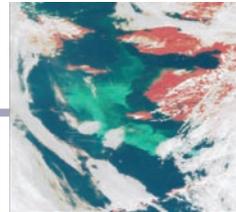


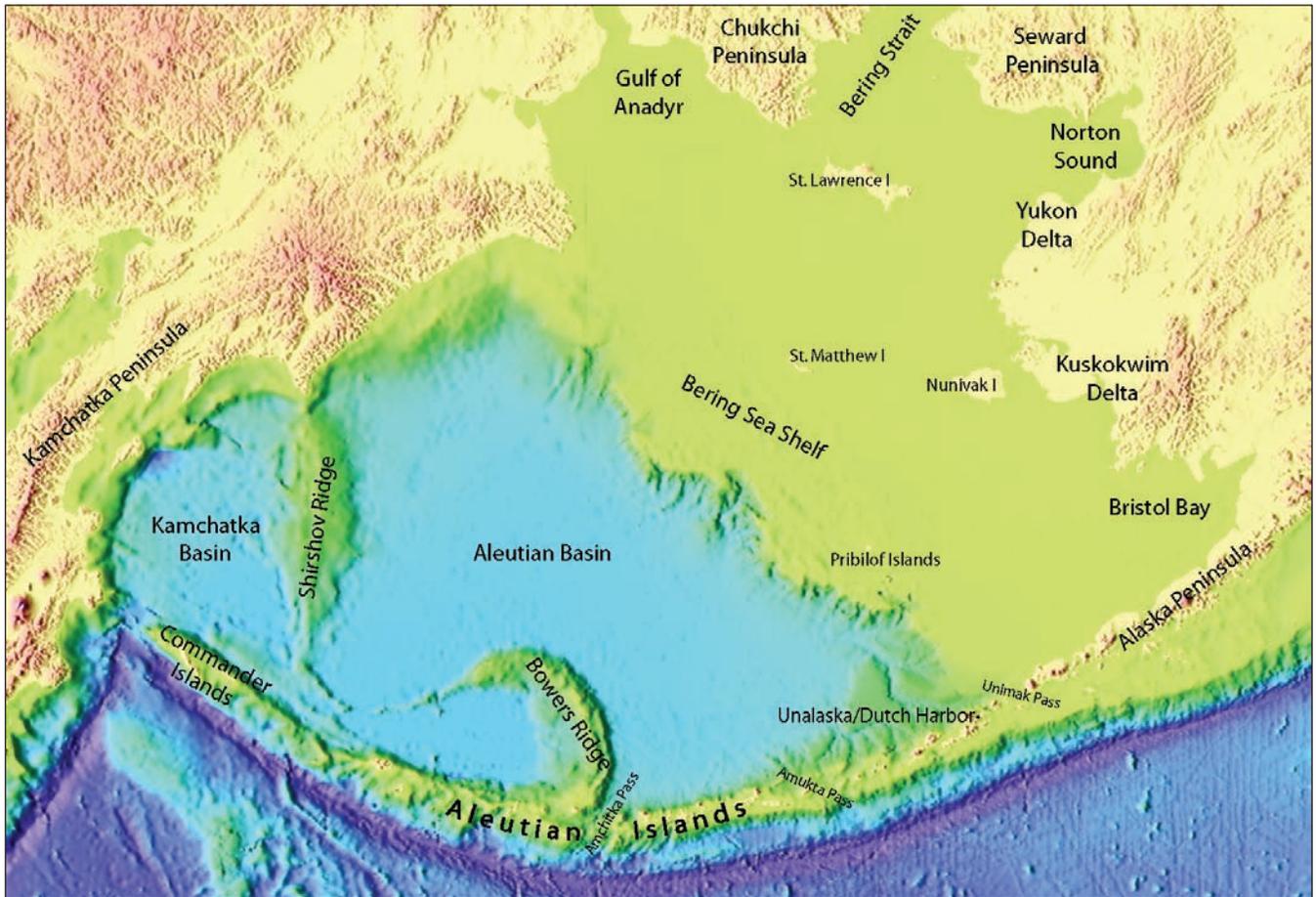
BEST



Bering Ecosystem Study

Science Plan





Major landmarks of the Bering Sea. Base map from U.S. Geological Survey Coastal and Marine Geology Program.

Cover photos

Harbor seals (*Phoca vitulina*)—© Patrick J. Endres/AlaskaPhotoGraphics.com

The trawler *Vaerdal*—Alaska Sea Grant

Coccolithophore bloom—National Aeronautics and Space Administration (NASA)

Drying salmon—National Park Service

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Bering Ecosystem Study

BEST

Science Plan

*Results of a
Planning Workshop*

Held 17–19 March 2003

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3535 College Road, Suite 101, Fairbanks, AK 99709 USA

Phone: 907-474-1600

Fax: 907-474-1604

www.arcus.org

info@arcus.org

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Foreword

The intent of this document is to outline a multi-year research initiative that will improve understanding of the effects of climate variability, at multiple temporal and spatial scales, on eastern Bering Sea marine ecosystems.

In recent decades, components of the eastern Bering Sea have changed in unexpected ways. The possibility that these changes were linked to climate led to the convening of an international workshop in Laguna Beach, California, in September 2002 to assess the need for a large-scale, integrated study of the Bering Sea (Appendix 1). Participants agreed unanimously on the urgent need to improve understanding of the linkages between climate variability and ecosystem responses of the Bering Sea, as detailed in the workshop report: *Ecosystem Studies of Sub-arctic Seas: Results of a Workshop Held in Laguna Beach, California, 6 September 2002* (<http://www.arcus.org/bering>). Such basic research will be the foundation of improved ecosystem models and will be key in helping to ameliorate the societal impacts of variability in this important ocean ecosystem. Workshop participants also agreed that the research effort should emphasize the eastern Bering Sea, in particular the eastern continental shelf and shelf-slope region, where the United States' commercial and subsistence activities are concentrated. This is also an area where earlier programs, such as the Outer Continental Shelf Environmental Assessment Program (OCSEAP, funded by NOAA 1975–85) and the Processes and Resources of the Bering Shelf (PROBES, funded by NSF 1979–81), focused, providing a strong basis for developing comprehensive regional studies.

In March 2003, a second planning workshop was convened in Seattle, Washington, the result of which is the development of this science plan for the Bering Ecosystem Study (BEST) Program (Appendix 2). The intent of this document is to outline a multi-year research initiative that will improve understanding of the effects of climate variability, at multiple temporal and spatial scales, on eastern Bering Sea ecosystems.

Drafts of this science plan were reviewed and discussed at Town Hall meetings in October 2003 in Seattle, Washington, in conjunction with the Study of Environmental Arctic Change (SEARCH) Open Science Meeting, in December 2003 in San Francisco, California, in conjunction with the American Geophysical Union (AGU) Fall Meeting, and in February 2004 in Honolulu, Hawaii, in conjunction with the American Society of Limnology and Oceanography (ASLO)/The Oceanography Society (TOS) Ocean Research Conference. The draft was also available for community review on the ARCUS web site for several months. In total, about 130 scientists participated in the discussion and review process.

This science plan provides background information and frames science questions to guide future integrated, interdisciplinary studies. The proposed studies focus on the mechanisms and

processes that determine the biological production and the fate of this production as it is transferred through the ecosystem to upper-trophic-level consumers, including humans. Thus, the BEST Program acknowledges, *a priori*, the need to understand the role of top predators, including marine mammals and people, as agents that structure the marine ecosystems on which they depend.

The BEST Program will be a major effort. As part of integrated field programs, BEST will require collaborative research among multiple institutions and disciplines, including international collaboration, the deployment of multiple ships and *in situ* long-term instrument arrays, and satellite-based remote sensing studies. Mathematical modeling studies will be an integral part of BEST from the outset, and they will provide frameworks for testing program hypotheses and sampling scenarios. Such an ambitious effort will of necessity require capacity building through targeted training programs, the involvement of social scientists, and strong public outreach efforts.

The BEST Program will interface with other national and international programs investigating the effects of climate change on high-latitude marine ecosystems. BEST is a component of the interagency Study of Environmental Arctic Change (SEARCH; <http://psc.apl.washington.edu/search>) and Ecosystem Studies of Sub-arctic Seas (ESSAS, a new regional program under Global Ocean Ecosystem Dynamics [GLOBEC]), and will interact with Arctic/Subarctic Ocean Fluxes (ASOF; <http://asof.npolar.no>), Climate Variability and Predictability (CLIVAR;

www.clivar.org), and North Pacific Marine Science Organization (PICES; www.pices.int). Moreover, the recent multidisciplinary studies of the Southern Ocean, undertaken as part of the Southern Ocean Global Ocean Ecosystem Dynamics (SO GLOBEC) Program, provide BEST with the opportunity to compare a subarctic marine system with another high-latitude system.

I thank the members of the International Planning Workshop who assembled in Laguna Beach, California, in September 2002 (Appendix 1). Their ideas and enthusiasm were of great importance in launching this endeavor. I also thank those who gathered in Seattle, Washington, in March 2003 for the science plan development workshop (Appendix 2). Their creativity, enthusiasm, and hard work, both during and after the workshop, have made possible this science plan. Numerous members of the marine science community provided unsolicited suggestions that added to the development of the science plan. In particular, I thank Bill Sydeman and David Hyrenbach for their critical reading and most helpful comments on the draft science plan. The staff at ARCUS provided superb support during the planning workshop and in the editing and production of the science plan. The strong support and enthusiasm of the Arctic Section of the Office of Polar Programs at the National Science Foundation is gratefully acknowledged.

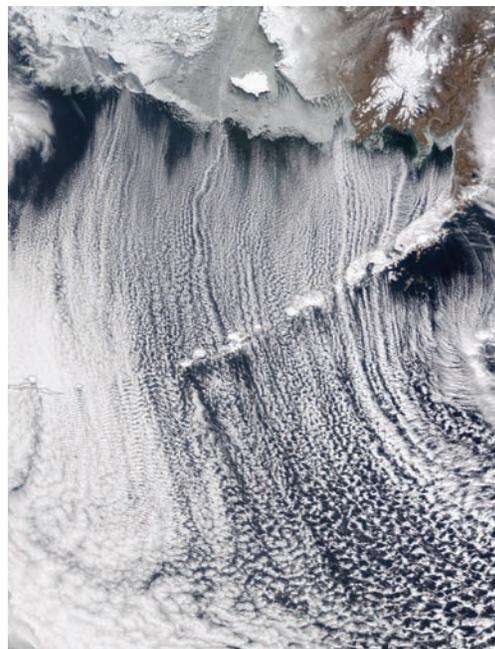
For the Planning Group

George L. Hunt, Jr.
Chair

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A Moderate Resolution Imaging Spectroradiometer (MODIS) image of the Bering Sea and the Gulf of Alaska. Over the ocean, clouds often align with a low-level wind, producing parallel rows, or streets, of clouds. The Aleutian Islands interrupt the airflow, leaving a sort of wake. The Aqua satellite captured this true-color image on March 14, 2003. Image by Jeff Schmaltz, MODIS Rapid Response Team, NASA/GSFC, courtesy NASA Visible Earth.

Approximately 1.5 million northern fulmars (*Fulmarus glacialis*) breed on the islands of the Bering Sea and Aleutian Archipelago. Corel photo.



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Executive Summary

The overarching question to be addressed in the BEST Program is—*How will climate change affect the marine ecosystems of the eastern Bering Sea?*

The eastern Bering Sea supports extraordinarily rich marine resources, including vast numbers of marine birds and mammals and stocks of commercial fish that generate more than 50% of all United States' fish and shellfish landings.

Unalaska/Dutch Harbor, Alaska, the principal port to which these landings are brought, has been, since 1989, the number one or two port in the nation for the dollar value of fisheries' landings. The Bering Sea is also directly or indirectly the source of over 25 million pounds of subsistence foods used by nearly 55,000 Alaska residents, primarily Alaska Natives in small rural communities (Mary Pete, personal communication).

Recent unprecedented changes in the marine ecosystems of the eastern Bering Sea have, in many cases, correlated with physical variability. For example, the eastern Bering Sea has been changing from a system dominated by cold-water, arctic species to a temperate system in which a new set of species may come to dominate; the rate of change appears to be accelerating. Population explosions of jellyfish have come and gone, and there have been sharp declines in seal and sea lion populations, as well as in salmon runs in the rivers of western Alaska. Understanding the underlying processes responsible for these ecosystem responses is the basis for providing good stewardship as this dynamic region evolves. The Bering Ecosystem Study (BEST) Program proposes to de-

velop a fundamental understanding of how climate change will affect the marine ecosystems of the eastern Bering Sea and the sustainable use of their resources.

Concern about the Bering Sea has engendered large and intense research efforts by many organizations. The results of prior and ongoing research in the eastern Bering provide a strong foundation for the BEST Program, which complements research efforts supported by agencies with management responsibilities in the region. BEST will leverage knowledge and resources from four important areas: 1) recently completed studies of the Bering and subarctic seas, 2) ongoing national and international programs, 3) national programs proposed for funding, and 4) international programs addressing global change.

BEST will investigate connections between external forcing mechanisms and hydrographic structure and physical processes. Two major external physical forcing mechanisms dominate the eastern Bering Sea—atmospheric forcing (solar insolation and winds) and transport of water through the Aleutian Passes and Bering Strait. Variability in these forcing mechanisms occurs on all spatial and temporal scales, including local episodic events (storms), interannual variability at the scale of the eastern Bering Sea, and decadal- and climatic-scale events at North Pacific and global scales. Issues of particular importance include resupply of

The BEST science plan addresses three major areas of inquiry:

- 1) What are the external forcing functions that link global and regional climate processes to the physical oceanography of the eastern Bering Sea?
- 2) How does variability in the physical aspects of the marine system affect ecosystem processes and structure?
- 3) How can spatial and temporal scales be integrated to permit forecasting how changes in climate will affect the productivity and sustainability of the marine ecosystems of the eastern Bering Sea?

nutrients to the eastern continental shelf, the role of flow through Bering Strait, and how the location, timing, frequency, and intensity of storms affect shelf ecosystems. Mechanisms linking atmospheric circulation patterns to currents, meanders, and eddies, and upwelling along the continental shelf-slope, and their impacts on nutrient replenishment in slope and shelf waters are not understood. Flow through the Bering Strait appears to be changing, but the effects of this change on the heat balance, nutrient flux, and ecosystem structure of the northeastern Bering Sea remain unknown. The location, strength and timing of storms are likely to be critical to eastern Bering Sea ecosystems, but the effects of changes in the pathways, strength, and duration of storms remain to be investigated. Changes in these parameters could have considerable impacts on top predators, including people, in this region.

BEST will investigate the connection between physical aspects of the marine environment and the responses of the biota of the eastern Bering Sea. Mechanisms of interaction that are particularly important include: 1) stratification of the water column, which affects the availability of light and nutrients needed to support primary production, as well as the vertical distribution of many of the smaller planktonic organisms, 2) sea ice, which affects light, water temperature, and the availability of substrate, and 3) water temperature, which affects the rates at which physiological processes occur and is also

a habitat variable to which fish respond behaviorally.

