent observational data, scientific analyses, model animations, management and proposal information, and historical perspectives. The site continues to provide a virtual network for the SE Bering Sea, with participation based on common interest and easy access to information.

5.5 Data Management

SEBSCC followed the lead of the U.S. GLOBEC data policy (U.S. Global Ocean Ecosystems Dynamics Report Number 10, February 1994). SEBSCC maintained that the intellectual investment and time committed to the collection and processing of a data set entitles an investigator to the fundamental benefits of the data set. Initial publication of descriptive or interpretive results derived immediately and directly from the data is the privilege and responsibility of the investigators responsible for each collection. Accordingly, SEBSCC generally allowed exclusive use of data for 1 year from the completion of data processing. Data were released for collaboration among scientists to promote interdisciplinary and comparative interpretation, development of collaborative approaches, and development and testing of new theories. Any scientist making substantial use of a data set was obligated to communicate with the investigators who acquired the data and anticipated that these scientists would be co-authors of published results.

In its request for proposals, SEBSCC's PMT required a data management plan from each investigator. This plan included documentation of adequate methods and equipment to meet the quality standards established for SEBSCC. As part of an interdisciplinary study, each plan was required to show coordination with other elements. Investigators submitted a schedule for collecting, processing, analyzing, archiving, and sharing data with other investigators consistent with SEBSCC standards. The investigators were responsible for archiving data with appropriate agencies and maintaining data for project sharing, preferably by on-line electronic means; SEBSCC facilitated data sharing. Applicants for research funds agreed to the following conditions: At least 3 months prior to execution of field sampling or scientific cruises, investigators will submit a plan to the SEBSCC data management office which documents the procedure to be used to collect, process, and analyze samples and data. SEBSCC will then derive a single plan for each cruise. From the collection of cruise summaries, SEBSCC will publish an annual data report describing its field operations.

The project developed data quality and timeliness standards following the GLOBEC model. SEBSCC's data management plan ensured that all data were processed, validated, and made available to other investigators. Metadata (descriptions of how data were collected, processed and analyzed) are part of the record. Retrospective data sets, numerical experiments, and field data are included in the database. Data information may be located through the SEBSCC web site and in the North Pacific Ecosystem Meta-database (<http://www.pmel.noaa.gov/bering/mdb>).

5.6 Research Structure and Methodology

SEBSCC was designed as a three-phase research project. The emphasis of Phase I was initialization of ecosystem monitoring and modeling, retrospective analysis, and beginning process studies. Phase II continued the monitoring and modeling effort. It also promoted more process studies to address specific objectives and began the important synthesis stage. Phase III was devoted to synthesis of results with limited monitoring to support synthesis activity. Research requirements were based on the following assertions:

- The southeastern Bering Sea shelf is a major region for groundfish, other commercial species, and marine mammals, containing as much as 50–85% of the pollock biomass in the Bering Sea.
- Walleye pollock is a nodal species in the Bering Sea ecosystem, i.e., it dominates the pelagic guild, and, in its juvenile stage, it serves as a major forage fish. Adult pollock are a major commercial asset for the United States.
- Because population dynamics processes that determine abundance appear to be chaotic, they are especially sensitive to initial conditions. The success of age-structured models for pollock in the Bering Sea shows that much variability in year class abundance is established by age two. There appears to be top-down predation control of pollock recruitment, spatial and temporal variability in food supply, and variability in transport processes affecting larval and juvenile pollock. The sequence of survival processes is non-linear.
- SEBSCC will test the hypothesis that interannual ocean variability influences the availability of prey, growth rate, predation, and distribution of juvenile pollock and higher trophic level species. Although we already know that ocean variability can influence fisheries, what is not known is how these factors specifically co-occur in the Bering Sea. We use the phrase “carrying capacity” in a general context as to what limits the potential size of the pelagic guild. From the results of testing these hypotheses, we will develop annual recruitment indices for pre-recruit pollock.

The scientific approach that SEBSCC pursued was interdisciplinary research balancing time-series measurements, process studies, models, and syntheses that were phased over the life of the project. Basic time series comprised a spring larval survey and autumn juvenile survey over the shelf and shelf break, moored biophysical platforms in several habitats over a 6-year period, and periodic hydrographic and water property surveys. The time series measurements tracked important climate changes, the ecosystem response to these changes, and provided data for model studies. Process and retrospective studies examined horizontal and vertical physical dynamics influencing the separation and overlap of aggregations of predators and prey, the feeding and switching behavior of juvenile pollock and their predators, nutrient transport onto the shelf, and the establishment

Table 5.1: Annual funds received by SEBSCC from NOAA Coastal Ocean Program.

1996	1997	1998	1999	2000	2001	2002
\$500,000	\$1,070,500	\$941,800	\$946,700	\$964,700	\$672,700	\$361,800

of pollock as the dominant species. Model-based research implemented a three-dimensional physical model, an individual-based model (IBM) for larval/juvenile processes, a trophic dynamics model, and a spatially dependent model of pollock, their predators, and alternate food sources. Synthesis efforts documented a contemporary understanding of the southeastern Bering Sea ecosystem and produced indices for predicting the abundance of age-1 pollock.

5.7 Resources

The project was awarded \$5,458,200 over its lifetime. Annual increments (Table 5.1) indicate the ramp-up, level-funding, and ramp-down character of the funding. Annual resources also included ~30 days aboard NOAA Ship *Miller Freeman*, ~30 days aboard a Class I research vessel, and a cooperative summer cruise aboard *Oshoro Maru*.

5.8 Leverage and Collaboration

Southeast Bering Sea Carrying Capacity was a highly leveraged program. It worked collaboratively with ongoing research by other National Marine Fisheries Service (NMFS) programs examining pollock resources and ecology of the Bering Sea (fishery acoustics group, stock assessment group, and Marine Mammal Protection Act studies), programs at the University and State of Alaska, Environmental Protection Agency, Shelikof Strait FOCI, Japan Far Seas Fisheries Laboratory, Ocean Research Institute of Tokyo University, Faculty of Fisheries of Hokkaido University, the Japanese Marine Science and Technology Center, Tokai University in Sapporo, Tohoku National Fisheries Institute, Korean Ocean Research and Development Institute and the Institute of Marine Biology, Far East Branch of the Russian Academy of Sciences. SEBSCC also coordinated with the inhabitants of St. Paul Island. The project promoted collaborative research with the Office of Naval Research, the National Science Foundation, and the National Aeronautics and Space Administration. Southeast Bering Sea Carrying Capacity was considered a component in the PICES-GLOBEC Climate Change and Carrying Capacity (CCCC) Program.

5.9 Research Components and Principal Investigators

SEBSCC advertised for research applicants to address the following scientific issues:

- How does climate variability influence the Bering Sea ecosystem? Is there historical evidence for a biophysical regime shift on the Bering Sea shelf? How is this reflected in ecological relationships and species mix? Are there “top-down” ecosystem effects associated with climate variations as well as “bottom-up” effects?
- What limits population growth on the Bering Sea shelf? Is there evidence of a single species carrying capacity, e.g., for pollock, or a more complex structure? What is the ecological role of pollock on the Bering Sea shelf, i.e., how are pollock, forage fish, and apex species linked through energetics and life history? How important is cannibalism?
- How do oceanographic conditions on the shelf influence biological distributions? How do the separate mixing domains, sea ice, and the cold pool influence the overlap or separation between predators and prey?
- What influences primary and secondary production regimes? What are the sources of nutrients to the southeastern Bering Sea shelf, and what processes affect their availability? Is the variability in sea ice extent and timing the primary factor influencing productivity? What determines the relative allocation of organic carbon going to benthos versus that remaining in the pelagic system? What are the lower trophic level structure and energetics on the shelf in summer and winter, especially regarding euphausiids? What is the role of gelatinous organisms?

Applicants were selected for the three research phases by the competitive process described in section 5.2 and according to the specific phase’s research requirements (section 5.6). Funded subprojects are listed by title, investigator, and institution for phases I, II, and III in Tables 5.2, 5.3, and 5.4, respectively.

Table 5.2: Research components and principal investigators for Phase I, 1996–1998.

Research Title	Investigators	Institution
Individual-based modeling of walleye pollock in the southeast Bering Sea	Hinckley, Sarah Megrey, Bern Hermann, Al	NOAA/NMFS/AFSC NOAA/NMFS/AFSC U. Washington/JISAO
A spatial model of upper-trophic level interactions in the eastern Bering Sea	Livingston, Pat Hinckley, Sarah	NOAA/NMFS/AFSC NOAA/NMFS/AFSC
Circulation modeling for the S.E. Bering Sea	Hermann, Al Stabeno, Phyllis Haidvogel, Dale Musgrave, David	U. of Washington/JISAO NOAA/OAR/PMEL Rutgers University U. Alaska Fairbanks
Monitoring and development of biophysical indices of the southeastern Bering Sea	Schumacher, Jim Stabeno, Phyllis Brodeur, Ric Napp, Jeff Hunt, George	NOAA/OAR/PMEL NOAA/OAR/PMEL NOAA/NMFS/AFSC NOAA/NMFS/AFSC U. California Irvine
An altimetric census of mesoscale eddy-like features in the Bering Sea	Okkonen, Steve	U. Alaska Fairbanks
Investigation of the origin and dynamics of nutrients on the southeast Bering Sea shelf in relation to dominant physical and biological processes	Whitledge, Terry	U. Texas at Austin
Isotopic and biomarker composition of sinking organic matter in the southeast Bering Sea: indicators of food web structure	Henrichs, Susan	U. Alaska Fairbanks
Using optical measurements to explore the influence of mesoscale eddies on the interaction of lower and higher trophic levels in the southeast Bering Sea	Stabeno, Phyllis	NOAA/OAR/PMEL
High-resolution acoustic and juvenile pollock retrospective data analysis	Swartzman, Gordie Brodeur, Ric	U. Washington NOAA/NMFS/AFSC
Habitat differences in frontal regions around the Pribilof Islands and their importance to juvenile pollock growth and survival in the Bering Sea	Brodeur, Ric Napp, Jeff Doyle, Miriam	NOAA/NMFS/AFSC NOAA/NMFS/AFSC U. Washington/JISAO
Low-temperature incubation of walleye pollock eggs (<i>Theragra chalcogramma</i>) from the southeast Bering Sea region	Blood, Debbie	NOAA/NMFS/AFSC
Natural scales of variability in coastal marine ecosystems of the eastern Bering Sea	Francis, Bob	U. Washington
Historical trends in the number of foraging trips made by lactating northern fur seals	Loughlin, Tom	NOAA/NMFS/AFSC
The role of atmospheric forcing on the cold pool and ecosystem dynamics of the Bering Sea shelf: A retrospective study	Niebauer, Joe Wyllie-Echeverria, Tina Bond, Nick Schumacher, Jim Stabeno, Phyllis	U. Alaska Fairbanks U. Washington/JISAO U. Washington/JISAO NOAA/OAR/PMEL NOAA/OAR/PMEL
A retrospective investigation into relationships between southeast Bering Sea pollock recruitment and biophysical correlates	Megrey, Bern Wespestad, Vidar	NOAA/NMFS/AFSC NOAA/NMFS/AFSC

Table 5.3: Research components and principal investigators for Phase II, 1999–2000.

Research Title	Investigators	Institution
Circulation modeling for the S.E. Bering Sea	Hermann, Al Haidvogel, Dale Stabeno, Phyllis Musgrave, David	U. Washington/JISAO Rutgers University NOAA/OAR/PMEL U. Alaska Fairbanks
Measures of ecosystem trends: an approach for synthesis and understanding	Schumacher, Jim	Two Crow Environ. Consult.
The regime shift of the 1970s: air-sea interactions crucial to walleye pollock	Bond, Nick Kachel, Nancy	U. Washington/JISAO U. Washington/JISAO
Environmental influences on the early life stages of walleye pollock, <i>Theragra chalcogramma</i> , in the southeastern Bering Sea during the late 1970s climate regime shift	Kendall, Art	NOAA/NMFS/AFSC
Monitoring and use of biophysical indices of the southeastern Bering Sea: phase II	Schumacher, Jim Stabeno, Phyllis Brodeur, Ric Napp, Jeff Hunt, George	Two Crow Environ. Consult. NOAA/OAR/PMEL NOAA/NMFS/AFSC NOAA/NMFS/AFSC U. California Irvine
Currents and transfer processes between shelf and slope waters: a Lagrangian perspective	Stabeno, Phyllis	NOAA/OAR/PMEL
In situ monitoring of nitrate concentrations on the Southeast Bering Sea shelf	Whitledge, Terry Stabeno, Phyllis	U. Alaska Fairbanks NOAA/OAR/PMEL
Sinking organic matter and pelagic food webs	Henrichs, Susan	U. Alaska Fairbanks
Investigation of origin of nutrients on the Southeast Bering Sea shelf in relation to physical processes and biological uptake	Whitledge, Terry	U. Alaska Fairbanks
Proximity of age-0 pollock, jellyfish, predators and prey	Swartzman, Gordie Coyle, Ken Brodeur, Ric Napp, Jeff	U. Washington U. Alaska Fairbanks NOAA/NMFS/AFSC NOAA/NMFS/AFSC
Habitat differences in frontal regions around the Pribilof Islands and their importance to juvenile pollock survival in the Bering Sea: Phase II	Brodeur, Ric Napp, Jeff Paul, A.J.	NOAA/NMFS/AFSC NOAA/NMFS/AFSC U. Alaska Fairbanks

Table 5.4: Research components and principal investigators for Phase III, 2001–2002.