Although seasonal sea ice cover is a dominant feature of the eastern Bering Sea, the ecosystem-level impact of changes in sea ice cover is not well understood. Sea ice is pivotal to structuring the physical environment and ecosystems on the shelf. Likewise, on the southeastern shelf, the timing of sea-ice retreat affects the timing and possibly the fate of the spring phytoplankton bloom, but the ecosystem consequences of the timing of the bloom need to be determined. Evidence indicates that water temperatures during the spring phytoplankton bloom affect the productivity of copepods and possibly the recruitment of important commercial fish species, such as walleye pollock (*Theragra chalcogramma*). Decadal-scale shifts in climate have the potential to shift the control of pollock populations between top-down (predation, fisheries) and bottom-up (production) mechanisms, and such differences have important implications for fisheries management.

Pools of cold bottom water are a signature feature of sea ice during spring on the Bering Sea shelf, but the effects of changes in the size, duration, and distribution of cold pools on the circulation and ecology on the shelf are open questions. The potential effects of changes in the distribution and extent of the cold pool has been observed on the southeastern Bering Sea shelf. There, changes in temperature affect the distribution of juvenile pollock and the likelihood that they will encounter fish predators, including cannibalistic adults. The effects of a loss of the cold pool in the central or northern Bering Sea are not known. If warming bottom water allowed the ranges of epibenthically feeding fish to expand, severe competitive pressures could impact benthic-foraging marine mammal populations, such as walrus (*Odobenus rosmarus*) and gray whales (*Eschrichtius robustus*).

The BEST Program will also develop tools for integrating the effects of climate change across spatial and temporal scales, with the goal of forecasting how the ecosystem might be expected to behave under different climate scenarios. Although some models address regional climate variability and others circulation patterns in the North Pacific or Bering Sea, no current models link global climate forcing through physical oceanography to the impact on individual organisms and then back up to the ecosystem consequences of the responses of the organisms to forcing.

Modeling the multiple linkages between climate, ocean productivity, and the physiological responses of individual organisms and how these in aggregate influence ecosystem function would be a major accomplishment. Such a series of linked models would have the prospect of providing not only intellectually exciting opportunities to investigate ways in which the ecosystem might respond to climate change, it would also

be a valuable fisheries management tool for the eastern Bering Sea. Although the Magnuson–Stevens Sustainable Fisheries Act of 1996 requires managers to consider ecosystem impacts on and of management decisions, at present managers lack the tools to incorporate ecosystem considerations in their models. Development of a model that would facilitate inclusion of ecosystem considerations in management models would be an important contribution toward sustainable management of the ecosystems of the eastern Bering Sea.

It is vital to the future economic and social well being of the region that we understand how processes controlled by climate influence the productivity of the Bering Sea. **Thus, the goal of the BEST program is to understand and predict the impacts of climate change on the marine ecosystems of the eastern Bering Sea and their sustainability.** The BEST Program will advance knowledge needed to facilitate the wise use and stewardship of this important marine ecosystem.

The BEST Science Plan

Rationale for the Program

Section 1

A comprehensive study of eastern Bering Sea marine ecosystems is needed to provide the scientific basis for understanding how global climate change may influence the structure and function of its marine ecosystems (IARPC, 2001).

1.1 Introduction

The Bering Sea region supports the United States' most productive and valuable fisheries, immense populations of marine birds and mammals, and subsistence activities of Native American communities.

This great biological productivity takes place in a dynamic ocean characterized by intense storms and substantial seasonal ice cover, the extent and nature of which affects all levels of the biological system. The Bering Sea is also an area where water flowing from the North Pacific Ocean into the Arctic Ocean is modified, giving the Bering Sea an important role in mediating climate change effects in the Arctic.

The past few decades of modern ocean observation have recorded significant year-to-year variations in both the extent and timing of seasonal ice cover, and this has been related to the ecological dynamics of the eastern Bering Sea shelf. The oceanographic processes linking ice cover and biological production, however, have yet to be fully resolved. Our ability to predict and prepare for fluctuations in important biological resources caused by regional short-term climate variability is therefore limited. Predictive ability is almost non-existent for more pervasive, longer-term climate changes that could alter ice extent for extended periods. Thus, improving our abilities to forecast ecological change provides a powerful motivation to

learn more about how climate change will affect eastern Bering Sea ecosystems and their connections to the North Pacific and Arctic Oceans. (NRC, 1996; IARPC, 2001).

Fully executed, the Bering Ecosystem Study (BEST) will provide a unique basis for managing sustainable commercial fisheries and subsistence harvests well into the future. To develop the needed understanding, the eastern Bering Sea continental shelf and shelf-slope must be studied as a whole, including inputs and outputs of properties such as heat, kinetic energy, nutrients, and biological production at multiple trophic levels. Moreover, to capture the signals of climate change, measurements of these parameters will be needed in all seasons, including winter, which is undersampled.

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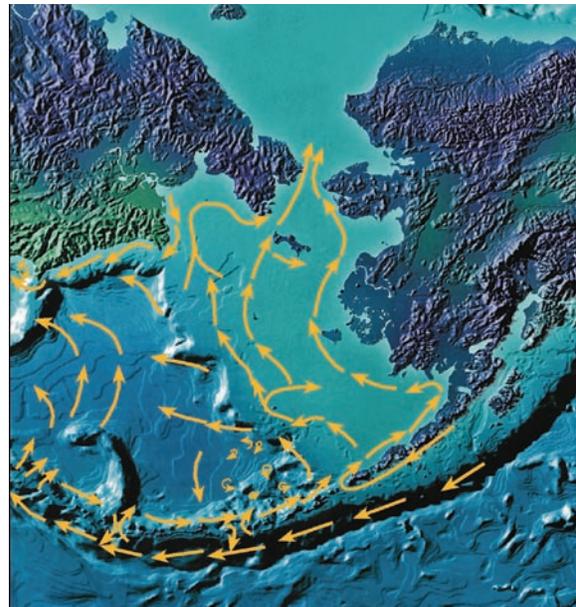
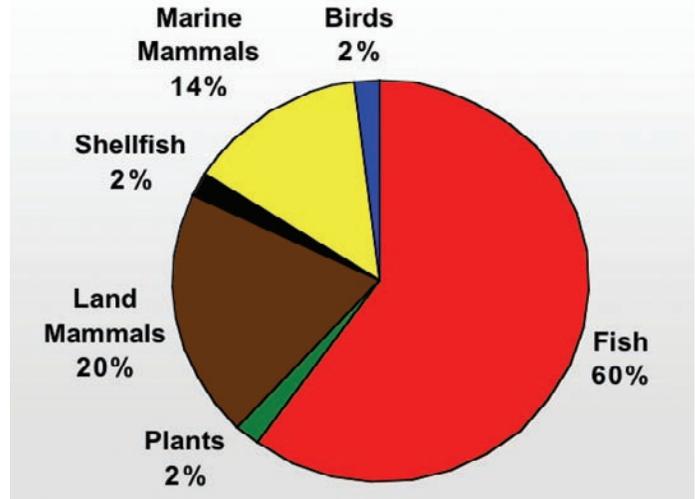


Figure 1. Map of the Bering Sea showing major currents (Stabeno et al., 1999a). Image by Karen Birchfield, NOAA Pacific Marine Environmental Laboratory.

Figure 3. Composition of subsistence harvest by rural Alaska residents. Figure from Mary Pete, Alaska Department of Fish and Game.



The Bering Sea is directly or indirectly the source of over 25 million pounds of subsistence foods used by nearly 55,000 Alaska residents, primarily Alaska Natives in small rural communities. Some of these same resources (Figure 3) also support important traditional hunting and fishing and sport harvest activities in which many Alaska residents participate for economic and cultural benefits (IARPC, 2001). Two major rivers, the Yukon and Kuskokwim, and numerous smaller ones, drain into the Bering Sea; these rivers host all five species of Pacific salmon, which are the central resource for many Native communities in western and interior Alaska. Since 1997, many of the western Alaska salmon fisheries have been designated as biological or economic disasters. Recent declines in salmon runs have had devastating effects on Native communities, especially those dependent on commercial salmon fishing. It has been hypothesized that changes in ocean conditions were responsible for these failures in salmon runs (Kruse, 1998).

Subsistence harvests may be the best indicator of changes in the populations of several species of marine mammals.

Walrus (*Odobenus rosmarus*), and ringed (*Phoca hispida*), ribbon (*P. fasciata*), spotted (*P. largha*), and bearded seals (*Erignathus barbatus*), which all use sea ice during part of their life cycle, are numerous secondary consumers in arctic and subarctic ecosystems and important to the subsistence cultures and economies of Alaska Natives living along the coasts of the Bering, Chukchi, and Beaufort Seas. These species may be affected by climate change (Tynan and DeMaster, 1997). Native hunters express increasing concern that changes in the thickness, persistence, and distribution of sea ice and in recent weather patterns have decreased the

populations and availability of ice seals and walrus and, consequently, human health and traditional culture (Krupnik and Jolly, 2002). Population estimates and trends for ice seals and walrus in the Bering Sea are not available due to the wide distribution of these animals and the inherent difficulties associated with conducting marine mammal surveys in remote, ice-covered waters. Changes in subsistence use of these species may provide an early warning of shifts in their populations.

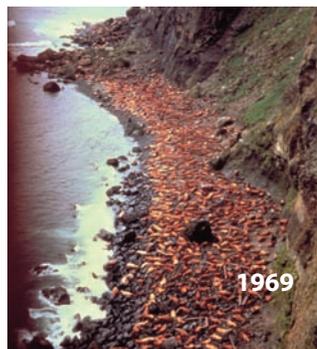
1.2.2 Recently, Significant Changes have Occurred in the Ecosystem

3

Bering Sea ecosystems are sensitive indicators of the effects of climate change in the subarctic region.

In the early 1980s some fish species increased in population, while others declined. Populations of seabirds and northern fur seals (*Callorhinus ursinus*) breeding on the Pribilof Islands have declined, as have Steller sea lions (*Eumetopias jubatus*) throughout most of the western part of their range (NRC, 2003). In 1997, there was a massive die-off of short-tailed shearwaters (*Puffinus tenuirostris*), a seabird that annually migrates from nesting grounds in Australia to for-

Steller sea lions on Ugamak Island, eastern Aleutians from 1969 to 1986. Photos from National Marine Mammal Laboratory, NOAA.



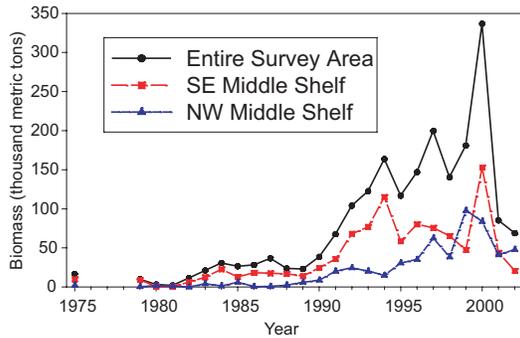


Figure 4. Biomass of large medusae caught in NOAA bottom trawl surveys 1975–2002. Figure modified from Brodeur et al., 2002.

age in the Bering Sea (Baduini et al., 2001, 2002; Hunt et al., 2002a,b). Coincident with these changes were a build-up and then crash in the biomass of large jellyfish (Figure 4; Brodeur 1999, 2002), and a massive coccolithophore bloom that whitened the waters of much of the eastern Bering Sea continental shelf in each summer from 1997 to 2001 (Figure 5; Sukhanova and Flint, 1998; Stockwell et al., 2001; Hunt et al., 2002a; Iida et al., 2002). Why these phenomena took place, and why they ceased to occur, remains unknown, yet many of these changes coincided with marked shifts in the physical environment. The biological shifts may be part of periodic fluctuations, or may be harbingers of longer-term change. In either case, the management implications of these changes are unclear. The BEST Program will be an important step toward filling the need for comprehensive knowledge of the mechanisms by which climate variability affects ecosystem function in the eastern Bering Sea.

Primary production and its ability to support top predators in the Bering Sea are strongly affected by climate-driven changes in sea ice cover, a feature not found in waters of any other area of the United States Exclusive Economic Zone.

Variations in sea ice cover provide a potential link between climate change and the timing, amount, and fate of primary production, and hence the recruitment of commercially and ecologically important populations in the Bering Sea. Small shifts in air or sea temperatures or wind patterns can create major changes in the timing, extent, and duration of ice cover. A recent study suggests that spring sea ice melt-back in the northern Bering Sea now occurs 2–3 weeks earlier than in the 1970s

(Stabeno and Overland, 2001). Changes in the spring melt-back have direct effects on the primary productivity of the eastern Bering Sea, and the amount of sea ice melting over the middle shelf affects bottom temperatures and benthic ecosystems there (Grebmeier and McRoy, 1989; Grebmeier and Dunton, 2000). The persistence and location of sea ice also affects the migratory routes of cetaceans, such as bowhead (*Balaena mysticetus*) and beluga (*Delphinapterus leucas*) whales. Thus, sea ice cover is one of the most important climate-related variables that directly affects the ecology of the eastern Bering Sea. Global warming may have a potentially immense impact on the Bering Sea, and this may first be apparent in the sea ice record, considered a sensitive indicator of a warming climate (IPCC, 2001, p. 124).

The elevated primary production found along the slope and over the eastern shelf also supports about 80% of the seabirds found in United States' coastal waters, and substantial populations of pinnipeds and cetaceans (NRC, 1996; IARPC, 2001). Among these upper trophic level predators are threatened (e.g., spectacled eider *Somateria fischeri*) and endangered species (e.g., short-tailed albatross *Phoebastria albatrus*, Steller sea lion; most large whales), and a number of species endemic to the region. In the 1970s, red-legged kittiwakes (*Rissa brevirostris*) and northern fur seals breeding at the Pribilof

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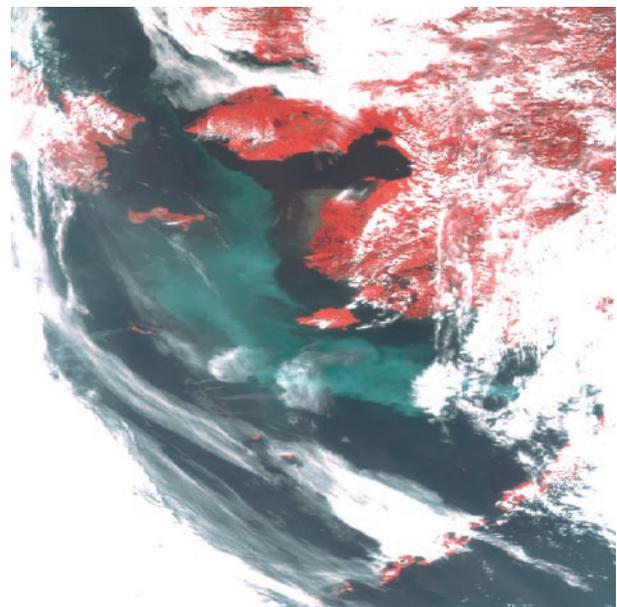


Figure 5. SeaWiFS false color image of a coccolithophore bloom in the eastern Bering Sea, 20 July 1998. Image courtesy of NASA, processed by Stephen I. Zeeman, University of New England.

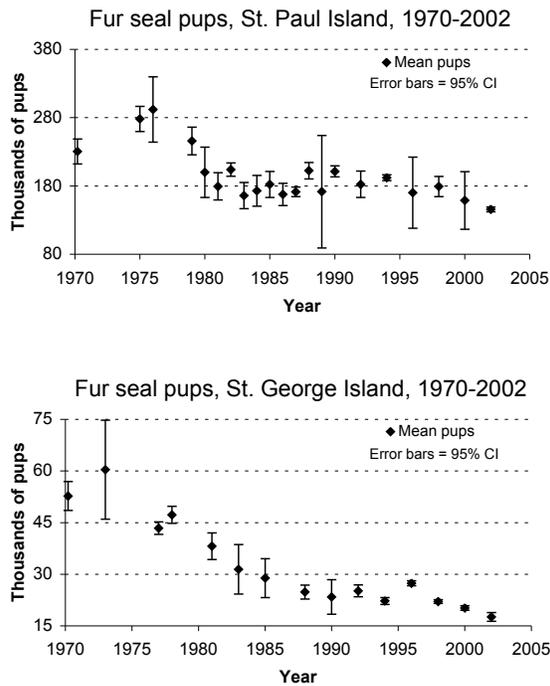


Figure 6. Changes in the annual counts of northern fur seal pups present in the Pribilof Islands. Figure from National Marine Fisheries Service, 2002.

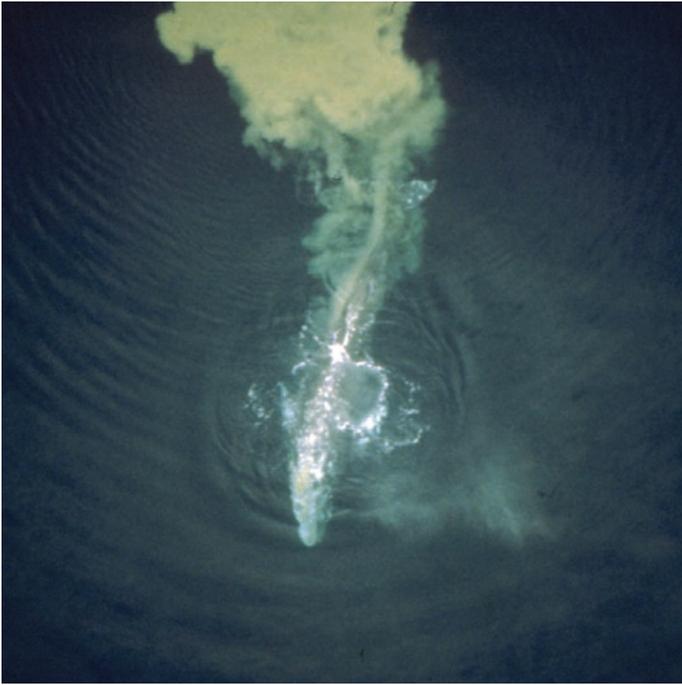
Islands constituted approximately 85% and 80%, respectively, of the world populations of these species. These populations have declined to between one-third to one-tenth of their former numbers (Figure 6; Springer, 1998; Hunt and Byrd, 1999; Hunt et al., 2002a). Changes in the diets and populations of seabirds and pinnipeds in the Bering Sea coincided with dramatic, decadal-scale changes in the physical environment (Hunt et al., 2002a), although the linking mechanisms have yet to be elucidated.

The Bering Sea affects global climate via its connections to the North Pacific and Arctic Oceans. As water flows poleward from the North Pacific through the Bering Sea to the Arctic Ocean, its heat, salt, and freshwater content are modified. Changes in water properties in the Bering Sea influence the strength of the permanent halocline in the Arctic Ocean, and the amount of freshwater and heat in the upper layers of the western Arctic Ocean (Aagaard and Carmack, 1994; McLaughlin et al., 1996). Cold, salty brine, rejected during the formation of sea ice in the northern Bering Sea, flows northward into the Arctic Ocean. Thus, flow patterns through Bering Strait and the amount of sea ice formed in the northeastern Bering Sea affect the amount of salt advected into

the Arctic Ocean. Heat from the North Pacific Ocean, advected through passes in the Aleutian Islands, warms the waters of the Bering Sea and is transported, in the Bering Slope Current and shelf currents, through the northern Bering Sea and into the Arctic Ocean. Similarly, freshwater is introduced via the near-shore Alaska Coastal Current from coastal rivers as far away as the Gulf of Alaska. Thus, modifications to these flows and/or water properties in the Bering Sea resulting from climate change processes will alter the pole-ward transport of heat, salt, and freshwater, which will ultimately affect the characteristics of the Arctic Ocean and its effects on global climate change. These transport and modification mechanisms have been neglected in global models of climate change. Some models of climate change predict that a warmer Arctic Ocean will result in decreased flow through Bering Strait, something that may already be occurring (Roach et al., 1995). Research shows that the northern Bering Sea and adjacent Arctic Ocean are already changing rapidly, with consequences that we do not fully understand.

1.3 Why a Program Now?

The eastern Bering Sea appears to be changing from a system dominated by coldwater, arctic species to a temperate system in which a new set of species may come to dominate. For example, a coldwater amphipod (*Themisto libellula*), once common in seabird diets at the Pribilof Islands, is now absent from the southeastern Bering Sea (K. Coyle, personal communication). Greenland turbot (*Reinhardtius hippoglossoides*), a coldwater species once an important component of commercial fisheries in the Bering Sea, is in severe decline (Witherell et al., 2000).



Benthic feeding gray whales trail plumes of mud and sediment after filtering out amphipods and other edible material. Photo by Sue Moore, NOAA National Marine Mammal Laboratory.

Warming of the northern Bering Sea may displace benthic-feeding species of fish northward, and amphipod beds necessary for gray whales (*Eschrichtius robustus*) and other benthic-foraging species may disappear. Some of these fish species are commercially important, which makes understanding the factors that limit or change their range of considerable economic interest.

6

In some areas of the eastern Bering Sea, primary production may be slowing. The eastern Bering Sea supports some of the highest rates of primary production reported for the world ocean. On the shelf-slope, in particular, an upwelling of nutrient-rich water results in a band of elevated primary production (the “Green Belt”; Springer et al., 1996; see section 3.2.2). In the northern Bering Sea, these nutrient-rich waters are carried onto the shelf and eventually through Bering Strait into the Arctic Ocean. When advected into areas that are stratified, these waters support rates of primary production of up to $570 \text{ g C m}^{-2} \text{ y}^{-1}$ (Springer et al., 1996). These rates are as high or higher than those recorded in the most productive upwelling regions of the world, most of which have much longer growing seasons. There is evidence that this extraordinarily high productivity may be slowing (Grebmeier

and Dunton, 2000; Grebmeier and Cooper, 2002), possibly because of a decrease in the currents flowing from the Bering Sea to the Arctic Ocean (Roach et al., 1995). If flow through the Bering Strait diminishes, advection of nutrients and high levels of primary production in the northern Bering and Chukchi Seas will also likely decrease (Grebmeier and Dunton, 2000; Cooper et al., 2002; Grebmeier and Cooper, 2002). Lower flows may also result in a decrease in sediment grain size on the northern Bering Sea continental shelf, displacing clams fed upon in winter by the world’s population of the threatened spectacled eider (Grebmeier and Cooper, 1995; Grebmeier and Dunton, 2000; Lovvorn et al., 2003). The connections between climate and these changes in transport have yet to be fully investigated, but a decline in the high rates of primary production in the northeastern Bering Sea will have major impacts on the availability of food for top predators that range from planktivorous seabirds to benthic-feeding gray whales.

Change in the Bering Sea appears to be accelerating, and understanding the underlying ecosystem processes is the basis for providing good stewardship as this dynamic region evolves. In recent years, it has become evident that this seasonally ice-covered, sub-arctic sea is subject to decadal-scale and secular changes in climate that have resulted in abrupt and unexpected changes in the ecosystem (Napp and Hunt, 2001). These changes have the potential to alter recruitment patterns of commercially important fish, affect the availability of ice seals and other marine resources necessary for subsistence harvests, and to fundamentally alter the structure and function of Bering Sea ecosystems. These changes in ecosystem function are already underway (Vance et al., 1998; Napp and Hunt, 2001). As an Alaska Native Elder said, “The Earth is faster now.” (Krupnik and Jolly, 2002).

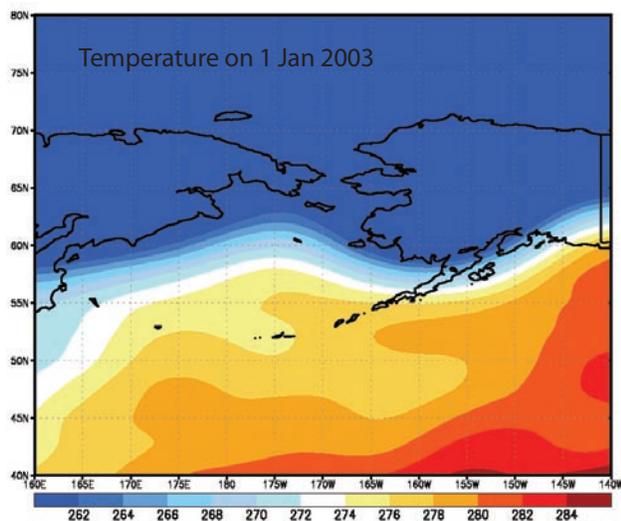
Threatened spectacled eider wintering at a lead in the St. Lawrence Island polynya. Photo by J. Lovvorn, inset of benthic invertebrates by J. Bump.

1.4 What about this Opportunity is Unique?

The Bering Sea is an excellent laboratory for studying the effects of climate change.

The tremendous interannual variation in almost every parameter in the Bering Sea environment allows investigators to study processes and mechanisms under a variety of climatic conditions that are as extreme as the warmest and coldest periods in recent history. Even over relatively short periods of time, the amplitude of variability is large, providing a strong signal-to-noise ratio, and the potential for detecting threshold phenomena that frequently characterize non-linear relationships in ecosystems.

The strong interannual climate variability provides the unique opportunity to observe how variations in climate affect the distribution, timing, and duration of sea ice cover, and through sea ice, the function of a marine ecosystem that supports major U.S fisheries. Sea ice has a central role in determining the timing, magnitude, and fate of primary production in the eastern Bering Sea. This connection between sea ice and ecosystem function invites comparison with processes, studies, and sites in both the Northern and Southern Hemispheres. Do these marginal ice zone systems behave similarly, or is the Bering Sea with its broad, shallow shelf and strong benthic–pelagic coupling fundamentally different? This offers an



excellent opportunity for synergy with the Antarctic Southern Ocean GLOBEC program.

The high spatial and temporal variability of the Bering Sea can be used, within the lifetime of a field program, as a proxy for studying the response of the Bering Sea system to variability at longer time scales. Over 1,200 km from north to south, the eastern Bering Sea provides strong spatial contrasts in climate, duration and timing of seasonal ice cover, water temperature, and biota. This spatial variation between the southeastern and northeastern Bering Sea can be used as a model for what temporal climate change may bring to the region. The northern and southern parts of the Bering Sea are influenced by the Arctic Oscillation (AO) and mid-latitude atmospheric forcing, respectively (Figure 7), thus facilitating examination of how different atmospheric systems interact. The climate of the Bering Sea also shows great temporal variability, with strong signals at seasonal, annual, El Niño–Southern Oscillation (ENSO; 3–7 years), and decadal scales. At temporal scales longer than the seasonal, the greatest variability is in the annual signal (Overland et al., 1999).

Although BEST's goal of characterizing processes that link climate to biological structure and function on the eastern Bering shelf is ambitious, it is attainable because of the convergence of several important features: 1) The region now has been the focus of three decades of modern oceanographic observations. Earlier

Figure 7. Daily temperature at 1000 hPa on 1 Jan 2003 based on NCEP/NCAR reanalysis. From Climate Prediction Center (CPC)/National Weather Service (NWS), NOAA, on-line plotting tool (http://wesley.wvb.noaa.gov/ncep_data/index.html).

studies, including the Outer Continental Shelf Environmental Assessment Program (OCSEAP, funded by NOAA 1975–85) and the Processes and Resources of the Bering Shelf (PROBES, funded by NSF 1979–81), provide a strong scientific basis to inform BEST research efforts. 2) The region's biological signals are large and dynamic. The short growing season produces some of the greatest primary production in the world ocean. Dramatic changes in fish, bird, and mammal populations and between diatom-dominated and coccolithophore-dominated communities have already been observed. 3) The system occupies the phase change region between the permanently open water of the subarctic region and the arctic pack ice. Thus, modest changes in atmospheric and oceanic forcing produce large changes in sea ice distribution. Marked year-to-year changes have already been recorded and have a high probability of recurring during the BEST field program.

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The results of prior research in the eastern Bering have helped to frame several important hypotheses that will be extended and refined by BEST. For example, prior research on the effects of ice on the timing, amount, and fate of primary production suggests that when sea ice retreats late in the spring, an ice-related phytoplankton bloom occurs in cold water. This pattern favors fluxes of energy to the benthic community (Walsh and McRoy, 1986; Stabeno et al., 1998; Hunt et al., 2002a). Sea ice retreat early in the spring delays the spring phytoplankton bloom until the surface waters become stratified. This late spring bloom occurs in warm water, favoring transfer of energy to a pelagic food web. These differences in the flow of energy in the food webs of the eastern Bering Sea shelf may shift control of recruitment to fish populations, especially the commercially important pollock, between top-down and bottom-up processes (Hunt et al., 2002a). Sea ice also affects the tempera-

ture of the bottom water over the middle shelf, which in turn affects the distribution of fish and their vulnerability to predation (Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1995; Wyllie-Echeverria and Wooster, 1998). Thus, several working hypotheses on how ice cover functions as one of the master variables in the eastern Bering Sea system have already been put forward (see section 4), and a growing time series of physical and biological variables exists for retrospective studies.

1.5 Connections with Other Research Programs

BEST will leverage knowledge and resources from four important areas:

1) recently completed studies of the Bering and subarctic seas, 2) ongoing national and international programs, 3) national programs proposed for funding beginning in FY04, and 4) international programs addressing global change. BEST will capitalize on syntheses and data from the recently completed NOAA Coastal Ocean Program (Bering Sea Fisheries Oceanography Coordinated Investigations [BSFOCI] and Southeast Bering Sea Carrying Capacity [SEBSCC]) and NSF (Inner Fronts Study) projects in the southeast Bering. Important syntheses of these programs have been published (Royer and Dagg, 2002; Macklin et al., 2002a,b; Macklin and Hunt, 2004), providing BEST with a solid basis on which to build its field program. Principal Investigators from each of these programs have helped to construct the BEST Science Plan.

The BEST Program will also benefit from partnerships with other studies, including the long-standing investigations of the Bering Sea by Japanese scientists at Hokkaido University (R/V

Groups of walrus congregate on ice floes to rest, give birth, and nurse pups. Photo by Marc Webber, U.S. Fish and Wildlife Service.

Oshoro Maru time series) and a relatively new international program, the Bering-Aleutian Salmon International Survey (BASIS), sponsored by the North Pacific Anadromous Fish Commission (Canada, Japan, South Korea, Russia, and the U.S.; www.npafc.org). BEST is already collaborating with the North Pacific Research Board (NPRB) and the Gulf Ecosystem Monitoring Program (GEM) of the Exxon Valdez Trustee Council to develop a coordinated research effort in the Bering Sea and adjacent North Pacific Ocean. The emerging Alaska Ocean Observing System (AOOS) emphasizes long-term observations and thus will complement the more process-oriented studies in BEST. BEST is a component of the interagency Study of Environmental Arctic Change (SEARCH). In addition, members of the BEST planning team are active members in the North Pacific Marine Science Organization (PICES) and serve on working groups and advisory panels of the PICES Climate Change and Carrying Capacity program (CCCC). BEST will interact with PICES as this international organization develops plans for research activities in the North Pacific region.