Research Title	Investigators	Institution
Synthesis of pinniped and seabird ecology	Sinclair, Beth Hunt, George Byrd, Vernon	NOAA/NMFS/NMML U. California Irvine USFandWS
Ecosystem trends of the southeastern Bering Sea	Schumacher, Jim Springer, Alan Ianelli, Jim Napp, Jeff Stabeno, Phyllis	Two Crow Environ. Consult. U. Alaska Fairbanks NOAA/NMFS/AFSC NOAA/NMFS/AFSC NOAA/OAR/PMEL
Synthesis of sediment trap, zooplankton, and biophysical data	Henrichs, Susan	U. Alaska Fairbanks
Habitat differences around the Pribilof Islands	Brodeur, Ric Napp, Jeff Francis, Robert	NOAA/NMFS/NWFSC NOAA/NMFS/AFSC U. Washington
Synthesis of acoustic and net data	Swartzman, Gordie Napp, Jeff Coyle, Ken	U. Washington NOAA/NMFS/AFSC U. Alaska Fairbanks
Biophysical monitoring of the southeastern Bering Sea	Stabeno, Phyllis Whitledge, Terry	NOAA/OAR/PMEL U. Alaska Fairbanks

5.10 Field Operations: SEBSCC Cruise Schedule

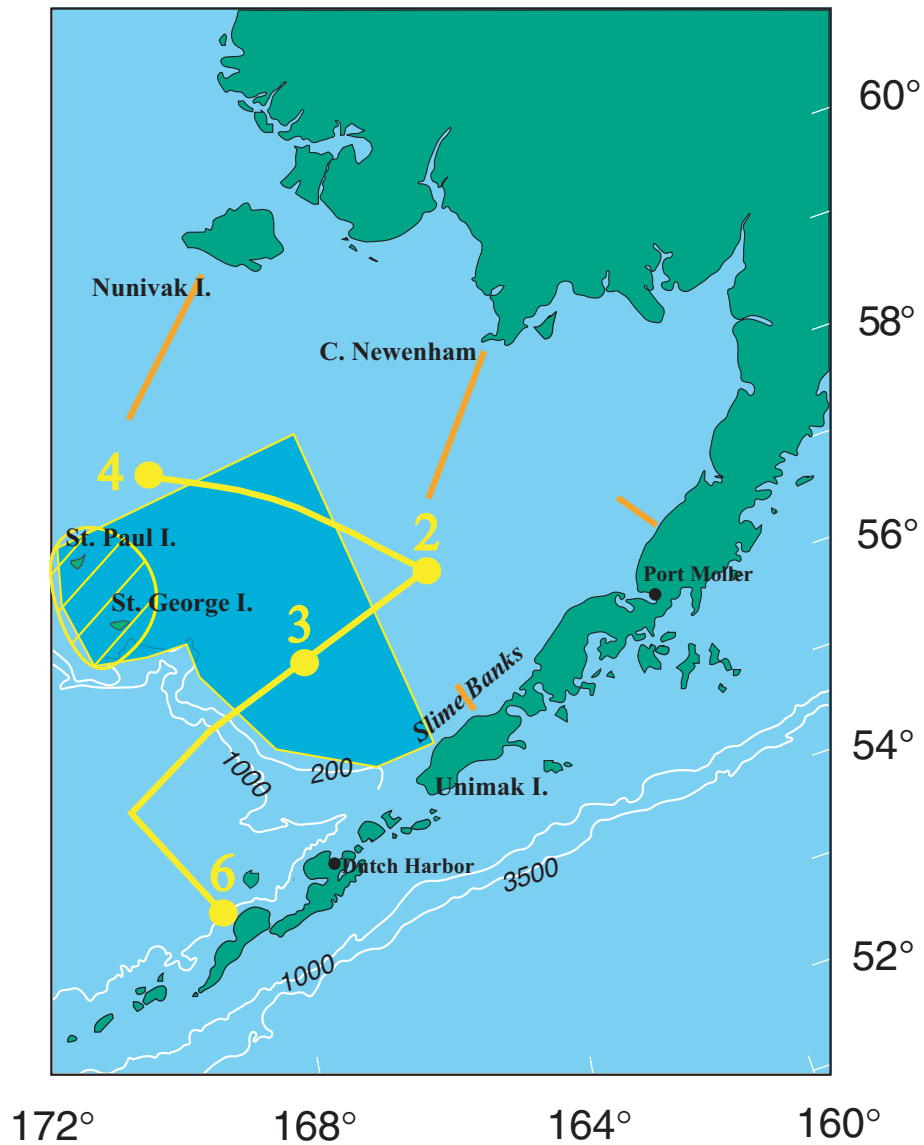


Figure 5.1: Field operations area for SEBSCC. Yellow numbers indicate mooring sites. Yellow lines connecting the moorings are transects for hydrographic, nutrient, phytoplankton, and zooplankton sampling. The crosshatched circular region on the left indicates the Pribilof Islands study area. The juvenile pollock sampling area of cooperative cruises aboard *Oshoro Maru* is shaded dark blue. Transects occupied by the Inner Front program are shown as orange lines.

Table 5.5: SEBSCC cruises.

Vessel	Cruise Designator	Departure and Return Dates	Departure and Return Ports	Sea Days	Activities
1996					
Miller Freeman	MF96-13	Sep 4 to Sep 16	Dutch Harbor to St. Paul	13	Age-0 monitoring, N. Pribilof mooring recovery
Miller Freeman	MF96-14a	Sep 16 to Sep 30	St. Paul to Larsen Bay	15	Bering Sea shelf and Shelkof mooring recoveries
1997					
Miller Freeman	MF97-01	Feb 10 to Feb 18 to Feb 26	Seattle to Dutch Harbor to Dutch Harbor	(8) 9	Test systems, deploy Bering Sea shelf subsurface moorings; NPZ samples, transect, Unimak stations
Miller Freeman	MF97-04	Mar 28 to Apr 13	Homer to Dutch Harbor	17	Drifters, line 8, egg collections, slope current
Miller Freeman	MF97-05A	Apr 15 to May 1	Dutch Harbor to Dutch Harbor	17	Recover/deploy moorings, NPZ samples, transect, Unimak stations, egg incubation
Miller Freeman	MF97-05B	May 3 to May 13	Dutch Harbor to Dutch Harbor	11	NPZ samples, larval feeding, egg incubation
Miller Freeman	MF97-06	May 14 to May 21	Dutch Harbor to Kodiak	8	Tsunami moorings, line 8, ADCP, drifters, egg incubation
Miller Freeman	MF97-07	May 23 to May 31 to Jun 6	Kodiak to Kodiak to Seattle	15	Larval index survey, drifters
Alpha Helix	HX196	May 29 to Jun 30	Seward to Seward	33	Inner front
Weconna	W9706A	Jun 4 to Jun 9	Dutch Harbor to Dutch Harbor	6	Deploy/recover moorings, test MPS gear
Weconna	W9706B	Jun 10 to Jun 27	Dutch Harbor to Dutch Harbor	18	Eddy studies, NPZ samples
Weconna	W9706C	Jun 30 to Jul 14	Dutch Harbor to Dutch Harbor	15	Habitat survey, ground truth, transect
Oshoro Maru	OM97	Jul 18 to Aug 2	Seward to Dutch Harbor	16	EBS shelf and St. Lawrence shelf survey: CTD, bottom trawl, NORPAC net, larval net, juvenile beam trawl
Alpha Helix	HX200	Aug 12 to Aug 28	Dutch Harbor to Dutch Harbor	17	Inner front
Miller Freeman	MF97-09A	Sep 8 to Sep 18	Dutch Harbor to St. Paul	10	Age-0 survey
Miller Freeman	MF97-09B	Sep 18 to Sep 27	St. Paul to Dutch Harbor	10	Mooring recovery, NPZ samples, transect
1998					
Miller Freeman	MF98-01	Feb 11 to Feb 16; Feb 17 to Feb 27	Seattle to Kodiak; Kodiak to Dutch Harbor	(6) 11	Moorings; NPZ samples, transect, Unimak stations
Miller Freeman	MF98-05B	Apr 14 to Apr 29	Dutch Harbor to Dutch Harbor	16	Moorings, NPZ samples, transect, Unimak stations
Weconna	(W9804C) and W9804D	Apr 24 to Apr 30 to May 5	Newport to Dutch Harbor to Dutch Harbor	(6) 5	Mooring or CTD / Unimak / nutrients
Weconna	W9805A	May 6 to May 22	Dutch Harbor to Dutch Harbor	17	NPZ samples and transects
Alpha Helix	HX209	May 22 to Jun 24	Seward to Seward	34	Inner front
Sir Wilfrid Laurier	LA-98-00	Jul 10 to Jul 15	Kodiak to Nome	6	Mooring Deployment, CTD
Oshoro Maru	OM98	Jul 18 to Aug 1	Seattle to Dutch Harbor	15	Ecology, biophysical control
Alpha Helix	HX213	Aug 15 to Sep 12	Seward to Dutch Harbor	29	Inner front
Professor Kaganovsky	PK-98-01	Sep 6 to Sep 18	Dutch Harbor to Dutch Harbor	13	Habitat survey, indices
Sir Wilfrid Laurier	LA-98-02	Sep 28 to Oct 9	Nome to Kodiak	11	Moorings, transects
1999					
Thomas G. Thompson	TGT99-01	Feb 4 to Feb 13	Dutch Harbor to Dutch Harbor	10	Moorings; NPZ samples, transects
Miller Freeman	MF99-04	Apr 10 to Apr 19	Kodiak to Dutch Harbor	10	Pollock eggs
Miller Freeman	MF99-05	Apr 21 to May 1	Dutch Harbor to Dutch Harbor	11	Moorings, NPZ samples, transects
Miller Freeman	MF99-06	May 1 to May 30	Dutch Harbor to Dutch Harbor	9	Hydrographic and NPZ transects
Miller Freeman	MF99-07	May 12 to May 20	Dutch Harbor to Dutch Harbor	9	Greenbelt water properties, drifters, midwater trawls
Alpha Helix	HX220	May 17 to Jun 18	Seward to Seward	33	CTDs, water samples
Alpha Helix	HX222	Jul 18 to Aug 22	Seward to Seward	36	CTDs, water samples
Oshoro Maru	OM99	Jul 20 to Aug 1	Juneau to Dutch Harbor	13	Ecology, biophysical control
Miller Freeman	MF99-11	Sep 2 to Sep 19	Kodiak to Dutch Harbor	18	Habitat survey
Miller Freeman	MF99-12	Sep 19 to Sep 29	Dutch Harbor to Dutch Harbor	11	Moorings, transects
2000					
Miller Freeman	MF00-01 Leg 3	Feb 17 to Feb 25	Dutch Harbor to Dutch Harbor	9	Transect; moorings; NPZ samples, transects; drifters
Miller Freeman	MF00-05	Apr 18 to Apr 30	Kodiak to Dutch Harbor	13	Moorings, NPZ samples, transects, drifters
Miller Freeman	MF00-06	May 1 to May 12	Dutch Harbor to Dutch Harbor	12	Hydrographic and NPZ transects, drifters
Oshoro Maru	OM00	Jul 21 to Aug 3	Victoria to Dutch Harbor	14	Ecology, biophysical control
Ron Brown	RB00-07 Leg 2	Sep 16 to Sep 23	Dutch Harbor to Dutch Harbor	8	Moorings, transects
2001					
Miller Freeman	MF01-01, Leg 2	Feb 5 to Feb 10	Dutch Harbor to Dutch Harbor	5	Bering Sea moorings
Miller Freeman	MF01-06	May 12 to May 14 to May 22	Dutch Harbor to Dutch Harbor	11	Moorings and ecosystem monitoring
Ron Brown	RB01-03, Leg 3	May 25 to Jun 8	Kodiak to Dutch Harbor	15	Mesoscale eddies, shelf-slope exchange
Oshoro Maru	OM01	Jul 14 to Jul 28	Seattle to Dutch Harbor	15	Age-0 pollock survey
Sir Wilfrid Laurier	LA-01-01	Oct 5 to Oct 9 to Oct 14	Nome to Dutch Harbor to Dutch Harbor	10	Moorings

Acknowledgments

The editors appreciate the artistic and word processing skills of Karen Birchfield, Ryan L. Whitney and Tracey Nakamura in producing this report. James E. Overland and Beth Turner contributed valuable comments to an early version of the manuscript. NOAA Coastal Ocean Program provided additional funds for this publication. We extend special thanks to the scientists, engineers, technicians and other personnel of the Southeast Bering Sea Carrying Capacity project and the NSF Inner Front study, and to the men and women of the many research vessels that supported this research.

Part 6—References and SEBSCC Publications*

- Alexander, V., and H.J. Niebauer (1981): Oceanography at the eastern Bering Sea ice edge zone in spring. *Limnol. Oceanogr.*, 26, 1111–1125.
- Anderson, P.J., and J.F. Piatt (1999): Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar. Ecol. Prog. Ser.*, 189, 117–123.
- Antonelis, G.A., E.H. Sinclair, R.R. Ream, and B.W. Robson (1997): Inter-island variation in the diet of female northern fur seals (*Callorhinus ursinus*) in the Bering Sea. *J. Zool. Soc. Lond.*, 242, 435–451.
- Baduini, C.L., K.D. Hyrenbach, K.O. Coyle, A. Pinchuk, V. Mendenhall, and G.L. Hunt, Jr. (2001a): Mass mortality of short-tailed shearwaters in the eastern Bering Sea during summer 1997. *Fish. Oceanogr.*, 10, 117–130.
- Baduini, C.L., J.R. Lovvorn, and G.L. Hunt, Jr. (2001b): Determining the body condition of short-tailed shearwaters: Implications for migratory flight ranges and starvation events. *Mar. Ecol. Prog. Ser.*, 222, 265–277.
- * Baier, C.T., and J.M. Napp (2003): Climate-induced variability in *Calanus marshallae* populations. *J. Plankton Res.*, 25, 771–782.
- Bailey, K.M., A.L. Brown, M.M. Yoklavich, and K.L. Mier (1996): Interannual variability of growth of larval and juvenile walleye pollock in the western Gulf of Alaska. *Fish. Oceanogr.*, 5(suppl. 1), 137–147.
- Bailey, K.M., M.F. Canino, J.M. Napp, S.M. Spring, and A.L. Brown (1995): Contrasting years of prey levels, feeding condition and mortality of larval walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. *Mar. Ecol. Prog. Ser.*, 119, 11–13.
- Bailey, E.P., and G.H. Davenport (1972): Die-off of murrelets on the Alaska Peninsula and Unimak Island. *Condor*, 74, 215–219.
- Bailey, K.M., and S.A. Macklin (1994): Analysis of patterns in larval walleye pollock *Theragra chalcogramma* and wind mixing events in Shelikof Strait, Alaska. *Mar. Ecol. Prog. Ser.*, 113, 1–12.
- Balch, W.M., P.M. Holligan, S.G. Ackleson, and K.J. Voss (1991): Biological and optical properties of mesoscale coccolithophore blooms in the Gulf of Maine. *Limnol. Oceanogr.*, 36, 629–643.
- Balch, W.M., P.M. Holligan, and K.A. Kilpatrick (1992): Calcification, photosynthesis and growth of the bloom-forming coccolithophore, *Emiliania huxleyi*. *Cont. Shelf Res.*, 12, 1353–1374.
- Balykin, P.A. (1996): Dynamics and abundance of western Bering Sea walleye pollock. In *Ecology of the Bering Sea: A Review of Russian Literature*, O.A. Mathisen, and K.O. Coyle (eds.), University of Alaska Sea Grant Report 96-01, Fairbanks, Alaska, 177–182.
- Baretta, L., and G.L. Hunt, Jr. (1994): Changes in the numbers of cetaceans near the Pribilof Islands, Bering Sea, between 1975–78 and 1987–89. *Arctic*, 47, 321–326.
- Barnston, A.G., and R.E. Livezey (1987): Classification, seasonality and persistence of low-frequency atmospheric circulation patterns. *Mon. Weather Rev.*, 115, 1083–1126.
- Beamish, R.J. (1995): Climate change and northern fish populations. *Can. Spec. Publ. Fish. Aquat. Sci.*, 121, 739.
- Beamish, R.J., K.D. Leask, O.A. Ivanov, A.A. Balanov, A.M. Orlov, and E.H. Sinclair (1999a): The ecology, distribution, and abundance of midwater fishes of the Subarctic Pacific gyres. *Prog. Oceanogr.*, 43, 399–442.

*SEBSCC publication

- Beamish, R.J., D.J. Noakes, G.A. McFarlane, L. Klyashtorin, V.V. Ivanov, and V. Kurashov (1999b): The regime concept and natural trends in the production of Pacific salmon. *Can. J. Fish. Aquat. Sci.*, 56, 516–526.
- * Blood, D.M. (2002): Low-temperature incubation of walleye pollock (*Theragra chalcogramma*) eggs from the southeast Bering Sea shelf and Shelikof Strait, Gulf of Alaska. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 6095–6108.
- * Bond, N.A., and J.M. Adams (2002): Atmospheric forcing of the southeast Bering Sea shelf during 1995–99 in the context of a 40-year historical record. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 5869–5887.
- * Bond, N.A., and J.E. Overland (2004): The importance of episodic weather events to the ecosystem of the Bering Sea shelf. *Fish. Oceanogr.* (in press).
- Braun, B.M., and G.L. Hunt (1983): Brood reduction in black-legged kittiwakes. *Auk*, 100, 469–476.
- * Brodeur, R.D. (2001): Habitat-specific distributions of Pacific ocean perch (*Sebastes alutus*) in Pribilof Canyon, Bering Sea. *Cont. Shelf Res.*, 21(3), 207–224.
- * Brodeur, R.D., and K.M. Bailey (2001): A different approach to understanding causes of recruitment variability in marine fishes. In *Fisheries Oceanography: An Integrative Approach to Fisheries Ecology and Management*, P.J. Harrison, and T.R. Parsons (eds.), Fish and Aquatic Resources, Series 4, Blackwell Science, 24–28.
- * Brodeur, R.D., C.E. Mills, J.E. Overland, G.E. Walters, and J.D. Schumacher (1999a): Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. *Fish. Oceanogr.*, 8(4), 296–306.
- * Brodeur, R.D., H. Sugisaki, and G.L. Hunt, Jr. (2002): Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Mar. Ecol. Prog. Ser.*, 233, 89–103.
- Brodeur, R.D., and M.T. Wilson (1999): Pre-recruit walleye pollock in the eastern Bering Sea and Gulf of Alaska ecosystems. In *Proceedings of GLOBEC International Marine Science Symposium on Ecosystem Dynamics*, 238–251.
- Brodeur, R.D., P.A. Livingston, T.R. Loughlin, and A.B. Hollowed (eds.) (1996): Ecology of juvenile walleye pollock, *Theragra chalcogramma*. NOAA Tech. Rept. NMFS-126, 227 pp.
- * Brodeur, R.D., M.T. Wilson, L. Ciannelli, M.J. Doyle, and J.M. Napp (2002): Interannual and regional variability in distribution and ecology of juvenile pollock and their prey in frontal structures of the Bering Sea. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 6051–6067.
- Brodeur, R.D., M.T. Wilson, G.E. Walters, and I.V. Melnikov (1999b): Forage fish in the Bering Sea: Distribution, species associations and biomass trends. In *Dynamics of the Bering Sea*, T.R. Loughlin, and K. Ohtani (eds.), University of Alaska Sea Grant, AK-SG-99-03, Fairbanks, Alaska, 509–536.
- Brown, C.W., and G.P. Podesta (1997): Remote sensing of coccolithophore blooms in the western South Atlantic Ocean. *Remote Sens. Environ.*, 83–91.
- Brown, C.W., and J.A. Yoder (1993): Blooms of *Emiliania huxleyi* (Prymnesiophyceae) in surface waters of the Nova Scotian shelf and the Grand Bank. *J. Plankton Res.*, 15, 1429–1438.
- Brueggerman, J.J., G.W. Oliver, C. Fowler, K. Frost, K. Fay, C. Cowles, K. Schneider, and D. Calkins (1987): Marine Mammals. In *The St. George Basin Environment and Possible Consequences of Planned Offshore Oil and Gas Development*, M.J. Hameedi (ed.), U.S. Depart. Commerce, U.S. Dept. Interior, Outer Continental Shelf Environmental Assessment Program, Juneau, Alaska, 55–81.

- Buckley, T.W., A. Greig, J. Ianelli, P. Livingston, and G. Walters (2001): Spatial distribution and ontogenetic movement of walleye pollock in the eastern Bering Sea. Presented at the North Pacific Marine Science Organization (PICES), Victoria, B.C., Canada, October 5–13, 2001, Alaska Fisheries Science Center, 7600 Sandpoint Way NE, Seattle, WA 98115.
- Bulatov, O.A. (1995): Biomass variations of walleye pollock in the Bering Sea in relation to oceanological conditions. In *Climate Change and Northern Fish Populations*, R.J. Beamish (ed.), *Can. Spec. Publ. Fish. Aquat. Sci.*, 121, 631–640.
- * Busby, M.S., K.L. Mier, and R.D. Brodeur. Habitat associations of demersal fishes and crabs in the Bering Sea near the Pribilof Islands, Alaska. *Fish. Bull.* (submitted).
- Capriulo, G.M., E.B. Sherr, and B.F. Sherr (1991): Trophic behavior and related community feeding activities of heterotrophic marine protists. In *Protozoa and Their Role in Marine Processes*, P.C. Reid, C.M. Turley, and P.H. Burkil (eds.), Springer, Berlin, 219–265.
- Cavaliere, D.J., and S. Martin (1994): The contribution of Alaskan, Siberian and Canadian coastal polynyas to the cold halocline layer of the Arctic Ocean. *J. Geophys. Res.*, 99, 18,343–18,362.
- Ciannelli, L. (2002): Cross-scale analysis of the Pribilof Archipelago, southeast Bering Sea, with a focus on age-0 walleye pollock (*Theragra chalcogramma*). Ph.D. Dissertation, University of Washington, Seattle, WA 98195, 226 pp.
- * Ciannelli, L. (2002): Effects of spatial variability, associated with a frontal structure, on predictions of age-0 walleye pollock (*Theragra chalcogramma*) growth around the Pribilof Islands, Bering Sea. *Estuar. Coast. Shelf Sci.*, 55(1), 151–165.
- * Ciannelli, L., R.D. Brodeur, and J.M. Napp (2004): Foraging impact on zooplankton by age-0 walleye pollock (*Theragra chalcogramma*) around a front in the southeast Bering Sea. *Mar. Biol.*, 144, 515–526.
- * Ciannelli, L., R.D. Brodeur, G.L. Swartzman, and S.A. Salo (2002): Physical and biological factors influencing the spatial distribution of age-0 walleye pollock (*Theragra chalcogramma*) around the Pribilof Islands, Bering Sea. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 6109–6126.
- * Ciannelli, L., A.J. Paul, and R.D. Brodeur (2002): Regional, interannual and size-related variation of age 0 year walleye pollock whole body energy content around the Pribilof Islands, Bering Sea. *J. Fish Biol.*, 60(5), 1267–1279.
- * Ciannelli, L., B.W. Robson, R.C. Francis, K. Aydin, and R.D. Brodeur (2004): Boundaries of open marine ecosystems: An application to the Pribilof Archipelago, southeast Bering Sea ecological applications. *Ecol. Appl.*, 14(3), 942–953.
- Coachman, L.K. (1986): Circulation, water masses and fluxes on the southeastern Bering Sea shelf. *Cont. Shelf Res.*, 5, 23–108.
- Coachman, L.K., K. Aagaard, and R.B. Tripp (1975): Bering Strait: Regional physical oceanography. University of Washington Press, Seattle, WA, 172 pp.
- * Coachman, L.K., T.E. Whitledge, and J.J. Goering (1999): Silica in Bering Sea deep and bottom water. In *Dynamics of the Bering Sea*, T.R. Loughlin, and K. Ohtani (eds.), University of Alaska Sea Grant, Fairbanks, Alaska, AK-SG-99-03, 285–310.
- Connors, M.E., A.B. Hollowed, and E. Brown (2002): Retrospective analysis of Bering Sea bottom trawl surveys: Regime shift and ecosystem reorganization. *Prog. Oceanogr.*, 55, 209–222.
- Cooney, R.T., J.R. Allen, M.A. Bishop, D.L. Eslinger, T. Kline, B.L. Norcross, C.P. McRoy, J. Milton, J. Olsen, V. Patrick, A.J. Paul, D. Salmon, D. Schell, G.L. Thomas, S.L. Vaughan, and T.M. Willette (2001): Ecosystem controls of

- juvenile pink salmon (*Onchorynchus gorbuscha*) and Pacific herring (*Clupea pallasii*) populations in Prince William Sound, Alaska. *Fish. Oceanogr.*, 10(suppl. 1), 1–13.
- Cooney, R.T., and K.O. Coyle (1982): Trophic implications of cross-shelf copepod distributions in the southeastern Bering Sea. *Mar. Biol.*, 70, 187–196.
- Corkett, C.J., and I.A. McLaren (1978): The biology of *Pseudocalanus*. *Adv. Mar. Biol.*, 15, 1–231.
- * Coyle, K.O., and A.I. Pinchuk (2002): The abundance and distribution of euphausiids and zero-age pollock on the inner shelf of the southeast Bering Sea near the inner front in 1997–1999. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 6009–6030.
- * Coyle, K.O., and A.I. Pinchuk (2002): Climate-related differences in zooplankton density and growth on the inner shelf of the southeastern Bering Sea. *Prog. Oceanogr.*, 55(1–2), 177–194.
- Cullen, J.T., Y. Rosenthal, and P.G. Falkowski (2001): The effect of anthropogenic CO₂ on the carbon isotope composition of marine phytoplankton. *Limnol. Oceanogr.*, 46, 996–998.
- Dagg, M.J., M.E. Clarke, T. Nishiyama, and S.L. Smith (1984): Production and standing stock of copepod nauplii, food items for larvae of the walleye pollock *Theragra chalcogramma* in the southeastern Bering Sea. *Mar. Ecol. Prog. Ser.*, 19, 7–16.
- * Davis, R.F., G. Lazin, J. Bartlett, A.M. Ciotti, and P.J. Stabeno (1997): Remote sensing of a pigment patch in the southeastern Bering Sea. In *Ocean Optics XIII*, S.G. Ackleson (ed.), SPIE, International Society for Optical Engineering, Vol. 2963, 654–657.
- Decker, M.B., G.L. Hunt, Jr., and G.V. Byrd, Jr. (1995): The relationships among sea surface temperature, the abundance of juvenile walleye pollock (*Theragra chalcogramma*), and the reproductive performance and diets of seabirds at the Pribilof Islands, southeastern Bering Sea. In *Climate Change and Northern Fish Populations*, R.J. Beamish (ed.), *Can. Spec. Publ. Fish. Aquat. Sci.*, 121, 425–437.
- Dragoo, D.E., G.V. Byrd, and D.B. Irons (2001): Breeding status, population trends and diets of seabirds in Alaska, 2000. U.S. Fish and Wildlife Service Report AMNWR 2001/07, 77 pp.
- * Duffy-Anderson, J.T., M.S. Busby, K.L. Mier, and C. Deliyaniades. Spatial and temporal patterns in summer ichthyoplankton assemblages on the eastern Bering Sea shelf from 1996–2000. *Fish. Oceanogr.* (submitted).
- Dussart, B.M. (1965): Les différentes catégories de plancton. *Hydrobiologica*, 26, 72–74.
- Dwyer, D.A., K.M. Bailey, and P.A. Livingston (1987): Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, with special reference to cannibalism. *Can. J. Fish. Aquat. Sci.*, 44, 1972–1984.
- Ebbesmeyer, C.C., D.R. Cayan, D.R. Milan, F.H. Nichols, D.H. Peterson, and K.T. Redmond (1991): 1976 step in the Pacific climate: Forty environmental changes between 1968–1975 and 1977–1984. In *Proceedings of the Seventh Annual Climate (PACLIM) Workshop, April 1990*, J.L. Betancourt, and V.L. Tharp (eds.), California Department of Water Resources, Interagency Ecological Studies Program Technical Report 26, 115–126.
- Eslinger, D.L., and R.L. Iverson (2001): The effects of convective and wind-driven mixing on spring phytoplankton dynamics in the southeastern Bering Sea middle shelf domain. *Cont. Shelf Res.*, 21, 627–650.