BEST is well positioned to collaborate with two newly proposed NOAA initiatives for FY04 and FY05 (North Pacific Climate and Ecosystem Productivity), as members of the BEST planning team were responsible for their development. Building upon these recently completed as well as extant programs, BEST will have a large resource base and access to up-to-date regional information on recently investigated questions and insights into emerging problems in this highly dynamic ecosystem. There may also be new opportunities for collaborative research with the joint Russian-American Long-term Census of the Arctic (RUSALCA), which will have its initial research cruise to the Bering and Chukchi Seas in summer 2004.



BEST will benefit from information developed in the Arctic/Subarctic Ocean Fluxes (ASOF; <http://asof.npolar.no>) and Climate Variability and Predictability (CLIVAR; www.clivar.org) programs, particularly as BEST synthesizes its results and attempts to develop models of what future global change may bring to the Bering Sea. For these goals, information on potential changes in climate forcing and flows through Bering Strait will be vital. In return, BEST will provide ASOF with information on how the properties of the water flowing from the Bering into the Arctic Ocean will change, given different climate scenarios. BEST will be an integral part of Ecosystem Studies of Sub-Arctic Seas (ESSAS), a new regional program recently accepted under Global Ocean Ecosystem Dynamics (GLOBEC).

Physical Oceanography and Climate of the Eastern Bering Sea

Section 2

The circulation of the northern North Pacific and Bering Sea transports heat and freshwater poleward and replenishes nutrients in the surface layers to support biological productivity. Changes in this transport system affect heat, salt, and food supply for the Bering Sea ecosystem.

2.1 Physical Oceanography of the Eastern Bering Sea

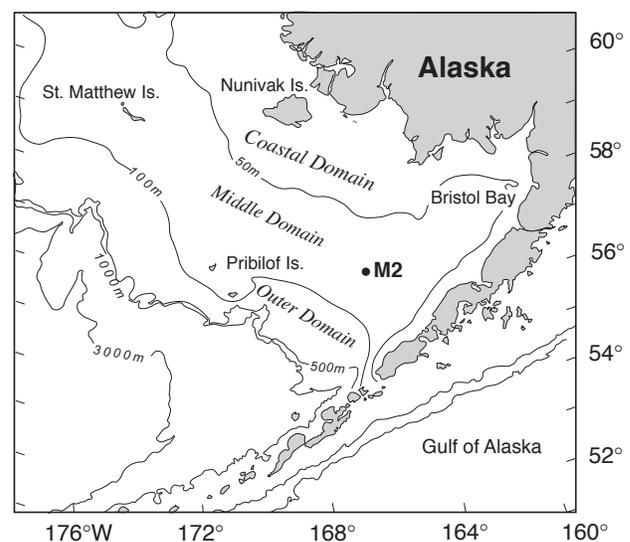
The Bering Sea consists of a deep central basin, a narrow northwestern shelf that extends south along the Kamchatka Peninsula, and a broad (500 km-wide) eastern shelf that stretches from the Alaska Peninsula to Russia and Bering Strait (Figure 1). The waters of the eastern Bering Sea can be divided into an oceanic regime in the basin and a shelf regime over the eastern shelf. The eastern shelf can be further sub-divided into the southeastern, central, and northeastern shelf (Schumacher and Stabeno, 1998). The divisions among these three regions have not been well delineated, but it is generally agreed that the central region is located between a line from St. Paul Island, Pribilof Islands, to Nunivak Island northward to an east-west line about half way between St. Matthew Island and St. Lawrence Island (Figure 8). The northeastern region of the shelf is dominated by advective processes and has relatively weak tides, whereas the southeastern region generally has relatively weak cross-shelf transport and strong tides. Little study has been devoted to the central region, but it is a transition area where cross-shelf transport may be important.

Figure 8. The southeastern Bering Sea, showing depth contours, the location of major hydrographic domains, and mooring 2 (M2), from which time series of sea water properties have collected since 1995.

Map courtesy of N. Kachel.

The following overview of the oceanic regime is based on Schumacher et al. (2003). The oceanic regime of the eastern basin is influenced by the Alaska Stream that enters the Bering Sea through the Aleutian Passes, particularly Amchitka and Amukta passes, and turns right to form the Aleutian North Slope Current (Figure 9; Reed and Stabeno, 1999, Stabeno et al., in press). This current, in turn, is the source of water for the Bering Slope Current 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).

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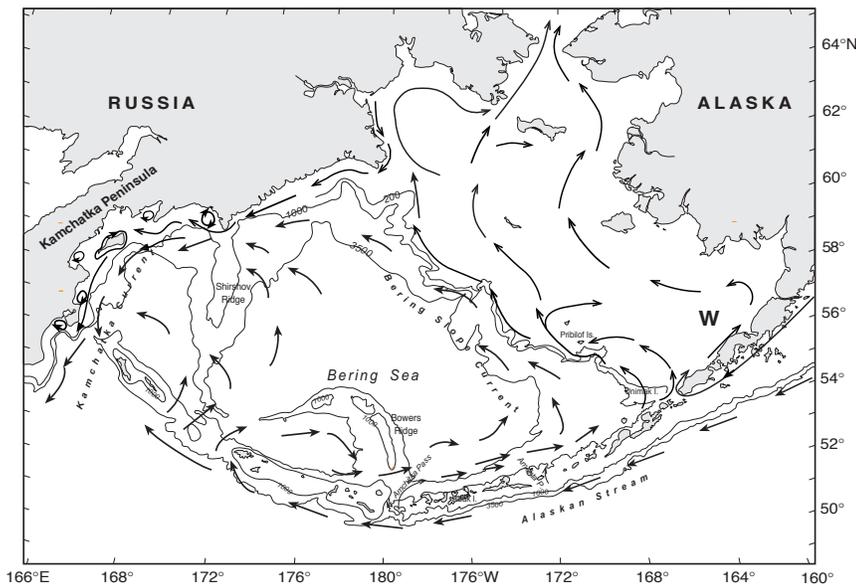


Figure 9. Major currents of the Bering Sea. The Aleutian North Slope Current flows eastward just north of the Aleutians. From Stabeno et al., 1999a.

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The broad continental shelf of the southeastern Bering Sea is differentiated into three bathymetrically-fixed domains: the Coastal Domain 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 which ranges from 100 m to 200 m in depth (Figure 8; Iverson et al., 1979; 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 (Kachel et al., 2002), the wider (> 50 km) middle transition zone between the Middle Shelf Domain and the Outer Shelf Domain, and the Slope 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 a strongly stratified two layer system with a tidally mixed bottom layer and wind mixed surface layer, and the Outer Shelf Domain has well mixed upper and lower layers separated by a zone of gradually increasing density. 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 (Stabeno et al., 2001; Hunt et al., 2002a).

The physical oceanography of the central portion of the Bering Sea shelf is not well studied, despite Coachman et al. (1975) having pointed out our lack of knowledge of this important connection between the southeastern and northeastern portions of the shelf. The circulatory connection between the southeastern and northern Bering shelf is at present largely inferred, because while

the flow over the northeastern and southeastern shelf are individually reasonably well-known, the circulation over the intervening connecting portion of the shelf, between Nunivak and St. Lawrence islands, has not been delineated (Coachman et al., 1975). This central, connecting portion of the shelf is also the region where both the Bering Shelf Water and the cold winter bottom water form, processes that Coachman et al. (1975) emphasized as being very poorly understood.

The hydrographic structure of the northeastern Bering Sea has been less well studied than that of the southeast. The shelf in the north is dominated by a wide "middle domain" of stratified water (Bering Shelf Water) in summer, and a coastal domain of well-mixed water. 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 (Muench et al., 1981). During summer in Norton Sound, a two-layered system can occur in water as shallow as 15 m. In winter, the water column is well mixed. In the Chirikov Basin, between St. Lawrence Island and Bering Strait, there are three water masses: fresh, warm Alaska Coastal Current Water in the east; Bering Shelf Water in the middle, and cold salty Anadyr Current Water in the west (Coachman et al., 1975). The Alaska Coastal Current Water and the Anadyr

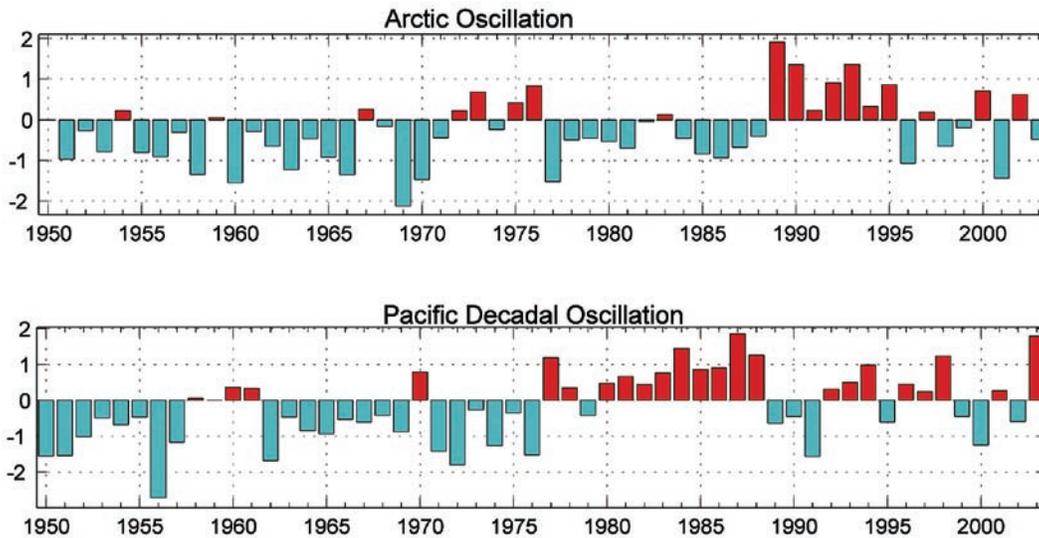


Figure 10. Time series of Arctic Oscillation and Pacific Decadal Oscillation. After Overland et al., 1999.

Current Water both tend to be well mixed, whereas the Bering Shelf water is stratified. The northeastern and central regions of the eastern Bering Sea shelf are usually covered by sea ice in winter, whereas sea ice cover in the southeastern Bering Sea varies greatly both inter- and intra-annually in extent and duration.

2.2 Climate Influences on the Southeastern Bering Sea

An important development in fisheries oceanography during the late twentieth century was the realization that climate variability, at the scale of decades, could have profound impacts on the function of marine ecosystems; relatively 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 of fisheries on fish stocks at a given rate of harvest may be quite different under different climate patterns (see section 5.2.1).

For the North Pacific Ocean, three well-studied indices of climate patterns depend on variability in winter: the Pacific

Decadal Oscillation (PDO), the Southern Oscillation (SO), and the Arctic Oscillation (AO). The AO has its largest variance in winter (January–March). A strong 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; Figure 10). The AO is defined as the leading mode of sea level pressure (SLP) 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., in preparation). The AO influences the Bering Sea through its effect on the Aleutian Low Pressure System, 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.

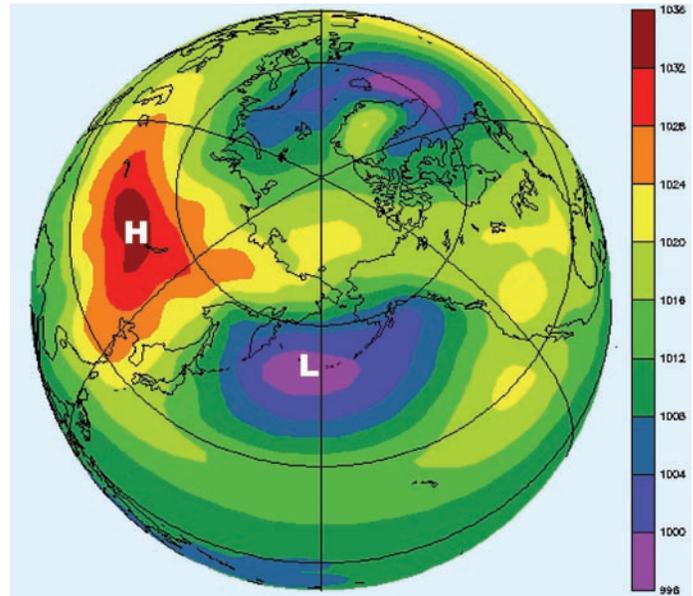
The SO plays a major role in global climate variability at time scales of 2–7 years, and has its greatest influence in the tropics. Recently, the SO has been shown to have a small but significant influence on marine climate of the Bering Sea via atmospheric teleconnections (Niebauer, 1998; Hollowed et al., 2001; Martin et al., 2001; Overland et al., 2001). A third index of atmospheric pressure, the North Pacific

Figure 11. The pressure gradient between the Siberian High (H) and the Aleutian Low (L) affects the intensity of storms and their tracks. From Overland et al., 1999.

(NP) pattern, represents the leading mode in spring of the 700 mb height, and is most prominent from March through July (Barnston and Livezey, 1987; Ladd et al., in preparation). 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).

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 50–60 years (Chavez et al., 2003; Ladd et al., in preparation; Figure 10). 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 most basic representation of atmospheric variability for the Bering Sea is the weekly to monthly average of the Siberian High SLP region and the Aleutian Low SLP region. The location and intensity of these two pressure fields influence the tracking and intensity of storms and other surface elements (Figure 11). Over the Bering Sea, there is a region of strong gradients in sea-level pressure 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 attributes of marine ecosystems (Minobe, 1999). By analyzing 100 time series of physical and biological variation, Hare and Mantua (2000) found evidence for regime-like jumps in these records near 1977 and 1989. The evidence was clearer in the biological data than in the physical time series. Their second mode showed strong co-variability between physical and biological variations in the Bering Sea over the past 40 years.

What are the External Forcing Functions and How do they Affect the Eastern Bering Sea?

Section 3

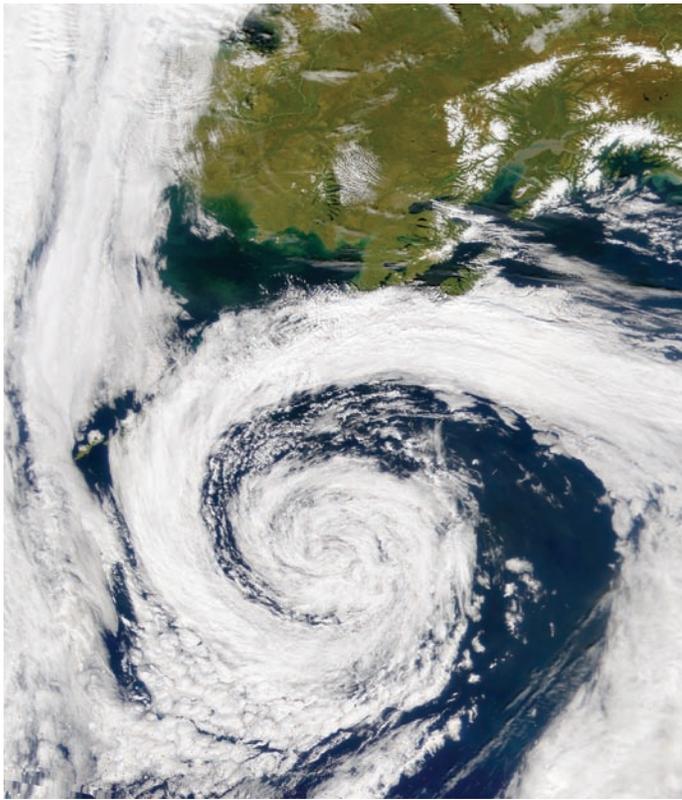
Two major external physical forcing mechanisms dominate the eastern Bering Sea: atmospheric forcing (solar insolation and winds) and transport of water through the Aleutian Passes and Bering Strait. In addition, tides and riverine inflows shape the hydrography of the shelf. Variability in these forcing mechanisms occurs on all spatial and temporal scales, including local episodic events (storms), interannual variability at the scale of the eastern Bering Sea, and decadal and long-term climate change at North Pacific- and global-scales. In addition to external physical forcing, productivity in the Bering Sea can be impacted by migratory species (whales, birds, etc.), and by the removal of a large biomass of fish and shellfish through commercial fishing. These top-down effects will be addressed in section 5.