*SEBSCC publication

- * Flint, M.V., I.N. Sukhanova, A.I. Kopylov, S.G. Poyarkov, and T.E. Whitledge (2002): Plankton distribution associated with frontal zones in the vicinity of the Pribilof Islands. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 6069–6093.
- Foukal, P. (2003): Can slow variations in solar luminosity provide the missing link between the sun and climate? *Eos Trans. AGU*, 84(22), 205, 208.
- Francis, R.C., and K.M. Bailey (1983): Factors affecting recruitment of selected gadoids in the northeastern Pacific and east Bering Sea. In *Year to Year: Interannual Variability of the Environment and Fisheries of the Gulf of Alaska and the Eastern Bering Sea*, W.S. Wooster (ed.), Washington Sea Grant, University of Washington, Seattle, WA, 17–22.
- Francis, R.C., S.R. Hare, A.B. Hollowed, and W.S. Wooster (1998): Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fish. Oceanogr.*, 7, 1–21.
- Goebel, M.E. (2002): Northern fur seal lactation, attendance and reproductive success in two years of contrasting oceanography. Ph.D. Thesis, University of California, Santa Cruz, 213 pp.
- Golet, G. H., and D.B. Irons (1999): Raising young reduces body condition and fat stores in black-legged kittiwakes. *Oecologia*, 120, 530–538.
- Golet, G.H., D.B. Irons, and J.A. Estes (1998): Survival costs of chick rearing in black-legged kittiwakes. *J. Anim. Ecol.*, 67, 827–841.
- Gower, J.R.F. (1997): Bright plankton blooms on the west coast of North America observed with AVHRR imagery. In *Monitoring Algal Blooms: New Techniques for Detecting Large-Scale Environmental Change*, M. Kahru, and C.W. Brown (eds.), Landes Bioscience, Austin, Texas, 25–41.
- Grebmeier, J.M. (1992): Benthic processes on the shallow continental shelf of the northern Bering and Chukchi Seas. In *Results of the Third Joint US-USSR Bering and Chukchi Seas Expedition (BERPAC), Summer 1988*, P.A. Nagel (ed.), U.S. Fish and Wildlife Service, Washington, DC, 243–251.
- Grebmeier, J.M., and L.W. Cooper (1994): A decade of benthic research on the continental shelves of the northern Bering and Chukchi Seas: Lessons learned. In *Bridges of Science Between North America and the Russian Far East*, R.H. Meehan, V. Serienko, and G. Weller (eds.), Fairbanks, Alaska: American Association for the Advancement of Science, Arctic Division, 87–98.
- Grebmeier, J.M., and L.W. Cooper (2002): Benthic processes in the Bering Strait region of the Arctic: Temporal/spatial variability and global change. *Eos Trans. AGU*, 83(4), Ocean Sciences Meeting Supplement, Abstract OS32M-01.
- Grebmeier, J.M., and K.H. Dunton (2000): Benthic processes in the northern Bering/Chukchi Seas: Status and global change. In *Impacts of Changes in Sea Ice and Other Environmental Parameters in the Arctic*, H.P. Huntington (ed.), Report of the Marine Mammal Commission Workshop, 15–17 February 2000, Girdwood Alaska. Available from the Marine Mammal Commission, Bethesda, Maryland.
- Haidvogel, D.B., H.G. Arango, K. Hedstrom, A. Beckmann, P. Malanotte-Rizzoli, and A.F. Shchepetkin (2000): Model evaluation experiments in the North Atlantic basin: Simulations in nonlinear terrain-following coordinates. *Dyn. Atmos. Oceans*, 32, 239–281.
- Hare, S.R., and R.C. Francis (1995): Climate change and salmon production in the northeast Pacific Ocean. In *Climate Change and Northern Fish Populations*, R.J. Beamish (ed.), *Can. Spec. Publ. Fish. Aquat. Sci.*, 121, 357–372.
- Hare, S.R., and N.J. Mantua (2000): Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog. Oceanogr.*, 47, 103–146.

- Hare, S.R., N.J. Mantua, and R.C. Francis (1999): Inverse production regimes: Alaskan and West Coast Pacific salmon. *Fisheries*, 24, 6–14.
- Hastie, T., and R. Tibshirani (1990): Generalized additive models. Chapman and Hall, London.
- Hatch, S.A. (1987): Did the 1982–1983 El Niño–Southern Oscillation affect seabirds in Alaska? *Wilson Bull.*, 99(3), 469–474.
- * Hermann, A.J., D.B. Haidvogel, D. Musgrave, and P.J. Stabeno (2002): A regional tidal/subtidal circulation model of the southeastern Bering Sea: development, sensitivity analyses and hindcasting. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 5945–5967.
- Hermann, A.J., P.J. Stabeno, D.B. Haidvogel, and D.L. Musgrave (2002): A regional tidal/subtidal circulation model of the southeastern Bering Sea: Development, sensitivity analyses and hindcasting. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49, 5945–5967.
- Hinckley, S. (1987): The reproductive biology of walleye pollock, *Theragra chalcogramma*, in the Bering Sea, with reference to spawning stock structure. *Fish. Bull.*, 85, 481–498.
- Hirons, A.C., D.M. Schell, and B.P. Finny (2001): Temporal records of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in North Pacific pinnipeds: Inferences regarding environmental change and diet. *Oecologia*, 129, 591–601.
- Holligan, P.M., M. Viollier, D.S. Harbour, P. Camus, and M. Champagne-Philippe (1983): Satellite and ship studies of coccolithophore production along a continental shelf edge. *Nature*, 304, 339–342.
- Hollowed, A.B., S.R. Hare, and W.S. Wooster (2001): Pacific basin climate variability and patterns of northeast Pacific marine fish production. *Prog. Oceanogr.*, 49, 257–282.
- Hollowed, A.B., and W.S. Wooster (1995): Decadal-scale variations in the eastern subarctic Pacific: II Responses of Northeast Pacific fish stocks. In *Climate Change and Northern Fish Populations*, R.J. Beamish (ed.), *Can. Spec. Publ. Fish. Aquat. Sci.*, 121, 373–385.
- Honkalehto, T., W. Patton, S. De Blois, and N. Williamson (2002): Echo integration-trawl survey results for walleye pollock (*Theragra chalcogramma*) on the Bering Sea shelf and slope during summer 2000. NOAA Tech. Memo. NMFS-AFSC-126, 66 pp.
- Hood, D.W. (1999): PROBES: Processes and resources of the eastern Bering Sea shelf. In *Dynamics of the Bering Sea*, T.R. Loughlin, and K. Ohtani (eds.), University of Alaska Sea Grant, AK-SG-99-03, Fairbanks, AK, 387–407.
- Howell-Kubler, A., E. Lessard, and J. Napp (1996): Springtime microprotozoan abundance and biomass in the southeastern Bering Sea and Shelikof Strait, Alaska. *J. Plankton Res.*, 18, 731–745.
- * Hunt, G.L., Jr., C.L. Baduini, R.D. Brodeur, K.O. Coyle, N.B. Kachel, J.M. Napp, S.A. Salo, J.D. Schumacher, P.J. Stabeno, D.A. Stockwell, T.E. Whitledge, and S.I. Zeeman (1999): The Bering Sea in 1998: A second consecutive year of extreme weather-forced anomalies. *Eos Trans. AGU*, 80(561), 565–566.
- * Hunt, G.L., Jr., C.L. Baduini, and J. Jahncke (2002): Diets of short-tailed shearwaters in the southeastern Bering Sea. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 6147–6156.
- * Hunt, G.L., Jr., and G.V. Byrd, Jr. (1999): Marine bird populations and carrying capacity of the eastern Bering Sea. In *Dynamics of the Bering Sea*, T.R. Loughlin, and K. Ohtani (eds.), University of Alaska Sea Grant, Fairbanks, Alaska, AK-SG-99-03, 631–650.

- Hunt, G.L., Jr., K.O. Coyle, S. Hoffman, M.B. Decker, and E.N. Flint (1996a): Foraging ecology of short-tailed shearwaters near the Pribilof Islands, Bering Sea. *Mar. Ecol. Prog. Ser.*, 141, 1–11.
- Hunt, G.L., Jr., M.B. Decker, and A.S. Kitaysky (1996b): Fluctuations in the Bering Sea ecosystem as reflected in the reproductive ecology and diets of kittiwakes on the Pribilof Islands, 1975 to 1990. In *Aquatic Predators and Their Prey*, S. Greenstreet, and M. Tasker (eds.), Blackwell, London, 142–153.
- Hunt, G.L., Jr., and N.M. Harrison (1990): Foraging habitat and prey taken by Least Auklets at King Island, Alaska. *Mar. Ecol. Prog. Ser.*, 65, 141–150.
- Hunt, G.L., Jr., N.M. Harrison, and T. Cooney (1990): Foraging of Least Auklets: The influence of hydrographic structure and prey abundance. *Stud. Avian Biol.*, 14, 7–22.
- Hunt, G.L., Jr., A.S. Kitaysky, M.B. Decker, D.E. Dragoo, and A.M. Springer (1996c): Changes in the distribution and size of juvenile walleye pollock as indicated by seabird diets at the Pribilof Islands and by bottom trawl surveys in the eastern Bering Sea. In *Ecology of Juvenile Walleye Pollock, *Theragra chalcogramma**, R.D. Brodeur, P.A. Livingston, T.R. Loughlin, and A.B. Hollowed (eds.), NOAA Tech. Rept. NMFS-126, 133–147.
- * Hunt, G.L., Jr., and P.J. Stabeno (2002): Climate change and the control of energy flow in the southeastern Bering Sea. *Prog. Oceanogr.*, 55(1–2), 5–22.
- * Hunt, G.L., Jr., P.J. Stabeno, G.E. Walters, E.H. Sinclair, R.D. Brodeur, J.M. Napp, and N.A. Bond (2002): Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 5821–5853.
- Huntley, M.E., and M.D.G. Lopez (1992): Temperature-dependent production of marine copepods: A global analysis. *Am. Nat.*, 140, 201–242.
- Ianelli, J.N., T. Buckley, T. Honkalehto, N. Williamson and G. Walters (2001): Bering Sea-Aleutian Islands Walleye Pollock Assessment for 2002. In *Stock assessment and Fishery Evaluation Report for the Groundfish Resources of the Bering Sea/Aleutian Islands Regions*, North Pacific Fishery Management Council, Anchorage, AK, Section 1:1–105.
- Ianelli, J., L.W. Fritz, T. Honkalehto, N. Williamson and G. Walters (1998): Eastern Bering Sea walleye pollock stock assessment with yield considerations for 1999. In *Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Bering Sea/Aleutian Islands Regions*, pp. 31–111, Groundfish Plan Team for the Bering Sea-Aleutian Islands Region (ed.), North Pacific Fishery Management Council, 605 W. 4th Ave., Suite 306, Anchorage, AK 99501, 560 pp.
- IARPC (Interagency Arctic Research Planning Committee) (2001): United States Arctic Research Plan: Biennial Revision 2002–2006. Office of Polar Programs, National Science Foundation, 84 pp.
- Iida, T., S-I. Saitoh, T. Miyamura, M. Toratani, H. Fukushima, and N. Shiga (2002): Temporal and spatial variability of coccolithophore blooms in the eastern Bering Sea, 1998–2001. *Prog. Oceanogr.*, 55, 165–175.
- Ingraham, W.J., Jr., and R.K. Miyahara (1988): Ocean surface current simulations in the North Pacific Ocean and Bering Sea (OSCURS-Numerical Model). NOAA Tech. Memo. NMFS-F/NWC-130, 155 pp.
- Irons, D.B. (1992): Aspects of foraging behavior and reproductive biology of the black-legged Kittiwake. Ph.D. Dissertation, University of California, Irvine, 143 pp.
- Iverson, R.L., L.K. Coachman, R.T. Cooney, T.S. English, J.J. Goering, G.L. Hunt, Jr., M.C. Macauley, C.P. McRoy, W.S. Reeburgh, and T.E. Whitledge (1979a):