3.1 Atmospheric Forcing

Global patterns of atmospheric forcing are changing, but we do not know how these changes will affect the physical and biological components of the eastern Bering Sea. The Bering Sea is subject to external forcing from neighboring regions, with cold, dry air masses from the Arctic, and warm, moist air masses from the Pacific Ocean. The arctic air masses that impact the Bering Sea show a long-term upward trend in spring temperatures (Stabeno and Overland, 2001). This warming will almost certainly be accompanied by a change in storm activity and the extent, duration, and location of sea ice cover. Atmospheric teleconnections also result in influences from more distant regions, such as the equatorial Pacific Ocean (e.g., the SO; Overland et al., 2001). Because atmospheric forcing occurs on all time scales, from daily to long-term trends, interacting processes may elicit chaotic responses

in Bering Sea ecosystem constituents (Overland et al., 2000).

Changing North Pacific climate indices are indicative of decadal-scale changes in wind forcing over the Bering Sea. The effects of such changes on the Bering Sea heat balance, and on production and composition of Bering Sea ecosystems remain unknown. In the North Pacific region, the wintertime atmospheric 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 30 years. One followed the winter of 1976–77, in which the PDO and the AO both shifted (Figure 10). A



A storm moves into the Bering Sea on 9 September 2001. Image from the SeaWiFS Project, NASA/Goddard Space Flight Center, and ORBIMAGE.

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second shift of the AO occurred after the winter of 1988–89 (Ebbesmeyer et al., 1991; Hare and Francis, 1995; Sugimoto and Tadokoro, 1998; Beamish et al., 1999; Brodeur et al., 1999a; Hare and Mantua, 2000). Evidence also indicates a third shift in the winter of 1998–99 (Schwing and Moore, 2000; Peterson et al., 2002). Although the SO appears to shift between alternate states, that does not appear to be the case for the southeastern Bering Sea, where the few regimes documented so far have each had unique characteristics. An important aspect of the AO is its trend toward a more persistent positive state since the late 1960s (Thompson and Wallace, 1998). The influences of the NP and AO modes in spring have resulted in an increase in southerly winds over the Bering Sea (Overland and Stabeno, 2004).

It is critical to understand how the timing, duration, and intensity of wind events interact with other mechanisms to influence the ecosystems of the eastern Bering Sea. There is a clear seasonal signal in the Bering Sea, with strong, frigid winds occurring in the winter and relatively weaker, warmer winds dominating

during the summer. The strong winds of winter mix water over the shelf to ~100 m (Coachman, 1986). In addition, wind-driven currents during the winter result in strong on-shelf and cross-shelf fluxes of water (Stabeno et al., 2001). This water is rich in nutrients, and wind-driven cross-shelf flux is the major mechanism for re-supplying nutrients to the productive eastern Bering Sea shelf (Stabeno et al., 2001, 2002). Interannual variation in cross-shelf advection may also be important in controlling year-class strength of ground fish (Wespestad et al., 2000; Wilderbuer et al., 2002). During summer, the winds weaken and the characteristic domains and fronts are formed (Coachman, 1986; Schumacher and Stabeno, 1998; Stabeno et al., 1999a). Fronts that separate the various regimes inhibit cross-shelf transport in summer.

The location, strength and timing of storms are likely to be critical to the shelf ecosystem, but the effects of changes in the pathways, strength and duration of storms is not understood (vis Overland and Pease, 1982). Prolonged winter storms would delay the formation of the fronts on the Bering Sea shelf (thus modifying the cross shelf transports), and/or could deepen the mixed layer (which could result in higher production in the spring and fewer nutrients available to support summer and fall production). Changes in the amount and timing of primary production, in turn, could impact the rest of the food web, such as survival of first feeding fish larvae and visiting migratory species (Walsh and McRoy, 1986; Baduini et al., 2001). Similarly, a change in the number and/or strength of summer storms will impact post-spring-bloom primary production (Ladd et al., in preparation). An increase in the number of storms could also impact cloud cover, in turn modifying insolation, and thus sea surface temperature (SST; Stone, 1997). A change in the wind stress curl would modify cur-

rents in the basin, particularly the Bering Slope Current, which interacts with topography along the eastern Bering Sea slope, resulting in instabilities that form eddies and meanders (Figure 12; Bond et al., 1994; Stabeno et al., 1999a). In general, how changes in storm tracks will combine with other forcing mechanisms is difficult to predict. Modeling and model validation with field data are needed to help clarify the potential effects of changes in storm intensity on the Bering Sea shelf ecosystem.

Atmospheric forcing largely drives ice formation and advection, but it is unclear how changes in atmospheric forcing will affect the duration and distribution of sea ice on the Bering Sea shelf. Since the presence of sea ice strongly influences the timing, duration, and fate of primary production on the shelf, mechanisms linking climate to ecosystem response cannot be fully understood without understanding the effects of climate on sea ice. In the Bering Sea, ice forms as early as November, and usually reaches a maximum in late February or March. During the winter season, ice generally forms in the north, and is then advected southward by the wind. Once the ice cover is established, polynyas form in the lees of the islands and coastal promontories. Polynya formation, location, and size depend on strong, frigid winds, usually out of the north (Pease, 1980; McNutt, 1980, 1981; Smith et al., 1990). Regions of high productivity and biological activity throughout the winter, polynyas are major sources of heat to the atmosphere and brine to the water column (Stirling, 1980; Dunbar, 1981). Sea ice effectively changes the salinity distribution across the shelf, both through brine rejection during sea

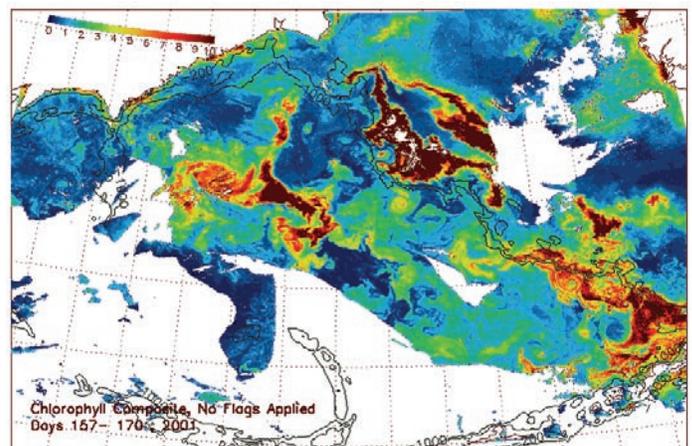
ice formation, and through the introduction of fresher water due to melting at the ice edge. Understanding how changes in the salinity of the water impacts the ecosystem is critical. Sea ice also gives rise to cold water on the shelf, which persists at depth over the middle shelf through summer. Temperature in this “cold pool” affects the distribution of juvenile pollock and their vulnerability to predation (Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1995, 1996; Wyllie-Echeverria and Wooster, 1998). Impacts of sea ice on the ecosystems of the Bering Sea shelf are discussed in section 4.

3.2 Transport in Currents

3.2.1 Inflows Through Aleutian Passes

Transport through the Aleutian passes and Bering Strait plays an important role in controlling the flux of heat, nutrients, and salts throughout the Bering Sea. The factors controlling transport through the deeper Aleutian passes, however, are not well understood. In addition, the influence of flow through Aleutian passes on southeastern Bering Sea ecosystems is recognized but not understood. There appears to be a division in the characteristics of the water flowing through the Aleutian Passes, with the Alaskan Stream water flowing through the deeper west-

Figure 12. A composite image of chlorophyll from SeaWiFS for 6–19 June 2001. The Bering Sea, particularly along the slope, is rich in mesoscale variability as evidenced in the chlorophyll. Eddies play an important, if not completely understood, role in causing this variability. For instance, an eddy in the southeast corner contains low concentrations of chlorophyll (blue) while the surrounding water has higher concentrations of chlorophyll. In contrast, near the center of the image, an eddy with higher concentrations of chlorophyll (yellow) is surrounded by lower concentrations. Figure courtesy Phyllis Stabeno.



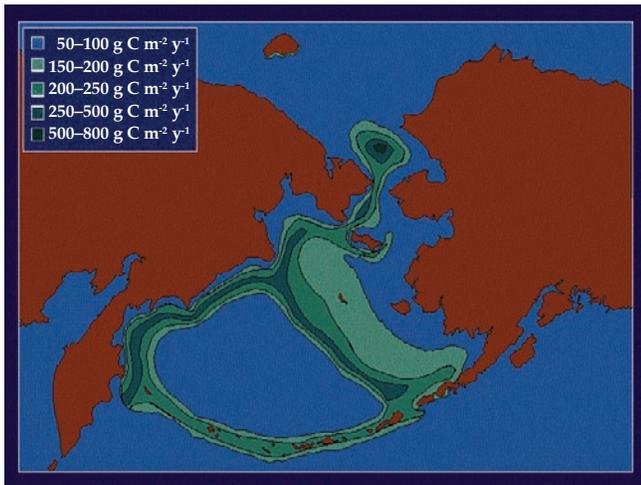


Figure 13. A composite pattern of primary productivity in the Bering Sea. The high productivity of the Green Belt (indicated by the dark green) is centered on the shelf edge. From Springer et al., 1996.

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ern passes, and a combination of Alaska Coastal Current (ACC) and Alaskan Stream water flowing through the shallow eastern passes (Ladd et al., in press). The ACC, which is freshened by runoff along the Gulf of Alaska coast, freshens the waters of the southeastern Bering Sea shelves (Stabeno et al., 2002; Ladd et al., In Press). Its transport through the eastern passes (Unimak, Akutan, and Samalga) is controlled in part by the along-shore wind stress (Schumacher et al., 1982; Stabeno et al., 2002; Stabeno et al., in press). The ACC introduces heat and zooplankton to the southern Bering. Since maximum northward flow through Unimak Pass is in the winter, this inflow may also play a role in limiting the maximum extent of ice along the Alaskan Peninsula.

Net transport through the passes varies on many scales, including a strong fortnightly component in the deeper passes (Reed and Stabeno, 1993; Stabeno et al., in press). Mesoscale eddies (of the order of 200 km across; observed from satellites and simulated with ocean models) along the Aleutian slopes in both the Bering Sea and the North Pacific likely impact Pacific-Bering exchanges (Figure 12; Schumacher and Stabeno, 1994; Okkonen, 2001). Flow through the passes provides a forcing mechanism for water mass modification in the southern Bering Sea at seasonal to interannual time scales, but their effects on marine ecosystems have yet to be determined.

Changes in transport through the Aleutian Passes would modify transport

in the Bering basin. Since approximately half of the Bering Sea gyre transport is related to inflow through the Aleutian Passes (the other half is driven by local wind stress curl; Bond et al., 1994), a reduction of flow could result in a less energetic Bering Slope Current, in turn modifying the flow of nutrient-rich water onto the eastern shelf. The primary result of reduced northward flow through the Aleutian Passes would be a reduction in transport of nutrients and heat. Reduction of nutrients may reduce the primary production of the Bering Sea ecosystems. The reduction of heat would allow an increased extent of sea ice. The magnitude of both of these changes is unknown.

3.2.2 Mechanisms for On-shelf Transport of Nutrients and Heat

The mechanisms linking atmospheric circulation patterns to currents, meanders, eddies, and upwelling along the continental shelf slope and their impacts on nutrient replenishment in slope and shelf waters are not understood. Water being transported through the Aleutian Passes is well mixed. Thus the deeper, nutrient-rich waters from the North Pacific and deep Bering Sea are mixed upward into the euphotic zone. This water is advected eastward as the Aleutian North Slope Current (ANSC) and subsequently turns northwestward as the Bering Slope Current (BSC; Figure 9; Stabeno et al., 1999a). The ANSC/BSC system bathes the Bering Slope in warm, saline, nutrient-rich water. The BSC experiences frequent along-slope mesoscale eddies (of the order of tens of km), which are believed to bring nutrient-rich and saline waters up the Bering shelf slope, thus affecting the slope region and the outer shelves, as well as the northern Bering Sea ecosystems via the Anadyr Current (Stabeno et al., 1999a). A region of high primary production (the "Green Belt") along the slope coin-

cides with the path of the BSC (Figure 13; Springer et al., 1996). This may be a region where nutrient-rich, but iron-poor water from the basin mixes with iron-rich water from the shelf, but the measurements critical for testing this hypothesis are lacking (Springer, 1999). When slope water upwells onto the northeastern shelf, it results in a region of high production to the south of St. Lawrence Island and northwards through Bering Strait (Shuert and Walsh, 1993; Springer and McRoy, 1993). Changes in atmospheric forcing will modify these processes in undetermined ways.

The relationship between atmospheric forcing and the formation, size, and trajectories of eddies along the eastern Bering Sea continental slope are unresolved. In the southeastern Bering Sea, eddies are a mechanism for on-shelf transport of nutrients originating in slope waters (Stabeno et al., 1999a; Stabeno and Van Meurs, 1999; Okkonen, 2001; Johnson et al., 2004). They occur not only in water seaward of the eastern shelf (Schumacher and Reed, 1992), but can occur in waters as shallow as 100–122 m deep (Reed, 1998). Potentially important as habitat for larval and juvenile pollock, these eddies can carry these fish, as well as nutrients, from the Oceanic Domain into the Outer Shelf Domain (Schumacher and Stabeno,

1994; Stabeno et al., 1999a). However, because eddies are rare in water less than 100 meters deep, other mechanisms are required to replenish nutrients in the Middle and Inner Domains.

Mechanisms for the on-shelf transport of nutrients and their susceptibility to atmospheric forcing are areas requiring substantial research effort. In the southeastern Bering Sea, two regions of preferential on-shelf flow are Bering Canyon, just north of the Aleutian Islands near Unimak Pass, and Pribilof Canyon, where the shelf break narrows (Stabeno et al., 1999a). There, acceleration of flow over the outer shelf (Schumacher and Stabeno, 1998) entrains slope water (Stabeno et al., 1999b). On-shelf flow west of the Pribilof Islands can move into the Middle Domain, 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, exhibit substantial variability (Stabeno et al., 2001), but it remains an open question how these influence on-shelf fluxes.

The mechanisms for nutrient transport across the southeastern Bering Sea shelf, their contribution to the nutrient pool relative to local remineralization, and their susceptibility to changes in atmospheric forcing are important and unanswered questions. Over the southeastern Bering Sea shelf, cross-shelf flux of nutrients is believed to provide about 50% of the nutrients that support new production on the southeastern Bering Sea shelf (Sambrotto et al., 1986; Whitley et al., 1986). This estimate remains to be verified. These cross-shelf fluxes were 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).

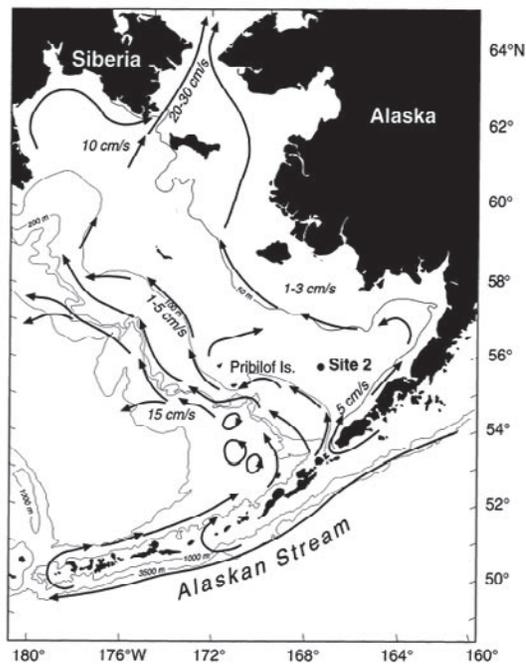


Figure 14. A schematic of flow on the eastern Bering Sea shelf in the upper 40 m of water column generated from a synthesis of moored current meters, satellite-tracked drift buoys and inferred geostrophic flow. Depths are in meters. After Schumacher and Stabeno, 1998; Stabeno et al., 1999a.

Two mechanisms have been proposed for driving cross-shelf advection. One mechanism is wind-forced circulation. Stabeno et al. (2001) hypothesized that strong winds during winter advect nutrient rich water onto the shelf, supplying nutrients for supporting productivity during the following spring and summer. Although mean annual current velocities over the middle shelf at a mooring (Mooring 2) in the central southeastern Bering Sea shelf (Figure 14) are weak, episodic (short-term) currents averaged over shorter periods (e.g., daily) can exceed 25 cm s^{-1} (Stabeno et al., 2001). 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). A second proposed mechanism that could contribute to replenishment of nutrients over the southeastern shelf and that may occur in response to the generally southward movement of sea ice in

winter is an onshore flow at depth, but this hypothesis has yet to be investigated (Schumacher and Alexander, 1999). In addition, there is a weak eastward flow originating north of St. Paul Island (Stabeno et al., 1999b). This eastward flow provides nutrients to the middle shelf between St. Paul and Nunivak Island, and is marked by a newly described front to the northeast of St. Paul Island (Flint et al., 2002).

3.2.3 Advective Processes in the Northern Bering Sea

On-shelf fluxes of nutrients from the Bering Sea basin are critical for the long-term productivity of the northern Bering Sea continental shelf, but the mechanisms responsible for forcing these fluxes are still not well understood. In the northern Bering Sea, cross shelf fluxes occur in the Anadyr Current (Figure 9) and from the northward flow along the 100 m isobath (Stabeno et al., 1999a). These waters then flow northward through Anadyr and Bering straits (Figure 9; Shuert and Walsh, 1993; Overland et al., 1994). These currents persist during the summer months. The Anadyr Current is an important source of nutrients to the northern shelf, and its flow is, at least in part, a response

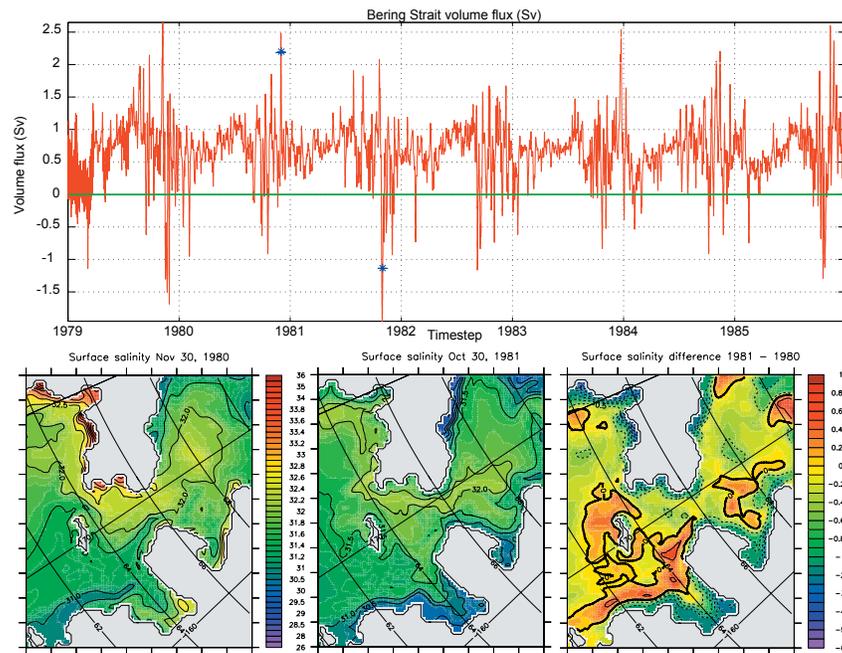


Figure 15. Top: total volume flux through Bering Strait 1975–86. Blue asterisks indicate the time of the surface salinity distribution plots below. Lower left: November 1980. Lower middle: October 1981. Lower right: difference between the two (with range of salinity change from -4 to 0.5 psu). From Clement et al., submitted.

On June 4, 2001 MODIS acquired this true-color image showing sediment discharge from the mouth of the Yukon River. Satellite: Terra. Image by Jacques Desclotres, MODIS Land Rapid Response Team, courtesy NASA Visible Earth.

to the northward flow through Bering Strait (Coachman et al., 1975; Nihoul et al., 1993). Nutrients in this water support the extraordinarily high rates of summertime production found in the Chirikov Basin and northward through Bering Strait (Springer and McRoy, 1993; Springer et al., 1996). This process also transports large oceanic copepods onto the northern shelf, where they support immense populations of planktivorous seabirds (Springer and Roseau, 1985; Springer et al., 1987, 1989; Hunt and Harrison, 1990; Hunt et al., 1990; Russell et al., 1999). The exact connections to the Bering Sea basin, however, remain unclear.

The along-shelf flow and BSC both advect heat northward. There is a net flux of heat from the ocean into the atmosphere over the Bering Sea shelf (Reed, 2003). The northward fluxes of water along the shelf break and over the shelf provide the necessary heat to balance the loss to the atmosphere. The source of this warm water is the Alaska Stream.

Flow through the Bering Strait appears to be changing, but the effect of this change on heat balance, nutrient flux, and ecosystem structure on the northern Bering Sea shelf remains unknown.

Bering Strait is relatively narrow, with $<1 \times 10^6 \text{ m}^3 \text{ s}^{-1}$ of flow (in contrast to a total transport of $\sim 15 \times 10^6 \text{ m}^3 \text{ s}^{-1}$ through all the Aleutian Passes). Net northward transport in Bering Strait results from the difference in the sea level heights between the Pacific and Atlantic Oceans (Overland and Roach, 1987). When strong winds blow southward in fall and winter, they can overcome the net northward flow through Bering Strait, causing a southward flow exceeding $1\text{--}2 \times 10^6 \text{ m}^3 \text{ s}^{-1}$ of cold, relatively fresh water from the southern Chukchi Sea into the northern Bering Sea (Figure 15; Roach et al., 1995; Overland et al., 1996; Clement et al., submitted). The likely impact of a long-term decrease (or increase) in flow through



Bering Strait would be more localized than that of a decrease in flow through the Aleutian passes. Although the area most impacted would likely be the shelf region north of 63°N , reduced flow through Bering Strait would reduce on-shelf flow of nutrients, and thus primary production on the northern Bering Sea shelf. It would also modify the advection of nutrients and particulate carbon into the Arctic Ocean.

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3.3 Riverine In-flows

Observations are needed to document how climate change is affecting the timing, magnitude, and pattern of riverine discharge, the temperature of the freshwater, and how these changes are impacting eastern Bering Sea ecosystems. The nearshore Bering Sea ecosystem (which has received little oceanographic attention generally) is strongly influenced by large, seasonally varying river inflows, an external forcing function that remains to be thoroughly investigated. In addition to the rivers flowing into the Bering Sea, riverine flow and glacial melt from the Gulf of Alaska are introduced to the Bering Sea through the eastern Aleutian passes, and flow northward along the western coast

of Alaska. These freshwater inflows, particularly from the Yukon River, provide a critical seasonal buoyancy flux to the coastal regions of the Bering Sea and may enhance the baroclinic flow of the Alaska Coastal Current on its way to the Chukchi and Beaufort Seas. Strongly marked by freshwater runoff, the central portion of the nearshore Bering shelf is an important conduit linking the southern and northern ecosystems and is prime habitat for many species, including migratory waterfowl and juvenile salmon beginning their out-migration to the open sea. Additionally, the nearshore ecosystem is vital to the numerous coastal residents who depend upon it for subsistence. Unfortunately, runoff measurements, which are important for ascertaining the role of riverine inflows, were discontinued in the 1990s, and temperature measurements (for heat flux estimates) are not available.

River influx also appears to play an important role in the formation of Bering Shelf Water, is indicated by $\delta^{18}\text{O}$ distribution (Coachman and Shigaev, 1992; Cooper et al., 1997). Both the isotopic signature field and remote sensing (Broerse et al., 2003) suggest that there is a substantial cross-shelf transfer of freshwater, sediments, and re-suspended biogenic material. In particular, satellite imagery, along with a pilot study involving satellite-tracked drifters (<http://www.ims.uaf.edu/NPRBdrifters/>), indicates major cross-shelf transport of freshwater in the region between St. Matthew and St. Lawrence islands. While the ecological significance of this flux is largely unknown, it likely redistributes macro- and micronutrients, and modifies Bering Shelf Water and the cold pool. For example, by changing the mid- and outer shelf salinities prior to freeze-up, this cross-shelf freshwater flux will alter the properties of the waters formed during winter ice formation. Cross-shelf transport and mixing on the Bering Sea shelf also have im-

portant downstream consequences for the salinity of the waters flowing northward through Bering Strait and thence into the Arctic Ocean, where they modify the density stratification in a manner that depends on the properties they acquired on the Bering shelf (Roach et al., 1995; Steele et al., 2004).

3.4 Tides

A clearer understanding is needed of the importance of tides, relative to other forcing factors, for cross-shelf flux of nutrients and organisms. Tides are important sources of mixing on the shelves and in the Aleutian Passes (Stabeno et al., 2001, in press). Over the eastern shelf they contribute to the formation of the hydrographic domains (Coachman, 1986; Schumacher and Stabeno, 1998). The coastal domain is weakly stratified because of the overlapping of mixing due to winds and tides, while the two-layer middle shelf domain forms by the abutment of the wind-mixed upper layer and tidally mixed lower layer (Schumacher and Stabeno, 1998). During some years prolonged production can occur along the inner front, which is the boundary between these two domains. This, in turn, supports the food web during the summer (Sambrotto et al., 1986; Kachel et al., 2002). In addition to tidal mixing, tides also contribute to the inflow through the Aleutian Archipelago. Tides are rectified in these passes, thus contributing to the net northward transport (Reed and Stabeno, 1993; Stabeno et al., in press). Tidal forcing can provide a stabilizing influence on the physical forcing of the Bering Sea, since tides are stationary and not modified by climatic variability. Tidal mixing may become particularly important under a scenario of increased stratification from higher solar warming and decreased wind mixing.

3.5 Questions Related to External Forcing Mechanisms

a. How would hemispheric climate change impact the Bering Sea?

While natural (solar variability, volcanoes) and anthropogenic (CO₂, greenhouse gases, aerosols) forcing have some direct impact on the subarctic region, their main impact is through changes in atmospheric circulation patterns caused by increased north/south gradients in radiative forcing. Thus there is not a uniform “global warming” of the Bering Sea, but spatial-, seasonal- and air mass-dependent impacts. As the Bering Sea responds to climate change, the influences of adjacent regions—the North Pacific, Siberia, and the Arctic—are likely to shift in relative importance.

b. How would changes in flow into the Bering Sea affect the circulation within the Bering Sea, and its output to adjacent seas?

Measurements of flow through the Aleutian Passes are extremely limited. Understanding what controls the flow through the passes is critical to understanding the strength of the Bering Slope Current (BSC) and the Aleutian North Slope Current (ANSC). Flow through these passes provides the nutrients necessary to drive the rich Bering Sea ecosystem. Freshwater discharges onto the eastern Bering Sea shelf constitute a second source of external forcing, the impact of which is not well studied. Thus, particularly in the under-studied central portion of the shelf, (e.g., between Nunivak and St. Lawrence islands), there is a need to determine circulation patterns and their impacts on shelf ecosystems. To investigate how changing flow in the passes

and rivers modifies the circulation, it will be necessary to employ a combination of moored observations, satellite-tracked drifters, and modeling.

c. How would changes in circulation through Bering Strait affect the circulation within the Bering Sea?

Flows through Bering Strait provide an exit for nutrient-rich waters advected from the basin and slope through Anadyr Strait, for the freshwater originating from the Alaska Coastal Current (ACC), for the riverine flow along the Alaskan coast, and for salty brine produced by the freezing of sea ice. If the Bering Strait flows were to diminish substantially or shut down, how would that affect the availability of nutrients and particulate carbon to fuel the benthic and pelagic communities of the northern Bering Sea? What would happen to the freshwater from the Alaska Coastal Current? If there were still substantial brine production, would it now flow into the basin? What would be the effect of brine flowing into the basin?

d. How does variation in atmospheric forcing (winds, solar radiation, and cloud cover) affect the physical structure of the Bering Sea?

Atmospheric forcing, together with tidal currents, determines the physical structure of the Bering Sea. Tides play a relatively important role in circulation and mixing in the southeastern Bering Sea, and a lesser role in Norton Sound and the northern Bering, where advective processes are more important. However, there is a lack of observational data over the central part of the shelf from St. Paul Island north to St. Lawrence Island. To understand the connections between the northern and southern shelves, observations over the central shelf, including how the atmo-

spheric forces interact with shelf currents, are critical. The relative importance of various external-forcing mechanisms is likely to vary with location on the eastern shelf. What are the implications of significant changes in these forcing mechanisms for the ecology of the eastern Bering Sea?

e. What is the importance of currents (e. g., ANSC, BSC, ACC, and Anadyr Current), mesoscale eddies and meanders for cross- and on-shelf fluxes and ecosystem structure in the Bering Sea?

Currents are major transport mechanisms for heat, nutrients, and plankton on and along the edge of the eastern Bering Sea continental shelf. At a limited number of sites, currents may impinge on the shelf and support cross-shelf advection. In other cases, eddies and meanders form in the currents. We need to identify where currents come onto the shelf, and the fate of the water and its nutrients and plankton once on the shelf. We need to know if there is a regularity to the formation of eddies and meanders, the role of these features in advecting water, nutrients, and organisms onto the shelf, and how changes in atmospheric forcing affects the frequency, magnitude and fate of on-shelf flows of all sorts.

f. How does atmospheric forcing affect the distribution, abundance and availability of nutrients over the eastern Bering Sea shelf?

On the shelf, tides, fronts, and wind are important in determining the distribution and availability of nutrients to phytoplankton, particularly once the spring phytoplankton bloom is completed. Cross-shelf flux of nutrients is enhanced by the currents and diminished by frontal systems. Vertical flux of nutrients is inhibited by stratification and enhanced by wind mixing and frontal processes. Stratification, wind mixing, and frontal strength are all subject to climate influence; tides are not. Similarly, the strength of tides and residual currents varies from north to south over the shelf. We need to know how changes in atmospheric forcing will affect the distribution and abundance of nutrients on the shelf and their availability to support primary production. What is the relative importance of currents versus in situ remineralization for nutrient supplies on the southeastern, central and northeastern shelf? How does the timing and magnitude of storm events influence nutrient distributions?