*SEBSCC publication

- Ecological significance of fronts in the southeastern Bering Sea. In *Ecological Processes in Coastal and Marine Systems*, R.J. Livingston (ed.), Plenum Press, New York, 437–466.
- Iverson, S.J., K.J. Frost, and S.L.C. Lang (2002): Fat content and fatty acid composition of forage fish and invertebrates in Prince William Sound, Alaska: Factors contributing to among and within species variability. *Mar. Ecol. Prog. Ser.*, 241, 161–181.
- Iverson, R.L., T.E. Whitley, and J.J. Goering (1979b): Chlorophyll and nitrate fine structure in the southeastern Bering Sea shelf break front. *Nature*, 281, 664–666.
- * Jahneke, J., K.O. Coyle, S.I. Zeeman, N.B. Kachel, and G.L. Hunt, Jr. Distribution of foraging shear waters with respect to the inner front of the southeastern Bering Sea. *Mar. Ecol. Prog. Ser.* (submitted).
- Johnson, G.C., P.J. Stabeno, and S.C. Riser (2004): The Bering Slope Current system revisited. *J. Phys. Oceanogr.*, 34(2), 384–398.
- * Jurado-Molina, J., and P.A. Livingston (2002): Climate forcing effects on trophically linked groundfish populations: Implications for fisheries management. *Can. J. Fish. Aquatic Sci.*, 59, 1941–1951.
- * Kachel, N.B., G.L. Hunt, Jr., S.A. Salo, J.D. Schumacher, P.J. Stabeno, and T.E. Whitley (2002): Characteristics and variability of the inner front of the southeastern Bering Sea. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 5889–5909.
- Kalnay, E., M. Kanamitsu, R. Kistler, W. Collins, D. Deaven, L. Gandin, M. Iredell, S. Saha, G. White, J. Woollen, Y. Zhu, A. Leetmaa, B. Reynolds, M. Chelliah, W. Ebisuzaki, W. Higgins, J. Janowiak, K. C. Mo, C. Ropelewski, J. Wang, R. Jenne, and D. Joseph (1996): The NCEP/NCAR 40-Year Reanalysis Project. *Bull. Am. Meteorol. Soc.*, 77, 437–472.
- Kendall, A.W. (2001): Specific gravity and vertical distribution of walleye pollock (*Theragra chalcogramma*) eggs. AFSC Processed Report 2001–01, January 2001, 45 pp.
- Kitaysky, A.S., G.L. Hunt, Jr., E.N. Flint, M.A. Rubega, and M.B. Decker (2000): Resource allocation in breeding seabirds: Responses to fluctuations in their food supply. *Mar. Ecol. Prog. Ser.*, 206, 283–296.
- Kitaysky, A.S., E.V. Kitayskaia, J.C. Wingfield, and J.F. Piatt (2001a): Dietary restriction causes chronic elevation of corticosterone and enhances stress response in red-legged kittiwake chicks. *J. Comp. Physiol., B*, 171, 701–709.
- Kitaysky, A.S., E.V. Kitaysky, J.F. Piatt, and J.C. Wingfield (2003): Benefits and costs of increased levels of corticosterone in seabird chicks. *Horm. Behav.*, 43, 140–149.
- Kitaysky, A.S., J.F. Piatt, and J.C. Wingfield (2002): Are seabirds breeding in the southeastern Bering Sea food-limited? Final Report to the North Pacific Marine Research Program, North Pacific Research Board, Anchorage, Alaska.
- Kitaysky, A.S., J.F. Piatt, J.C. Wingfield, and M. Romano (1999a): The adrenocortical stress-response of black-legged kittiwake chicks in relation to dietary restrictions. *J. Comp. Physiol., B*, 169, 303–310.
- Kitaysky, A.S., J.C. Wingfield, and J.F. Piatt (1999b): Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. *Funct. Ecol.*, 13, 577–584.
- Kitaysky, A.S., J.C. Wingfield, and J.F. Piatt (2001b): Corticosterone facilitates begging and affects resource allocation in the black-legged kittiwake. *Behav. Ecol.*, 12, 619–625.
- Klyashtorin, L.B., and F.N. Rukhlov (1998): Long-term climate change and pink salmon stock fluctuations. *N. Pac. Anadromous Fish Comm. Bull.*, 1, 464–479.

- Kruse, G.H. (1998): Salmon run failures in 1997–98: a link to anomalous conditions? *Alaska Fish. Bull.*, 5, 55–63.
- * Ladd, C., G.L. Hunt, Jr., and P.J. Stabeno: Climate, mixing, and phytoplankton on the southeastern Bering Sea shelf: A synthesis (unpublished manuscript).
- Lang, G.M., R.D. Brodeur, J.M. Napp, and R. Schabetsberger (2000): Variation in groundfish predation on juvenile walleye pollock relative to hydrographic structure near the Pribilof Islands, Alaska. *ICES J. Mar. Sci.*, 57, 265–271.
- Lang, G.M., C.W. Derrah, and P.A. Livingston (2003): Groundfish food habits and predation on commercially important prey species in the eastern Bering Sea from 1993 to 1996. U.S. Department of Commerce AFSC Processed Report 2003–2004. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, 351 pp. preparation).
- Leatherwood, S., A.E. Bowles, and R.R. Reeves (1983): Aerial surveys of marine mammals in the southeastern Bering Sea. National Oceanic and Atmospheric Administration/Outer Continental Shelf Environmental Assessment Program, Environmental Assessment of the Alaskan Continental Shelf, Final Reports of Principal Investigators, 42, 147–473.
- Lee, S.H. (2000): Use of Beaufort Sea as feeding habitat by bowhead whales (*Balaena mysticetus*) as indicated by stable isotope ratios. MS Thesis, University of Alaska Fairbanks, Fairbanks, AK 99775, 95 pp.
- Livingston, P.A. (ed.) (1991): Groundfish food habits and predation on commercially important prey species in the eastern Bering Sea from 1984 to 1986. NOAA Tech. Memo. NMFS-F/NWC-207, 240 pp.
- Livingston, P.A. (1993): The importance of predation by groundfish, marine mammals, and birds on walleye pollock *Theragra chalcogramma* and Pacific herring *Clupea pallasii* in the eastern Bering Sea. *Mar. Ecol. Prog. Ser.*, 102, 205–215.
- Livingston, P.A., and Y. deReynier (1996): Groundfish food habits and predation on commercially important prey species in the eastern Bering Sea from 1990 to 1992. U.S. Department of Commerce AFSC Processed Report 96-04, 214 pp.
- Livingston, P.A., and J. Jurado-Molina (2000): A multispecies virtual population analysis of the eastern Bering Sea. *ICES J. Mar. Sci.*, 57, 294–299.
- Livingston, P.A., and G.M. Lang (1996): Interdecadal comparisons of walleye pollock, *Theragra chalcogramma*, cannibalism in the eastern Bering Sea. In *Ecology of Juvenile Walleye Pollock, Theragra chalcogramma*, R.D. Brodeur, P.A. Livingston, T.R. Loughlin, and A.B. Hollowed (eds.), NOAA Tech. Rept. NMFS-126, 115–124.
- Livingston, P.A., and R.D. Methot (1998): Incorporation of predation into a population assessment model of eastern Bering Sea walleye pollock. In *Fishery Stock Assessment Models*, Alaska Sea Grant College Program, AK-SG-98-01, 16 pp.
- Livingston, P.A., L.-L. Low, and R.J. Marasco (1999): Eastern Bering Sea trends. In *Large Marine Ecosystems of the Pacific Rim: Assessment, Sustainability, and Management*, K. Sherman, and Q. Tang (eds.), Blackwell Science, Inc., Malden, MA, USA, 140–162.
- Livingston, P.A., A. Ward, G.M. Lang, and M.-S. Yang (1993): Groundfish food habits and predation on commercially important prey species in the eastern Bering Sea from 1987 to 1989. NOAA Tech. Memo. NMFS-AFSC-11, 192 pp.
- Loughlin, T.R., G.A. Antonelis, J.D. Baker, A.E. York, C.W. Fowler, R.L. DeLong, and H.W. Braham (1994): Status of the northern fur seal population in the United States during 1992. In *Fur Seal Investigations, 1994*, E.H. Sinclair (ed.), NOAA Tech. Memo. NMFS-AFSC-45.
- Mackas, D.L., R. Goldblatt, and A.G. Lewis (1998): Interdecadal variation in de-

*SEBSCC publication

- velopmental timing of *Neocalanus plumchrus* populations at Ocean Station P in the subarctic North Pacific. *Can. J. Fish. Aquatic Sci.*, 55, 1878–1893.
- Mackenzie, B.R., T.J. Miller, S. Cyr, and W.C. Leggett (1994): Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. *Limnol. Oceanogr.*, 39(8), 1790–1799.
- Macklin, S.A. (1999a): Bering Sea FOCI. In *Dynamics of the Bering Sea*, T.R. Loughlin, and K. Ohtani (eds.), Univ. of Alaska Sea Grant AK-SG-99-03, Fairbanks, Alaska, 733–751.
- * Macklin, S.A. (1999b): Southeast Bering Sea Carrying Capacity (SEBSCC). *PICES Press*, 7(2), 24–28, 34.
- * Macklin, S.A. (2001): Bering Sea and North Pacific Ocean theme page: Providing Internet-based information to scientists, managers and educators for six years. *PICES Press*, 9(1), 29–30, 34.
- * Macklin, S.A., G.L. Hunt, Jr., and J.E. Overland (2002): Collaborative research on the pelagic ecosystem of the southeastern Bering Sea shelf. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 5813–5819.
- * Macklin, S.A., V.I. Radchenko, S. Saitoh, and P.J. Stabeno (2002): Variability in the Bering Sea ecosystem. *Prog. Oceanogr.*, 55(1–2), 1–4.
- * Macklin, S.A., and P.J. Stabeno (2001): Marine ecosystem studies of physical and biological interactions in the eastern Bering Sea and western Gulf of Alaska. In *Arctic Research of the United States*, 14(2), National Science Foundation, Arlington, Virginia, 25–32.
- Mantua, N.J., and S.R. Hare (2002): The Pacific Decadal Oscillation. *J. Oceanogr.*, 58, 35–44.
- Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace, and R.C. Francis (1997): A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.*, 78, 1069–1079.
- Marchesiello, P., J.C. McWilliams, and A.F. Shchepetkin (2001): Open boundary conditions for long-term integration of regional oceanic models. *Ocean Model.*, 3, 1–20.
- Martin, J.E., R.D. Grauman, and N. Marsili (2001): Surface cyclolysis in the North Pacific Ocean. Part I: A synoptic climatology. *Mon. Weather Rev.*, 129, 748–765.
- McFarlane, G.A., J.R. King, and R.J. Beamish (2000): Have there been recent changes in climate? Ask the fish. *Prog. Oceanogr.*, 47, 147–169.
- McGowan, J.A. (1990): Climate and change in oceanic ecosystems: the value of time-series data. *Trends in Ecological Evolution*, 5, 293–299.
- McLaren, I.A. (1963): Effects of temperature on growth of zooplankton and the adaptive significance of vertical migration. *J. Fish. Res. Board Can.*, 20, 685–727.
- McRoy, C.P., and J.J. Goering (1974): The influence of ice on the primary productivity of the Bering Sea. In *Oceanography of the Bering Sea With Emphasis on Renewable Resources*, D.W. Hood, and E.J. Kelly (eds.), Occasional Publication No. 2, Institute of Marine Sciences, University of Alaska, Fairbanks, Alaska, 403–421.
- Megrey, B.A., and S. Hinckley (2001): Effect of turbulence on feeding of larval fishes: a sensitivity analysis using an individual-based model. *ICES J. Mar. Sci.*, 58, 1015–1029.
- Megrey, B.A., A.B. Hollowed, S.R. Hare, S.A. Macklin, and P.J. Stabeno (1996): Contribution of FOCI research to forecasts of year-class strength of walleye pollock in Shelikof Strait, Alaska. *Fish. Oceanogr.*, 5(suppl. 1), 189–203.

*SEBSCC publication

- Merrick, R.L. (1997): Current and historical roles of apex predators in the Bering Sea ecosystem. *J. Northwest Atl. Fish. Sci.*, 22, 343–355.
- Merrick, R.L., M.K. Chumbley, and G.V. Byrd (1997): A potential relationship between the diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska. *Can. J. Fish. Aquatic Sci.*, 54, 1342–1348.
- Minobe, S. (1999): Resonance in bidecadal and pentadecadal climate oscillations over the North Pacific: Role in climate regime shifts. *Geophys. Res. Lett.*, 26, 855–858.
- Mitchell-Innes, B.A., and A. Winter (1987): Coccolithophores: A major component in mature upwelled waters off Cape Peninsula, South Africa in March, 1983. *Mar. Biol.*, 95, 25–30.
- Mock, D.W., H. Drummond, and C.H. Stinson (1990): Avian siblicide. *Am. Sci.*, 78, 438–449.
- Moore, S.E., J.M. Waite, N.A. Friday, and T. Honkalehto (2002): Cetacean distribution and relative abundance on the central-eastern and the southeastern Bering Sea shelf with reference to oceanographic domains. *Prog. Oceanogr.*, 55, 249–261.
- Moore, S.E., M. Waite, L. Mazzuca, and R.C. Hobbs (2000): Provisional estimates of Mysticete whale abundance on the central Bering Sea shelf. *J. Cetacean Res. Manage.*, 2, 227–234.
- Nakatani, T., and T. Maeda (1984): Thermal effect on the development of walleye pollock eggs and on their upward speed to the surface. *Bull. Jap. Soc. Sci. Fish.*, 50, 937–942.
- * Napp, J.M., C.T. Baier, K.O. Coyle, R.D. Brodeur, N. Shiga, and K.L. Mier (2002): Interannual and decadal variability in zooplankton communities of the southeast Bering Sea shelf. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 5991–6008.
- * Napp, J.M., and G.L. Hunt, Jr. (2001): Anomalous conditions in the south-eastern Bering Sea 1997: Linkages among climate, weather, ocean, and biology. *Fish. Oceanogr.*, 10(1), 61–68.
- Napp, J.M., A.W. Kendall, Jr., and J.D. Schumacher (2000): A synthesis of biological and physical processes affecting the feeding environment of larval walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. *Fish. Oceanogr.*, 9, 147–162.
- NCDC (National Climatic Data Center) (2004): Global surface temperature anomalies. <http://www.ncdc.noaa.gov/oa/climate/research/anomalies/anomalies.html>.
- Niebauer, H.J. (1983): Multiyear sea ice variability in the eastern Bering Sea: an update. *J. Geophys. Res.*, 88, 2733–2742.
- * Niebauer, H.J. (1998): Variability in Bering Sea ice cover as affected by a regime shift in the North Pacific in the period 1947–1996. *J. Geophys. Res.* 103(C12), 27,717–27,737.
- Niebauer, H.J., V. Alexander, and R.T. Cooney (1981): Primary production at the eastern Bering Sea ice edge: The physical and biological regimes. In *The Eastern Bering Sea Shelf: Oceanography and Resources*, D.W. Hood, and J.A. Calder (eds.), Vol. 1, U.S. Government Printing Office, Washington, D.C., 763–780.
- Niebauer, H.J., V. Alexander, and S.M. Henrichs (1990): Physical and biological oceanographic interaction in the spring bloom at the Bering Sea marginal ice edge zone. *J. Geophys. Res.*, 95, 22,229–22,242.
- Niebauer, H.J., V. Alexander, and S.M. Henrichs (1995): A time-series study of the spring bloom at the Bering Sea ice edge I: Physical processes, chlorophyll and nutrient chemistry. *Cont. Shelf Res.*, 15, 1859–1878.