What are the Biophysical Mechanisms that Control the Observed Biological Variability?

Section 4

Biological processes interact with physical aspects of the marine environment in many ways. Three mechanisms of interaction that are important in the eastern Bering Sea are: 1) stratification of the water column, which affects the availability of light and nutrients supporting primary production and the vertical distribution of many of the smaller plankton organisms; 2) sea ice, which affects light, nutrient distributions, the availability of substrate for benthic taxa, and water temperature; and 3) water temperature, which affects the rates at which physiological processes occur, and which is a habitat variable to which fish respond behaviorally by seeking waters of preferred temperatures. The roles of sea ice and its closely related variable water temperature are discussed below.

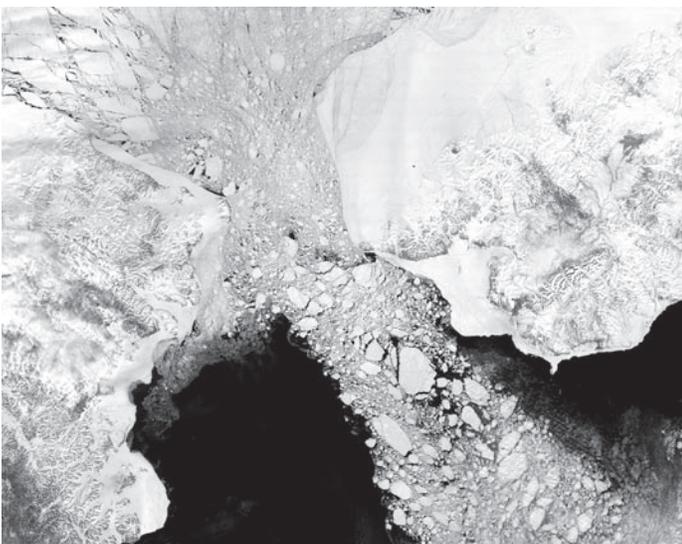
4.1 What are the Roles of Sea Ice?

Sea ice is one of the defining characteristics of the Bering Sea continental shelf.

Ice integrates the effects on the ocean of atmospheric forcing, especially wind and air temperature, and long-term teleconnection patterns. Sea ice formation over the eastern shelf begins as early as November, and sea ice may remain into June of the following year. Most of the sea ice is formed in the northern portions of

the shelf and is then advected southward due to the prevailing north-northeasterly winds (Pease, 1980; McNutt, 1981, 1980). Formation, melt, and retreat of sea ice provide the physical conditions that influence the structure and function of Bering Sea continental shelf ecosystems through: (1) brine formation, (2) development of polynyas, (3) formation of “cold pools” in the bottom layer, and (4) freshwater and nutrient input to the water column. Sea ice also serves as habitat for microfauna, birds, and marine mammals. The advance and retreat of the ice also affect the migration routes of arctic marine mammals and seabirds.

In the Bering Sea, sea ice modifies water temperature, salinity, and baroclinic currents. The formation, advection, and melting of the ice edge influence heat and salt flux on the Bering Sea continental shelf. Ice formation produces cold, saline



MODIS image of sea ice in the Bering Strait, acquired on May 7, 2000. Image courtesy NASA Goddard Distributed Active Archive Center.



Sea ice. Photo by Paul Lethaby.

cover in the region (Figure 16; Overland and Stabeno, 2004).

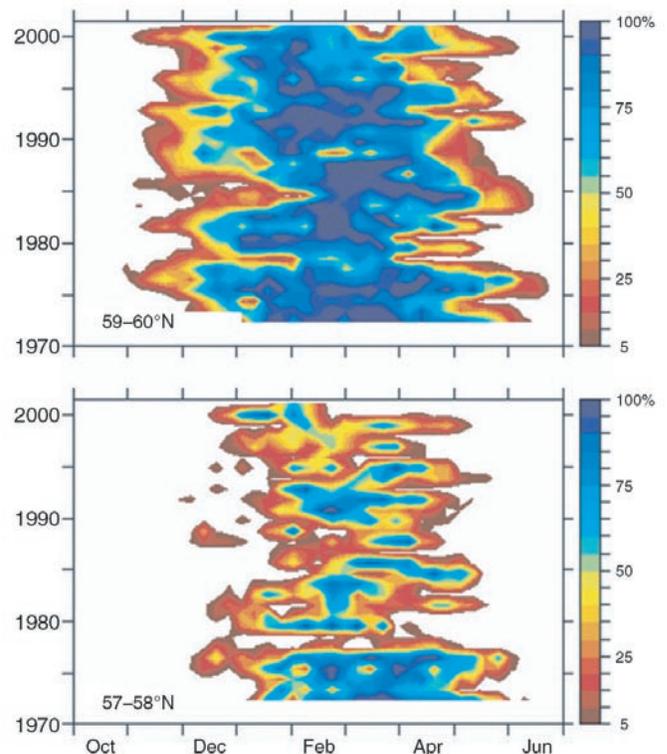
4.1.1 Climate Variability and Sea Ice Responses

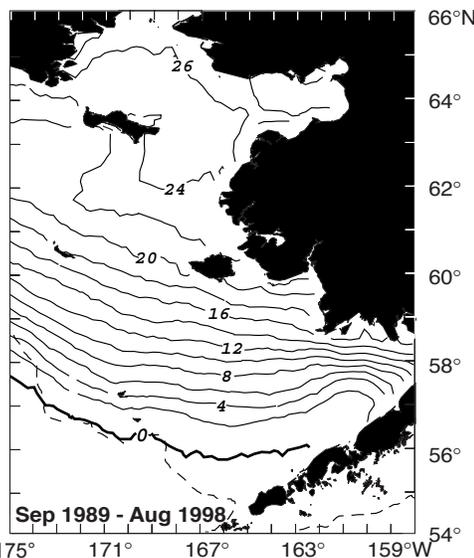
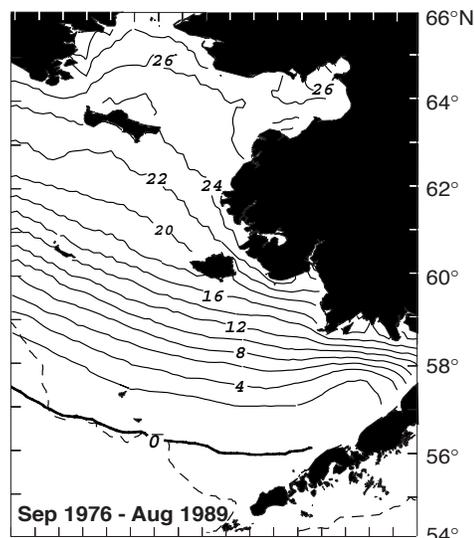
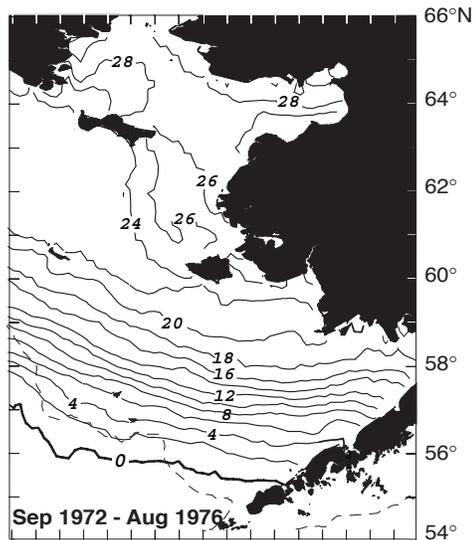
A better understanding of how sea ice responds to longer-term variations in atmospheric forcing and teleconnections is required to evaluate how the Bering Sea will react to changing climate.

Fluctuations in atmospheric forcing cause large (hundreds of kilometers) variations in the timing and location of the sea ice maximum extent, the persistence of ice on the shelf, its thickness distribution, polynya development, fast ice formation, and ice dynamics. Sea ice exhibits short-term variations associated with storm passage, annual variations, and longer-period fluctuations, ranging from interannual to decadal (teleconnection patterns) and trends forced by climate change (Niebauer, 1981; Niebauer and Day, 1989; Niebauer, 1998; Schumacher and Alexander, 1999). For instance, interannual variability of the Bering Sea ice edge and ocean temperatures, both at the surface and the bottom, correlate strongly

(as high as 34 psu) water through brine rejection, while melting at its leading edge introduces cold (-1.7°C) freshwater. Under some circumstances, melting sea ice releases remineralized nutrients to the water column (Arrigo, 2003), but this has not been documented in the Bering Sea. In the northern Bering Sea, the cold, highly saline water that sinks to the bottom is exported to the Arctic Ocean and strengthens the halocline there (Aagaard and Carmack, 1994; Cavalieri and Martin, 1994; McLaughlin et al., 1996). Thus, ice modifies the horizontal density structure, resulting in baroclinic currents that advect heat and salts over the shelf. Over the past 40 years, we have observed a trend towards a later onset of freezing, an earlier ice-melt, and a less persistent, thinner ice

Figure 16. 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).



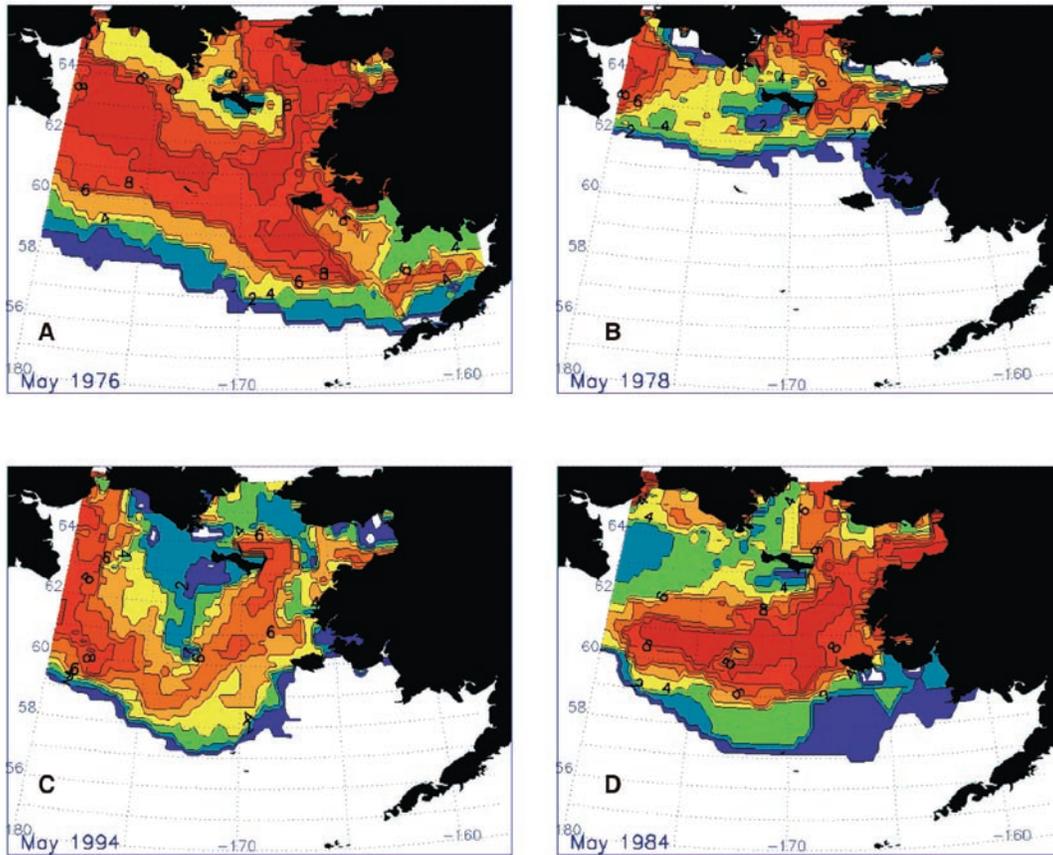


($r > 0.7$) with storm track climatologies and low pressure anomalies associated with the Aleutian Low, thus making sea ice extent an important index of environmental change (Overland and Pease, 1982; Niebauer and Day, 1989; Niebauer, 1998; Overland et al., 1999; Bond and Adams, 2002; Overland et al., 2002). To evaluate how the Bering Sea will react to changing climate conditions, however, we need a better understanding of how sea ice responds to longer-term variations in atmospheric forcing and teleconnections. This will require examination of available time series of satellite remote sensing.

Decadal-scale changes in sea ice cover provide a means of assessing how changes in climate may affect sea ice in the Bering Sea.

During the past thirty years, three different sea ice regimes have affected the Bering Sea shelf: 1972–76 (cold), 1977–88 (warm), and 1989–2001 (cool; Stabeno et al., 2001). During the cold period, ice extended south to St. Paul Island near the shelf break (Figure 17, dashed line) and persisted there for a month or more. The abrupt shift in the Bering Sea climate regime in 1977, from cold to warm (Overland et al., 1999) was followed by changes in the sea ice extent, air and ocean temperatures, sea level pressure, and surface winds. In the warm period, the ice did not extend as far seaward, and the residence time was 2–4 weeks less than that during the colder regimes (McNutt, 1983; Stabeno et al., 2001). There have also been marked differences in the ice distribution along the Alaska Peninsula during these three periods (Figure 16; Stabeno et al., 2001). These differences may be related to increased transport of warm water onto the shelf near the Alaska Peninsula, or to a shift to more southerly winds, which would both melt the ice and advect it northward. We need a better understanding of why the waters north of the Alaska Peninsula are now largely ice-free, and how this change affects shelf ecosystems.

Figure 17. Contours of the number of weeks that > 10% sea ice cover was present over the eastern Bering Sea for three time periods: 1972–76, 1976–89, and 1989–98. Note the decrease in ice distribution along the Alaska Peninsula in the later two periods. From Stabeno et al., 2001.



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Figure 18. Four distinct ice meltback patterns have been documented in the Bering Sea. The maps show averaged May conditions derived from National Ice Center (NIC) ice charts. Colors indicate relative ice concentration (noted in tenths), with dark red indicating heaviest ice concentrations and blue indicating more diffuse ice; white is open water; black is land. The heavier ice concentrations (>5/10ths) generally represent the regions of thicker sea ice, while the lighter concentrations show thinner, more diffuse ice (<5/10ths), where melt is most likely occurring, caused by winds and warmer water. The location of regions of heavier sea ice concentration is important to creation of the cold pool, especially on the western shelf. Patterns of ice meltback contribute to the regional distributions of the nutrients required for the annual phytoplankton bloom, critical to the entire ecosystem.

Panel A: Patterns of ice retreat during the cold period before the regime shift of 1976 showed heavy ice across the shelf. Since the regime shift of 1976 the extensive ice seen in panel A has not recurred. Since 1977, three meltback patterns have emerged (Panels B–D).

Panel B: During the warm period of 1977–88, extreme melt from the southeast left a patch of heavy ice in the western shelf.

Panel C: During the cool period of 1989–2001, melt from the east and north left heavy ice on both the eastern and western shelves.

Panel D: A second distinct pattern seen during the warm period was melt from the west, leaving the heaviest ice on the eastern shelf.

The patterns seen in panels C and D may indicate changes to the flow of warmer water across the shelf. A western melt pattern similar to that seen in panel D occurred in the years preceding the phytoplankton bloom of 1997 and may have been an indication of changing conditions on the shelf. Pacific Marine Environmental Lab figure.