- * Niebauer, H.J., N.A. Bond, L.P. Yakunin, and V.V. Plotnikov (1999): An update on the climatology and sea ice of the Bering Sea. In *Dynamics of the Bering Sea*, T.R. Loughlin and K. Ohtani (eds.), University of Alaska Sea Grant, Fairbanks, Alaska, AK-SG-99-03, 29–60.
- Nishiyama, T. (1974): Energy requirements of sockeye salmon in Bristol Bay in the eastern Bering Sea. In *Oceanography of the Bering Sea With Emphasis on Renewable Resources*, D.W. Hood, and E.J. Kelly (eds.), Institute of Marine Sciences Occasional Publication 2, University of Alaska, Fairbanks, Alaska, 321–343.
- NMFS (National Marine Fisheries Service) (1993): Final conservation plan for the northern fur seal (*Callorhinus ursinus*). Prepared by the NMFS/Alaska Fisheries Science Center/National Marine Mammal Laboratory, Seattle, WA and the NMFS/Office of Protected Resources, Silver Spring, MD, 80 pp.
- NMFS (National Marine Fisheries Service) (1995): Status review of the United States Steller sea lion (*Eumetopias jubatus*) population. Prepared by the NMFS/Alaska Fisheries Science Center/National Marine Mammal Laboratory, Seattle, WA, 45 pp.
- NMFS (National Marine Fisheries Service) (2002): Fewer northern fur seal pups born in 2002. National Marine Fisheries Service, Alaska Region Press Release, 19 December 2002, <http://www.fakr.noaa.gov>.
- NMML (National Marine Mammal Laboratory) (1994): Status review of Steller sea lions (*Eumetopias jubatus*). National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, Seattle, WA, 40 pp.
- NPAFC (North Pacific Anadromous Fish Commission) (2001): Draft plan for NPAFC Bering-Aleutian International Survey (BASIS). NPAFC Doc. 579, Rev. 1, 27 pp.
- NPFMC (North Pacific Fishery Management Council) (2000): Stock Assessment and Fishery Evaluation document.
- NPFMC (North Pacific Fishery Management Council) (2001): Stock Assessment and Fishery Evaluation document.
- NPFMC (North Pacific Fishery Management Council) (2002): Stock Assessment and Fishery Evaluation document.
- NRC (National Research Council) (1996): The Bering Sea Ecosystem. National Academy Press, Washington, D.C., 324 pp.
- NRC (National Research Council) (2003): Decline of the Steller sea lion in Alaskan waters: Untangling food webs and fishing nets. National Academy Press, Washington, D.C.
- Ohtani, K., and T. Azumaya (1995): Influence of interannual changes in ocean conditions on the abundance of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. In *Climate Change and Northern Fish Populations*, R.J. Beamish (ed.), *Can. Spec. Publ. Fish. Aquat. Sci.*, 121, 87–95.
- Oka, N., and N. Maruyama (1986): Mass mortality of short-tailed shearwaters along the Japanese coast. *Tori*, 34, 97–104.
- Okkonen, S.R. (2001): Altimeter observations of the Bering Slope Current eddy field. *J. Geophys. Res.*, 106, 2465–2476.
- * Olson, M.B., and S.L. Strom (2002): Phytoplankton growth, microzooplankton herbivory and community structure in the southeast Bering Sea: Insight into the formation and temporal persistence of an *Emiliania huxleyi* bloom. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 5969–5990.
- Overland, J.E., J.M. Adams, and N.A. Bond (1999): Decadal variability in the Aleutian low and its relation to high-latitude circulation. *J. Clim.*, 12, 1542–1548.

- * Overland, J.E., J.M. Adams, and H.O. Mofjeld (2001): Chaos in the North Pacific: spatial modes and temporal irregularity. *Prog. Oceanogr.*, 47, 337–354.
- * Overland, J.E., N.A. Bond, and J.M. Adams (2001): North Pacific atmospheric and SST anomalies in 1997: Links to ENSO? *Fish. Oceanogr.*, 10(1), 69–80.
- * Overland, J.E., N.A. Bond, and J.M. Adams (2002): The relation of surface forcing of the Bering Sea to large-scale climate patterns. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 5855–5868.
- Overland, J.E., and C.H. Pease (1982): Cyclonic climatology of the Bering Sea and its relation to sea ice extent. *Mon. Weather Rev.*, 110, 5–13.
- Overland, J.E., M.C. Spillane, H.E. Hurlburt, and A.J. Wallcraft (1994): A numerical study of the circulation of the Bering Sea basin and exchange with the North Pacific Ocean. *J. Phys. Oceanogr.*, 24, 736–758.
- * Overland, J.E., and P.J. Stabeno (2004): Is the climate of the Bering Sea warming and affecting the ecosystem? *Eos, Trans. AGU* (in press).
- Pease, C.H. (1980): Eastern Bering Sea ice processes. *Mon. Weather Rev.*, 108, 2015–2023.
- Percival, D.B., J.E. Overland, and H.O. Mofjeld (2001): Interpretation of North Pacific variability as a short- and long-memory process. *J. Clim.*, 14, 4545–4559.
- Peterson, R.T., and J. Fisher (1955): *Wild America*. Houghton Mifflin Co., Boston, MA, 434 pp.
- Peterson, W.T., J.E. Kister, and L.R. Feinberg (2002): The effects of the 1997–1999 El Niño-La Niña events on the hydrography and zooplankton off the Central Oregon coast. *Prog. Oceanogr.*, 54, 381–398.
- Piatt, J.F., and P. Anderson (1996): Response of common murrelets to the Exxon Valdez oil spill and long-term changes in the Gulf of Alaska marine ecosystem. *Am. Fish. Soc. Symp.*, 18, 720–737.
- Piatt, J.F., and T.I. van Pelt (1997): Mass-mortality of guillemots (*Uria aalge*) in the Gulf of Alaska in 1993. *Mar. Pollut. Bull.*, 34, 656–662.
- Polovina, J.J. (1984): The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs*, 3, 1–11.
- Polovina, J.J., G.T. Mitchum, and G.T. Evans (1995): Decadal and basin-scale variations in mixed layer depth and the impact on biological production in the Central and North Pacific. *Deep-Sea Res.*, 42, 1701–1716.
- Price, J.F., R.A. Weller, and R. Pinkel (1986): Diurnal cycling: Observations and models of the upper ocean response to diurnal heating, cooling and wind mixing. *J. Geophys. Res.*, 91, 8411–8427.
- Quinn, T.J., and H.J. Niebauer (1995): Relation of eastern Bering Sea walleye pollock (*Theragra chalcogramma*) recruitment to environmental and oceanographic variables. In *Climate Change and Northern Fish Populations*, R.J. Beamish (ed.), *Can. Spec. Publ. Fish. Aquat. Sci.*, 121, 497–507.
- Reed, R.K. (1995): On the variable subsurface environment of fish stocks in the Bering Sea. *Fish. Oceanogr.*, 4, 317–323.
- Reed, R.K. (1998): Confirmation of a convoluted flow over the Southeastern Bering Sea Shelf. *Cont. Shelf Res.*, 18, 99–103.
- Reed, R.K. (1999): A time series of temperature, salinity, and geopotential across the southeastern Bering Sea shelf, 1995–1999. NOAA Tech. Rept. ERL 455-PMEL 43 (NTIS PB2000-100564), 15 pp.
- Reed, R.K., and P.J. Stabeno (1996): On the climatological mean circulation over the eastern Bering Sea shelf. *Cont. Shelf Res.*, 16(10), 1297–1305.

- Reed, R.K., and P.J. Stabeno (1999): The Aleutian North Slope Current. In *Dynamics of the Bering Sea*, T.R. Loughlin, and K. Ohtani (eds.), University of Alaska Sea Grant, AK-SG-99-03, 177–192.
- * Reed, R.K., and P.J. Stabeno (2002): Surface heat fluxes and subsurface heat content at a site over the southeastern Bering Sea shelf, May–July 1996. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 5911–5917.
- Rho, T. (2000): Carbon and nitrogen uptake dynamics during 1997 and 1998: Anomalous conditions in the Bering Sea. M.S. Thesis, University of Alaska Fairbanks, 95 pp.
- * Rho, T., J.J. Goering, T.E. Whitley, and D.A. Stockwell. Carbon and nitrogen uptakes and nutrients response to the warm conditions in the southeastern Bering Sea during 1997 and 1998. *Cont. Shelf Res.* (in revision).
- Rivkin, R.B., J.N. Putland, M.R. Anderson, and D. Deibel (1999): Microzooplankton bacterivory and herbivory in the NE subarctic Pacific. *Deep-Sea Res. (2 Top. Stud. Oceanogr.)*, 46, 2579–2618.
- Roach, A.T., K. Aagaard, C.H. Pease, S.A. Salo, T. Weingartner, V. Pavlov, and M. Kulakov (1995): Direct measurements of transport and water properties through Bering Strait. *J. Geophys. Res.*, 100, 18,443–18,457.
- Robertson, J.E., C. Robinson, D.R. Turner, P. Holligan, A.J. Watson, P. Boyd, E. Fernandez, and M. Finch (1994): The impact of a coccolithophore bloom on oceanic carbon uptake in the northeast Atlantic during summer 1991. *Deep-Sea Res.*, 41, 297–314.
- Robson, B.W. (2002): The relationship between foraging areas and breeding sites of lactating northern fur seals, *Callorhinus ursinus* in the eastern Bering Sea. M.S. Thesis, University of Washington, Seattle, WA, 62 pp.
- Rosenkranz, G.E., A.V. Tyler, and G.H. Kruse (2001): Effects of water temperature and wind on year-class strength of Tanner crabs in Bristol Bay, Alaska. *Fish. Oceanogr.*, 10(1), 1–12.
- Royer, T.C. (1982): Coastal fresh water discharge in the Northeast Pacific. *J. Geophys. Res.*, 87, 2017–2021.
- Russell, R.W., N.M. Marrison, and G.L. Hunt, Jr. (1999): Foraging at a front: hydrography, zooplankton and avian planktivory in the northern Bering Sea. *Mar. Ecol. Prog. Ser.*, 182, 77–93.
- Sambrotto, R.N., and J.J. Goering (1983): Interannual variability of phytoplankton and zooplankton production on the southeast Bering Sea shelf. In *From Year to Year*, W.S. Wooster (ed.), Washington Sea Grant, Seattle, WA, 161–177.
- Sambrotto, R.N., H.J. Niebauer, J.J. Goering, and R.L. Iverson (1986): Relationships among vertical mixing, nitrate uptake and phytoplankton growth during the spring bloom in the Southeast Bering Sea middle shelf. *Cont. Shelf Res.*, 5, 161–198.
- * Schabetsberger, R.D., R.D. Brodeur, L. Ciannelli, J.M. Napp, and G.L. Swartzman (2000): Diel vertical migration and interaction of zooplankton and juvenile walleye pollock (*Theragra chalcogramma*) at a frontal region near Pribilof Islands, Bering Sea. *ICES J. Mar. Sci.*, 57(4), 1283–1295.
- Schell, D.M. (2000): Declining carrying capacity in the Bering Sea: Isotopic evidence from whale baleen. *Limnol. Oceanogr.*, 45, 459–462.
- Schell, D.M. (2001): Carbon isotope ratio variations in the Bering Sea biota: The role of anthropogenic carbon dioxide. *Limnol. Oceanogr.*, 46, 999–1000.
- Schell, D.M., B.A. Barnett, and K. Vinette (1998): Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi, and Beaufort Seas. *Mar. Ecol. Prog. Ser.*, 162, 11–23.

*SEBSCC publication

- Schnute, J.T. (1994): A general framework for developing sequential fisheries models. *Can. J. Fish. Aquat. Sci.*, 51, 1676–1688.
- * Schumacher, J.D. (2000): Regime shift theory: A review of changing environmental conditions in the Bering Sea and eastern North Pacific. In *Proceedings of the Fifth North Pacific Rim Fisheries Conference*, 1–3 December 1999, Anchorage, Alaska, 127–142.
- Schumacher, J.D., and V. Alexander (1999): Variability and the role of the physical environment in the Bering Sea ecosystem. In *Dynamics of the Bering Sea*, T.R. Loughlin, and K. Ohtani (eds.), University of Alaska Sea Grant, AK-SG-99-03, Fairbanks, Alaska, 147–160.
- Schumacher, J.D., N.A. Bond, R.D. Brodeur, P.A. Livingston, J.M. Napp, and P.J. Stabeno (2003): Climate change in the southeastern Bering Sea and some consequences for biota. In *Large Marine Ecosystems of the World: Trends in Exploitation, Protection and Research*, G. Hemple, and K. Sherman (eds.), Amsterdam: Elsevier Science, 17–40.
- Schumacher, J.D., and T.H. Kinder (1983): Low frequency currents over the Bering Sea Shelf. *J. Phys. Oceanogr.*, 13, 607–623.
- Schumacher, J.D., and R.K. Reed (1992): Characteristics of currents over the continental slope of the eastern Bering Sea. *J. Geophys. Res.*, 97, 9423–9433.
- Schumacher, J.D., and P.J. Stabeno (1994): Ubiquitous eddies of the eastern Bering Sea and their coincidence with concentrations of larval pollock. *Fish. Oceanogr.*, 3, 182–190.
- Schumacher, J.D., and P. J. Stabeno (1998): Continental shelf of the Bering Sea. In *The Sea, Vol. 11, The Global Coastal Ocean: Regional Studies and Synthesis*, John Wiley & Sons, Inc., New York, NY, 789–822.
- Schwing, F.B., and C.S. Moore (2000): A year without summer for California: Or a harbinger of a climate shift. *Eos Trans. AGU*, 81, 301.
- SEBSCC (1995): Concept Paper. <http://www.pmel.noaa.gov/sebscc>.
- Shchepetkin, A.F., and J.C. McWilliams (1998): Quasi-monotone advection schemes based on explicit locally adaptive dissipation. *Mon. Weather Rev.*, 126, 1541–1580.
- Sherr, E.B., and B.F. Sherr (1992): Trophic roles of pelagic protists: Phagotrophic flagellates as herbivores. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, 37, 165–172.
- Shuert, P.G., and J.J. Walsh (1993): A coupled physical-biological model of the Bering-Chukchi Seas. *Cont. Shelf Res.*, 13, 543–574.
- Sinclair, E.H., G.A. Antonelis, B.W. Robson, R.R. Ream, and T.R. Loughlin (1996): Northern fur seal, *Callorhinus ursinus*, predation on juvenile walleye pollock, *Theragra chalcogramma*. In *Ecology of Juvenile Walleye Pollock, Theragra chalcogramma*, R.D. Brodeur, P.A. Livingston, T.R. Loughlin, and A.B. HOLLOWED (eds.), NOAA Tech. Rept. NMFS 126, 167–178.
- Sinclair, E.H., A.A. Balanov, T. Kubodera, V.I. Radchenko, and Y.A. Fedorets (1999): Distribution and ecology of mesopelagic fishes and cephalopods. In *Dynamics of the Bering Sea*, T.R. Loughlin, and K. Ohtani (eds.), University of Alaska Sea Grant, AK-SG-99-03, Fairbanks, Alaska, 485–508.
- * Sinclair, E.H., and P.J. Stabeno (2002): Mesopelagic nekton and associated physics of the southeastern Bering Sea. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 6127–6145.
- Sinclair, E.H., T. Loughlin, and W. Pearcy (1994): Prey selection by northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea. *Fish. Bull.*, 92, 144–156.
- * Sinclair, E.H., G.L. Hunt, Jr., L. Vlietstra, T.K. Zeppelin, G.V. Byrd, and A.M. Springer: Trends in diet and population of apex predators in the Pribilof Islands: 1975–2000. *Can. J. Fish. Oceanogr.*, in preparation.

- * Sinclair, E.H., T.K. Zeppelin, and R.R. Ream (2003): Synthesis of pinniped diets at the Pribilof Islands. Final Report of the Synthesis of Information on Marine Birds, Fur Seals and Steller Sea Lions in the Eastern Bering Sea. SEBSCC report, NOAA/PMEL, 7600 Sand Point Way NE, Seattle, WA 98115.
- * Smith, S.L., S.M. Henrichs, and T. Rho (2002): Stable C and N isotopic composition of sinking particles and zooplankton over the southeastern Bering Sea shelf. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 6031–6050.
- Smith, S.L., and J. Vidal (1984): Spatial and temporal effects of salinity, temperature, and chlorophyll on the communities of zooplankton in the southeastern Bering Sea. *J. Mar. Res.*, 42, 221–257.
- Smith, S.L., and J. Vidal (1986): Variations in the distribution, abundance and development of copepods in the southeast Bering Sea in 1980 and 1981. *Cont. Shelf Res.*, 5, 215–239.
- Smith, S.L., S.M. Henrichs, and T. Rho (2002): Stable C and N isotopic composition of sinking particles and zooplankton over the southeastern Bering Sea shelf. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49, 6031–6050.
- Sogard, S.M., and B.L. Olla (1993): Effects of light, thermoclines and predator presence on vertical distribution and behavioral interactions of juvenile walleye pollock, *Theragra chalcogramma* Pallas. *J. Exp. Mar. Biol. Ecol.*, 167, 179–195.
- Springer, A.M. (1991): Seabird relationships to food webs and the environment: examples from the North Pacific Ocean. In *Studies of High-Latitude Seabirds. 1. Behavioral, Energetic, and Oceanographic Aspects of Seabird Feeding Ecology*, W.A. Montevecchi, and A.J. Gaston (eds.), Ottawa, Canadian Wildlife Service, 39–48.
- Springer, A.M. (1992): A review: Walleye pollock in the North Pacific—how much difference do they really make? *Fish. Oceanogr.*, 1, 80–96.
- Springer, A.M. (1998): Is it all climate change? Why marine bird and mammal populations fluctuate in the North Pacific. In *Proceedings of the 10th 'Aha Huliko'a Hawaiian Winter Workshop on Biotic Impacts of Extratropical Climate Variability in the Pacific*, 26–30 January 1998, G. Holloway, P. Muller, and D. Henderson (eds.), SOEST Special Publication, University of Hawaii, Honolulu, HI, 121–125.
- Springer, A.M., and G.V. Byrd (1989): Seabird dependence on walleye pollock in the southeastern Bering Sea. In *Proceedings of the International Symposium on the Biology and Management of Walleye Pollock*, Alaska Sea Grant, AK-SG-89-01, 667–677.
- Springer, A.M., and C.P. McRoy (1993): The paradox of pelagic food webs in the northern Bering Sea—III. Patterns of primary production. *Cont. Shelf Res.*, 13, 575–599.
- Springer, A.M., and D.G. Roseaneau (1985): Copepod-based food webs: Auklets and oceanography in the Bering Sea. *Mar. Ecol. Prog. Ser.*, 21, 229–237.
- Springer, A.M., C.P. McRoy, and M. Flint (1996a): The Bering Sea green belt: shelf-edge processes and ecosystem production. *Fish. Oceanogr.*, 5, 205–223.
- Springer, A.M., C.P. McRoy, and K.R. Turco (1989): The paradox of pelagic food webs in the northern Bering Sea—II. Zooplankton communities. *Cont. Shelf Res.*, 9, 359–386.
- Springer, A.M., E.C. Murphy, D.G. Roseaneau, C.P. McRoy, and B.A. Cooper (1987): The paradox of food webs in the northern Bering Sea—I. Seabird food habits. *Cont. Shelf Res.*, 7(8), 895–911.
- Springer, A.M., J.F. Piatt, and G.B. Van Vliet (1996): Seabirds as proxies of marine habitats and food webs in the western Aleutian Arc. *Fish. Oceanogr.*, 5, 45–55.

*SEBSCC publication

- * Stabeno, P.J., N.A. Bond, N.B. Kachel, S.A. Salo, and J.D. Schumacher (2001): On the temporal variability of the physical environment over the south-eastern Bering Sea. *Fish. Oceanogr.*, 10(1), 81–98.
- * Stabeno, P.J., and G.L. Hunt, Jr. (2002): Overview of the Inner Front and South-east Bering Sea Carrying Capacity Programs. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 6157–6168.
- * Stabeno, P.J., N.B. Kachel, M.E. Sullivan, and T.E. Whitledge (2002): Variability of physical and chemical characteristics along the 70-m isobath of the south-eastern Bering Sea. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 5931–5943.
- * Stabeno, P.J., and J.E. Overland (2001): The Bering Sea shifts toward an earlier Spring transition. *Eos Trans. AGU*, 29, 317, 321.
- Stabeno, P.J., and R.K. Reed (1994): Circulation in the Bering Sea basin observed by satellite-tracked drifters: 1986–1993. *J. Phys. Oceanogr.*, 24, 848–854.
- * Stabeno, P.J., R.K. Reed, and J.M. Napp (2002): Transport through Unimak Pass, Alaska. *Deep-Sea Res. II, Top. Stud. Oceanogr.*, 49(26), 5919–5930.
- Stabeno, P.J., J.D. Schumacher, R.F. Davis, and J.M. Napp (1998): Under-ice observations of water column temperature, salinity and spring phytoplankton dynamics: Eastern Bering Sea shelf, 1995. *J. Mar. Res.*, 56, 239–255.
- Stabeno, P.J., J.D. Schumacher, and K. Ohtani (1999a): The physical oceanography of the Bering Sea. In *Dynamics of The Bering Sea*, T.R. Loughlin, and K. Ohtani (eds.), Alaska Sea Grant, AK-SG-99-03, Fairbanks, AK, 1–28.
- Stabeno, P.J., J.D. Schumacher, S.A. Salo, G.L. Hunt, Jr., and M. Flint (1999b): Physical environment around the Pribilof Islands. In *Dynamics of the Bering Sea*, T.R. Loughlin, and K. Ohtani (eds.), Alaska Sea Grant, AK-SG-99-03, Fairbanks, AK, 193–215.
- Stabeno, P.J., and P. Van Meurs (1999): Evidence of episodic on-shelf flow in the southeastern Bering Sea. *J. Geophys. Res.*, 104(C12), 29,715–29,720.
- * Stockwell, D.A., T.E. Whitledge, S.I. Zeeman, K.O. Coyle, J.M. Napp, R.D. Brodeur, A.I. Pinchuk, and G.L. Hunt, Jr. (2001): Anomalous conditions in the south-eastern Bering Sea, 1997: Nutrients, phytoplankton and zooplankton. *Fish. Oceanogr.*, 10(1), 99–116.
- Sugimoto, T., and K. Tadokoro (1997): Interannual-interdecadal variations in zooplankton biomass, chlorophyll concentration and physical environment in the subarctic Pacific and Bering Sea. *Fish. Oceanogr.*, 6, 74–93.
- Sugimoto, T., and K. Tadokoro (1998): Interdecadal variations of plankton biomass and physical environment in the North Pacific. *Fish. Oceanogr.*, 7, 289–299.
- Sukhanova, I.N., and M.V. Flint (1998): Anomalous blooming of coccolithophorids over the eastern Bering Sea shelf. *Oceanography*, 38, 502–505.
- Sukhanova, I.N., H.J. Semina, and M.V. Venttsel (1999): Spatial distribution and temporal variability of phytoplankton in the Bering Sea. In *Dynamics of the Bering Sea*, T.R. Loughlin, and K. Ohtani (eds.), University of Alaska Sea Grant, AK-SG-99-03, Fairbanks, AK, 193–215.
- Sverdrup, H.U. (1953): On conditions for the vernal blooming of phytoplankton. *J. Conseil Exp. Mer*, 18, 287–295.
- * Swartzman, G.L., R.D. Brodeur, J.M. Napp, G.L. Hunt, Jr., D. Demer, and R.P. Hewitt (1999): Spatial proximity of age-0 walleye pollock (*Theragra chalcogramma*) to zooplankton near the Pribilof Islands, Bering Sea, Alaska. *ICES J. Mar. Sci.*, 56(4), 545–560.
- * Swartzman, G.L., and G.L. Hunt, Jr. (2000): Spatial association between murrens (*Uria* spp.), puffins (*Fratercula* spp.) and fish shoals near the Pribilof Islands, Alaska. *Mar. Ecol. Prog. Ser.*, 206, 297–309.

- * Swartzman, G.L., J.M. Napp, R.D. Brodeur, A.G. Winter, and L. Ciannelli (2002): Spatial patterns of pollock and zooplankton distribution in the Pribilof Islands, Alaska nursery area and their relationship to pollock recruitment. *ICES J. Mar. Sci.*, 59(6), 1167–1186.
- * Swartzman, G.L., A.G. Winter, K.O. Coyle, R.D. Brodeur, T. Buckley, L. Ciannelli, G.L. Hunt, Jr., J. Ianelli, and S.A. Macklin (2004): Relationship of age-0 pollock abundance and distribution around the Pribilof Islands with other shelf regions of the eastern Bering Sea. *Fish. Res.* (submitted).
- Thompson, D.W.J., and J.M. Wallace (1998): The Arctic Oscillation signature in the wintertime geopotential height and temperature fields. *Geophys. Res. Lett.*, 25, 1297–1300.
- Townsend, D.W., L.M. Cammen, P.M. Holligan, D.E. Campbell, and N.R. Pettigrew (1994a): Causes and consequences of variability in the timing of spring phytoplankton blooms. *Deep-Sea Res.*, 41, 747–765.
- Townsend, D.W., M.D. Keller, P.M. Holligan, S.G. Ackleson, and W.M. Balch (1994b): Blooms of the coccolithophore *Emiliana huxleyi* with respect to hydrography in the Gulf of Maine. *Cont. Shelf Res.*, 14, 979–1000.
- Traynor, J., and D. Smith, 1996. Summer distribution and abundance of age-0 walleye pollock, *Theragra chalcogramma*, in the Bering Sea. (Abstract). In *Ecology of Juvenile Walleye Pollock, Theragra chalcogramma*, NOAA Tech. Rept. NMFS 126.
- Trenberth, K.E. and J.W. Hurrell (1994): Decadal atmospheric-ocean variations in the North Pacific. *Clim. Dyn.*, 9, 303–319.
- Trenberth, K.E., and J.W. Hurrell (1995): Decadal coupled atmospheric-ocean variations in the North Pacific Ocean. In *Climate Change and Northern Fish Populations*, R.J. Beamish (ed.), *Can. Spec. Publ. Fish. Aquat. Sci.*, 121, 15–24.
- Trites, A.W., and M.A. Bigg (1996): Physical growth of northern fur seals: Seasonal fluctuations and migratory influences. *J. Zool. (Lond.)*, 238, 459–482.
- Trites, A.W., and P.A. Larkin (1996): Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: How many were there? *Aquat. Mamm.*, 22, 153–166.
- Tynan, C.T. (1998): Coherence between whale distributions, chlorophyll concentration, and oceanographic conditions on the southeast Bering Sea shelf during a coccolithophore bloom, July–August, 1997. *Eos Trans. AGU*, 79, 127.
- Tynan, C.T. (1999): Redistribution of cetaceans in the southeast Bering Sea relative to anomalous oceanographic conditions during the 1997 El Niño. In *Proceedings of the 1998 Science Board Symposium on the Impacts of the 1997–1998 El Niño Event on the North Pacific Ocean and Its Marginal Seas*, H.J. Freeland, W.T. Peterson, and A. Tyler (eds.), PICES Scientific Report 10, 115–117.
- USGS (United States Geological Survey), (2004): Investigations of the linkages between climate, growth, and production of sockeye salmon populations in Bristol Bay, Alaska. http://www.nrel.colostate.edu/brd_global_change/proj-25_ak_salmon.html. March 17, 2004.
- * Vance, T.C., C.T. Baier, R.D. Brodeur, K.O. Coyle, M.B. Decker, T. Wyllie-Echeverria, G.L. Hunt, Jr., J.M. Napp, J.D. Schumacher, P.J. Stabeno, D.A. Stockwell, C. Tynan, T.E. Whitledge, and S.I. Zeeman (1998): Union ecosystem anomalies in the eastern Bering Sea: Including blooms, birds and other biota. *Eos Trans. AGU*, 79(10), 121, 126.
- * Vance, T.C., and S.A. Macklin (1998): Anomalies of the eastern Bering Sea ecosystem during Summer and Fall 1997. *Alaska Fish. J.*, 21(3), 36–37.
- Vidal, J. (1980): Physioecology of zooplankton II: Effects of phytoplankton concen-

- tration, temperature, and body size on the development and molting rates of *Calanus pacificus* and *Pseudocalanus* spp. *Mar. Biol.*, 56, 135–146.
- Vidal, J., and S.L. Smith (1986): Biomass, growth and development of population of herbivorous zooplankton in the southeastern Bering Sea. *Deep-Sea Res.*, 33, 523–566.
- * Vlietstra, L., A. Springer, G.V. Byrd, G.L. Hunt, Jr. (2003). Control of seabird population dynamics at the Pribilof Islands, Alaska. Final Report of the Synthesis of Information on Marine Birds, Fur Seals and Steller Sea Lions in the Eastern Bering Sea. SEBSCC report, NOAA/PMEL, 7600 Sand Point Way NE, Seattle, WA 98115.
- Wallace, J.M., C. Smith, and C.S. Bretherton (1992): Singular value decomposition of wintertime sea surface temperature and 500-hPa height anomalies. *J. Clim.*, 5, 561–576.
- Walsh, J.J., and C.P. McRoy (1986): Ecosystem analysis in the southeastern Bering Sea. *Cont. Shelf Res.*, 5, 259–288.
- Welch, D.W., B.R. Ward, B.D. Smith, and J.P. Eveson (1998): Influence of the 1990 ocean climate shift on British Columbia steelhead (*O. mykiss*) and coho (*O. kisutch*) populations. In *Proceedings of the 10th 'Aha Huliko'a Hawaiian Winter Workshop on Biotic Impacts of Extratropical Climate Variability in the Pacific*, 26–30 January 1998, G. Holloway, P. Muller, and D. Henderson, (eds.), SOEST Special Publication, University of Hawaii, Honolulu, HI, 77–87.
- Wespestad, V.G. (1994): Walleye Pollock. Report and data submitted for the Third International Pollock Assessment Workshop, Seattle, WA, 119–143.
- Wespestad, V.G., L.W. Fritz, W.J. Ingraham, Jr., and B.A. Megrey (2000): On relationships between cannibalism, climate variability, physical transport and recruitment success of Bering Sea walleye pollock, *Theragra chalcogramma*. *ICES J. Mar. Sci.*, 57, 272–278.
- Wespestad, V.G., and T.J. Quinn, II (1996): Importance of cannibalism in the population dynamics of walleye pollock, *Theragra chalcogramma*. In *Ecology of Juvenile Walleye Pollock Theragra chalcogramma*, R.D. Brodeur, P.A. Livingston, T.R. Loughlin, and A.B. Hollowed (eds.), NOAA Tech. Rept. NMFS 126, 212–226.
- * Whitledge, T.E., and V.A. Luchin (1999): Summary of chemical distributions and dynamics in the Bering Sea. In *Dynamics of the Bering Sea*, T.R. Loughlin, and K. Ohtani (eds.), University of Alaska Sea Grant, Fairbanks, Alaska, AK-SG-99-03, 217–250.
- * Wilderbuer, T.K., A.B. Hollowed, W.J. Ingraham, Jr., P.D. Spencer, M.E. Conners, N.A. Bond, and G.E. Walters (2002): Flatfish recruitment response to decadal climatic variability and ocean conditions in the eastern Bering Sea. *Prog. Oceanogr.*, 55(1–2), 235–247.
- * Wilson, M.T., A.H. Andrews, A.L. Brown, and E.E. Cordes (2002): Axial rod growth and age estimation of the sea pen, *Halipteris willemoesi* kölliker. *Hydrobiologia*, 471(1–3), 133–142.
- * Winter, A.G., G.L. Swartzman, and L. Ciannelli. Early- to late-summer population growth and prey consumption by age-0 pollock in two years of contrasting pollock abundance near the Pribilof Islands, Bering Sea (submitted).
- Wyllie-Echeverria, T. (1995): Sea-ice conditions and the distribution of walleye pollock (*Theragra chalcogramma*) on the Bering and Chukchi shelf. In *Climate Change and Northern Fish Populations*, R.J. Beamish, (ed.), *Can. Spec. Publ. Fish. Aquat. Sci.*, 121, 131–136.
- Wyllie-Echeverria, T. (1996): The relationship between the distribution of one-year-old walleye pollock, *Theragra chalcogramma*, and sea-ice characteristics.

*SEBSCC publication

- In *Ecology of Juvenile Walleye Pollock, Theragra chalcogramma*, R.D. Brodeur, P.A. Livingston, T.R. Loughlin, and A.B. Hollowed (eds.), NOAA Tech. Rept. NMFS 126, 47–56.
- Wyllie-Echeverria, T., and K. Ohtani (1999): Seasonal sea ice variability and the Bering Sea ecosystem. In *Dynamics of the Bering Sea*, T.R. Loughlin, and K. Ohtani (eds.), University of Alaska Sea Grant, AK-SG-99-03, Fairbanks, AK, 435–451.
- Wyllie-Echeverria, T., and W.S. Wooster (1998): Year-to-year variations in Bering Sea ice cover and some consequences for fish distributions. *Fish. Oceanogr.*, 7, 159–170.
- York, A.E., and J.R. Hartley (1981): Pup production following harvest of female northern fur seals. *Can. J. Fish. Aquat. Sci.*, 38, 84–90.
- York, A.E., and P. Kozloff (1987): On the estimation of numbers of northern fur seal, *Callorhinus ursinus*, pups born on St. Paul Island, 1980–86. *Fish. Bull.*, 85, 367–375.
- York, A.E., R.G. Towell, R.R. Ream, J.D. Baker, and B.W. Robson (2000): Population assessment, Pribilof Islands, Alaska. In *Fur Seal Investigations, 1998*, B.W. Robson, (ed.), NOAA Tech. Memo. NMFS-AFSC-113, 7–26.

OTHER TITLES IN THE DECISION ANALYSIS SERIES

- No. 1. Able, Kenneth W. and Susan C. Kaiser. 1994. Synthesis of Summer Flounder Habitat Parameters.
- No. 2. Matthews, Geoffrey A. and Thomas J. Minello. 1994. Technology and Success in Restoration, Creation and Enhancement of *Spartina Alterniflora* Marshes in the United States. 2 vols.
- No. 3. Collins, Elaine V., Maureen Woods, Isobel Sheifer, and Janice Beattie. 1994. Bibliography of Synthesis Documents on Selected Coastal Topics.
- No. 4. Hinga, Kenneth R., Heeseon Jeon, and Noelle F. Lewis. 1995. Marine Eutrophication Review.
- No. 5. Lipton, Douglas W., Katherine Wellman, Isobel C. Sheifer, and Rodney F. Weiher. 1995. Economic Valuation of Natural Resources: A Handbook for Coastal Policymakers.
- No. 6. Vestal, Barbara, Alison Reiser, et al. 1995. Methodologies and Mechanisms for Management of Cumulative Coastal Environmental Impacts. Part I — Synthesis with Annotated Bibliography, Part II — Development and Application of a Cumulative Impacts Assessment Protocol.
- No. 7. Murphy, Michael L. 1995. Forestry Impacts on Freshwater Habitat of Anadromous Salmonids in the Pacific Northwest and Alaska — Requirements for Protection and Restoration.
- No. 8. William F. Kier Associates. 1995. Watershed Restoration — A Guide for Citizen Involvement in California.
- No. 9. Valigura, Richard A., Winston T. Luke, Richard S. Artz, and Bruce B. Hicks. 1996. Atmospheric Nutrient Inputs to Coastal Areas — Reducing the Uncertainties.
- No. 10. Boesch, Donald F., et al. 1997. Harmful Algal Blooms in Coastal Waters: Options for Prevention, Control and Mitigation.
- No. 11. McMurray, Gregory R., and Robert J. Bailey, editors. 1998. Change in Pacific Northwest Coastal Ecosystems.
- No. 12. Fonseca, Mark S., W. Judson Kenworthy, and Gordon W. Thayer. 1998. Guidelines for the Conservation and Restoration of Seagrasses in the United States and Adjacent Waters.
- No. 13. Macklin, S. Allen (editor). 1998. Bering Sea FOCI Final Report.
- No. 14. Wiseman, William, Jr., Rabalais, Nancy N., Dagg, Michael J., and Whitledge, Terry E. (editors). 1999. Nutrient Enhanced Coastal Ocean Productivity in the Northern Gulf of Mexico.
- No. 15. Rabalais, Nancy N., R. Eugene Turner, Dubravko Justic, Quay Dortch, and William Wiseman, Jr. 1999. Characterization of Hypoxia: Topic 1 Report for the Integrated Assessment on Hypoxia in the Gulf of Mexico.
- No. 16. Diaz, Robert J., and Andrew Solow. 1999. Ecological and Economic Consequences of Hypoxia: Topic 2 Report for the Integrated Assessment on Hypoxia in the Gulf of Mexico.
- No. 17. Goolsby, Donald A., William A. Battalin, Gregory B. Lawrence, Richard S. Artz, Brent T. Aulenbach, Richard P. Hooper, Dennis R. Kenney, and Gary J. Stensland. 1999. Flux and Sources of Nutrients in the Mississippi-Atchafalaya River Basin: Topic 3 Report for the Integrated Assessment on Hypoxia in the Gulf of Mexico.
- No. 18. Brezonik, Patrick L., Victor Bierman, Jr., Richard Alexander, James Anderson, John Barko, Mark Dortch, Lorin Hatch, Gary Hitchcock, Dennis Kenney, David Mulla, Val Smith, Clive Walker, Terry Whitledge, and William J. Wiseman, Jr. 1999. Effects of Reducing Nutrient Loads to Surface Waters within the Mississippi River Basin and the Gulf of Mexico: Topic 4 Report for the Integrated Assessment on Hypoxia in the Gulf of Mexico.
- No. 19. Mitsch, William J., John W. Day, Jr., J. Wendell Gilliam, Peter M. Groffman, Donald L. Hey, Gyles W. Randall, and Naiming Wang. 1999. Reducing Nutrient Loads, Especially Nitrate-Nitrogen to Surface Water, Ground Water, and the Gulf of Mexico: Topic 5 Report for the Integrated Assessment on Hypoxia in the Gulf of Mexico.
- No. 20. Doering, Otto C., Francisco Diaz-Hermelo, Crystal Howard, Ralph Heimlich, Fred Hitzhusen, Richard Kazmierczak, John Lee, Larry Libby, Walter Milon, Tony Prato, and Marc Ribaud. 1999. Evaluation of the Economic Costs and Benefits of Methods for Reducing Nutrient Loads to the Gulf of Mexico: Topic 6 Report for the Integrated Assessment on Hypoxia in the Gulf of Mexico.
- No. 21. Donald F. Boesch, John C. Field, and Donald Scavia (editors). 2000. COASTAL: The Potential Consequences of Climate Variability and Change.
- No. 22. Kelty, Ruth A. and Steve Bliven. 2003. Environmental and Aesthetic Impacts of Small Docks and Piers.
- No. 23. Science-Based Restoration Monitoring of Coastal Habitats, Vols. 1 and 2.



US Department of Commerce
National Oceanic and Atmospheric Administration
Pacific Marine Environmental Laboratory
7600 Sand Point Way NE
Seattle, WA 98115