During the past three decades, there have been distinct patterns of sea ice melt-back in the Bering Sea associated with the cold, warm, and cool periods, but the causes of these differences and their effects on the ecosystem remain to be investigated. The regime shift of 1976 marks the end of the last cold period (Figure 18.a). During the warm period of the 1980s, ice melted from east to west across the Bering Sea, contributing to a reduced ice cover in the eastern Bering Sea (Figure 18.b; Stabeno et al., 2001). In the 1990s, a cool period, ice melted early in the western Bering, creating large areas of open water within the sea ice in the west and leaving sea ice in the eastern Bering Sea (Figure 18.c). In a third pattern seen during some warm years, ice melted “in situ,” leaving streamers of ice scattered across the shelf (Figure 18.d). These melt-back patterns may result from atmospheric forcing or changes in the location of “warm” water on the shelf.

4.1.2 Sea Ice and Primary Production

In the southeastern Bering Sea, the type of phytoplankton bloom depends on the timing of ice retreat. The timing and magnitude of the spring phytoplankton bloom and the species involved correlate strongly with the extent and condition of the sea ice on the shelf during the winter and spring (Niebauer and Day, 1989; Niebauer et al., 1995; Alexander et al., 1996; Stabeno et al., 1998). Phytoplankton

blooms in the Bering Sea can occur in two different ways: they can be initiated either by ice melt (early bloom) or by insolation (late bloom; Figure 19; Eslinger and Iverson, 2001; Stabeno et al., 2001; Hunt et al., 2002a). Thus, climate-forcing acting on sea ice can affect biota (Schandelmeier and Alexander, 1981; Niebauer and Alexander, 1989; Niebauer et al., 1990; Niebauer et al., 1995; Francis et al., 1998). These food web fluctuations may be transmitted up the food web, since different zooplankton preferentially graze small or large phytoplankton cells.

The timing, species composition, and type of spring phytoplankton bloom appear to have changed in the southeastern Bering Sea. Observations in the 1970s showed the predominant bloom in the Bering Sea occurred along the ice edge in early spring as the sea ice retreated (Alexander and Niebauer, 1981; Niebauer, 1981). In the 1980s, the blooms in the southeastern Bering Sea were not tied spatially to the location of the ice edge, since the ice retreated early in the season. Peak primary productivity during this warm period took place mainly in May and June and consisted of different species assemblages than those found in the ice-edge blooms (Alexander et al., 1996; McRoy et al., 1986; Niebauer and Alexander, 1989). By the 1990s, the blooms again began appearing in March and April in association with the retreat of the ice edge. Yet, they were not as regular and intense as the ice-edge blooms of the 1970s (Stabeno

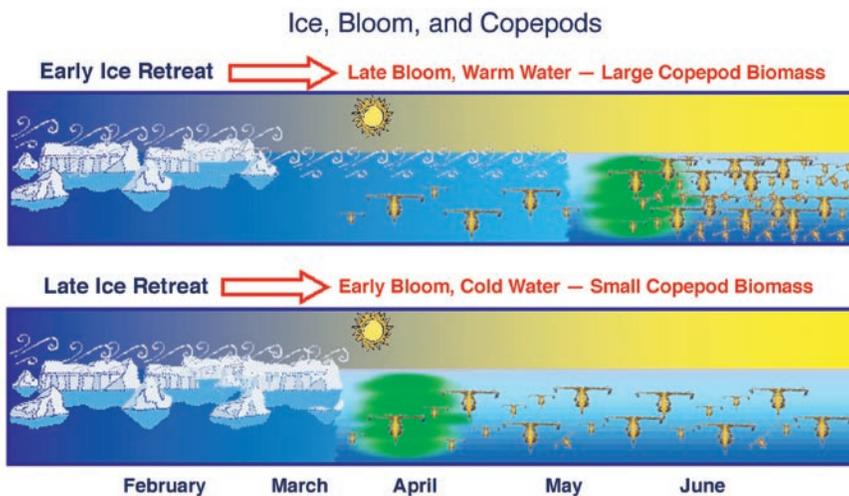


Figure 19. Early ice retreat leads to a late bloom in warm water and high copepod production (top), whereas late ice retreat leads to an early, ice-associated bloom in cold water and weak copepod production (bottom). After Hunt et al., 2002a.



Diatoms in sea ice.
Image courtesy NOAA Arctic Theme Page.

et al., 1998a, 2001; Napp and Hunt, 2001; Stockwell et al., 2001). The ecosystem effects of this variability in the timing and ice-association of the bloom have been hypothesized to include shifts in the fate of carbon between the pelagic and benthic components (Walsh and McRoy, 1986; Alexander et al., 1996), but this hypothesis has yet to be tested (see section 4.3.4).

The species composition of sea ice algal communities in the Bering Sea has received little attention since the early work of Schandelmeier and Alexander (1981). Likewise, little is known about how the species composition of ice-associated blooms affects the fate of this production. The extensive pack and fast ice that forms in arctic regions provides a unique habitat for microbial assemblages. Algal communities, in particular, are known to flourish within the distinct microhabitats created as sea ice forms and ages. Sea ice provides a platform from which algae can remain suspended in the upper ocean where light is sufficient for photosynthesis and growth. These autotrophic organisms are critical in polar marine ecology. For example, although rates of primary production by sea ice algae are generally low compared to their phytoplankton counterparts, they are often virtually the sole source of fixed carbon for higher trophic levels in ice-covered waters. Furthermore, sea ice algae have been shown to sustain a wide variety of organisms, including krill, through the winter months when other sources of food are lacking.

The growth of sea ice microalgae in pack and landfast ice is limited by available light and nutrients. In landfast ice, the growth of sea ice microalgae in the skeletal layer is determined primarily by salinity (Arrigo and Sullivan, 1992) and by the thickness of the overlying snow cover through its effect on light attenuation (Arrigo et al., 1991). In contrast, pack ice algae frequently grow at or near the sea ice surface where light levels are generally high. Under these conditions, pack ice microalgae have high photosynthetic capacities, comparable to those of phytoplankton from the same region (Lizotte and Sullivan, 1992).

The greatest fraction of sea ice microalgae typically grow in the bottom 20 cm of the ice sheet where environmental conditions are generally stable and more favorable for growth. Bottom ice communities form in the skeletal layer and extend upward as far as 0.2 m, their upward distribution generally being limited by nutrient availability and high brine salinity characteristic of the sea ice interior when temperatures are low (Arrigo and Sullivan, 1992). Less common sea ice assemblages include those that grow at the sea ice surface and in a “strand” layer just beneath the sea ice. Surface communities form in regions of the pack that become flooded with seawater, either as a result of rafting or snow loading. These are relatively common in the Arctic on rafted multi-year ice surfaces.

The highest algal biomass reported for arctic sea ice is approximately 300 mg Chl *a* m⁻² in the congelation ice of Resolute Passage, with a spring-summer average for all studies of 87.5 mg Chl *a* m⁻² (Arrigo, 2003). Three of the four highest Chl *a* accumulations in the Arctic were reported in landfast congelation ice. Pack ice, however, exhibits consistently higher rates of primary production than landfast ice in the Arctic, generally by a factor of four or more. Pack ice may thus represent the

more important sea ice habitat in terms of providing a food source for upper trophic level organisms. Evidence of production rates as much as four-fold higher than landfast ice with only half the accumulated algal biomass (and little expected difference in sinking losses) suggests that a much larger fraction of the primary production in pack ice is being consumed by higher trophic levels compared to landfast ice. The importance of these differences in food web structure is further magnified by the fact that pack ice is so much more prevalent than fast ice in the Arctic.

The few studies that have been conducted indicate annual primary production in sea ice in the Arctic Ocean ranges from 5–15 g C m⁻² yr⁻¹ (Arrigo, 2003). These values are consistent with biomass accumulation data from the region, which represent a minimum estimate of annual production. For example, assuming a carbon:Chl *a* ratio for sea ice diatoms of 40, then annual production estimated from maximum spring/summer Chl *a* abundance ranges from 0.2–12 g C m⁻² yr⁻¹ for the Arctic. Despite the small sample sizes, it is still probably fair to conclude that even in the most productive sea ice habitats, annual production in the Arctic is well below 50 g C m⁻² yr⁻¹, an amount similar in magnitude to the oligotrophic central gyres of the open oceans.

Recent estimates of basin-wide production in the Arctic are crude, but indicate that approximately 70 Tg C are fixed annually by ice algae (Arrigo, 2003). It is not known what fraction of this total originates in the Bering Sea. Until more *in*

situ data become available to describe the large-scale variability in sea ice algal production, numerical models should be developed and utilized, as has been done for Antarctic sea ice. This is particularly necessary for the Arctic where no models at any level (e.g., 1-D or 3-D) currently exist. These models can provide a framework for testing our understanding of how these ecosystems operate and can also be used as a predictive tool for estimating the production of ice algae in regions where data are currently lacking.

4.1.3 Sea Ice and Modification of Shelf Habitats

Regions of cold bottom water are a signature feature of sea ice during spring on the Bering Sea shelf, but the effects of changes in the size, duration, and distribution of these cold pools on circulation and ecology are open questions. The winter sea ice cover affects the ecosystems of the eastern Bering Sea continental shelf through polynya development and the formation of cold pools. Polynyas are persistent areas of open water in the sea ice, formed in the lee of islands and coasts. They are most often generated during northerly winds. The St. Lawrence Island Polynya (SLIP) is a commonly occurring feature on the shelf, covering hundreds of kilometers. Polynyas generate large volumes of new ice, rejecting cold, salty brine in the process. This dense saline water sets up periodic baroclinic currents that transport water, and possibly entrained organic matter, westward and northward and eventually through Bering Strait. Persistence of the SLIP aids in creation of cold pools on the northern and central shelf that are maintained throughout the summer (Grebmeier and Cooper, 1995), and are often marked by high nutrient distributions (Whitledge et al., 1988). A “footprint” of high carbon deposition and benthic productivity occurs under these

The St. Lawrence Island Polynya (SLIP) is a commonly occurring feature on the shelf, covering hundreds of kilometers. It supports threatened spectacled eiders, which winter there feeding on benthic mollusks. Photo by J. Lovvorn.



cold pools. High oxygen uptake (an indicator of carbon supply to the benthos) and benthic biomass (an interannual integrator of overlying water column processes) occur in these regions, indicating interannually persistent ecosystem features (Cooper et al., 2002).

A third cold pool occurs in the lower central shelf and in the middle shelf domain of the southeastern Bering Sea. Cold bottom waters here form when sea ice melts, and storms mix the cold (-1.7°C), fresh melt-water throughout the water column (Stabeno et al., 1998). The capping of this cold melt-water by a strong thermocline insulates the bottom water from solar 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., in preparation). This central and southern cold pool impacts distributions of species of fish such as pollock (Ohtani and Azumaya, 1995; Wyllie-Echeverria 1995; Wyllie-Echeverria and Wooster, 1998).

Changes in the patterns of persistent features such as the SLIP and cold pools may have significant effects on the ecosystems of the region. Water-column primary production and the final location of carbon deposition to the benthos are related to ice production and brine formation in the SLIP during late winter–early spring. Benthic productivity is directly linked to higher trophic levels, since the regional food web is dominated by marine mammal and eider predation on benthic bivalves and amphipods (Fay, 1982; Lowry et al., 1982; Lovvorn et al., 2003; Moore et al., 2003). Changes in benthic populations can thus cascade rapidly to higher trophic levels. We need to know how reduced ice production south of the SLIP might influence the renewal of nutrients for early-season production by ice algae

and phytoplankton, and how the baroclinic currents that would transport this material to the southwest might respond. We need to understand the relative importance of the regional sea surface warming observed south of St. Lawrence Island in the 1990s compared to the 1980s (Stabeno and Overland, 2001) versus the declining flow in Bering Strait (Roach et al., 1995) as factors influencing the apparent decline in productivity observed in this region (Grebmeier and Dunton, 2000). If there is a warming trend in the northern Bering Sea, the “cold pool” could be diminished. Since this low temperature region is believed to inhibit northward migration of demersal fish, any warming trend may allow these fishes to shift northward and increase competition for prey between bottom-feeding fish and benthic-feeding marine mammals and birds. It is critical that we have a better understanding of the effects of polynyas and cold pools on shelf circulation, transport through Bering Strait, and the decline in productivity observed in the northeastern shelf region.

4.1.4 Sea Ice as a Habitat

We do not know why spotted seals have changed their habitat use patterns, though this issue is vital to subsistence hunters who depend upon these seals for food. Sea ice not only affects the timing and intensity of events in the water column, it is also a substrate on and in which organisms spend part or all of their lives (Schandelmeier and Alexander, 1981; Lowry et al., 1998, 2000). For instance,



A female spotted seal objects to humans intruding too close to her pup. Photo courtesy NOAA Photo Library.

changes associated with the advance and retreat of sea ice affect spotted seal behavior (Lowry et al., 1998, 2000), as well as when and where migratory fish are available to avian and mammalian predators. In the late 1970s during periods of heavy sea ice cover extending to the shelf break, spotted seals were most numerous within 25 km of the ice edge (Braham et al., 1984). During light ice periods such as 1991–94, satellite-tagged spotted seals were distributed up to 300 km from the ice edge, although the sea ice still extended to the shelf break area (Lowry et al., 2000).

Annual fluctuations in the location of the sea ice front may affect the reproductive success of female spotted seals. Spotted seals require ice floes thick enough to serve as a stable platform on which to haul out and raise their pups. In warm years of lighter-than-average ice coverage, the ice edge region where seals haul out may be several hundreds of kilometers from the richest feeding grounds over the shelf edge. Seals are then required to travel farther to reach prime feeding areas or to spend more time and energy foraging locally to obtain the same amount of food. In this situation, seals may have difficulty maintaining adequate body condition, particularly through the energetic demands of lactation. Changes in the physical environment of the Bering Sea appear to have altered the behavior of spotted seals and may be having an adverse effect on the health of their population and on subsistence hunters who rely on the seals for food (J. Bengtson, personal communication). Although ice seals and walrus are key ecological components of Bering Sea ecosystems and important resources for subsistence culture throughout the coastal Arctic (Wolfe and Mischler, 1995), relatively little is known of the population structure, feeding ecology, or seasonal distribution of these mammals.

The presence or absence of sea ice also affects the distributions and migratory

patterns of birds and cetaceans, especially bowhead and beluga whales. Coastal residents have reported shifts in the availability of marine mammals that they attribute to recent changes in climate and its effects on sea ice characteristics (Huntington, 2000). Because of the importance of sea ice in the life history and ecology of ice seals and walrus, and in the migratory patterns of beluga and bowheads, these species may be particularly vulnerable to climatic change or other environmental impacts that will alter this habitat. Thus, these taxa may serve as indicator species, reflecting changes to the ecosystem as a whole.

4.2 Questions Related to the Role of Sea Ice

a. How do the various climatological variables, such as storm-tracks, prevailing winds, surface air temperature (SAT), SST, and ocean currents, interact to determine the spatial and temporal variability of sea ice?

Sea ice in the eastern Bering Sea has complex interactions with various physical forcing functions across many different spatial and temporal scales. Often it exhibits chaotic patterns on longer time scales, while responding quickly to changes in local forcing, such as storm track climatology. The sea ice also serves as an integrator of the interaction of atmospheric and oceanic forcing. For example, until recently ice retreated relatively slowly from the Bering Sea shelf, but the retreat of ice has accelerated (see section 4.1.1). Even if ice has remained later on the southern shelf, it is gone earlier from the Bering Sea as a whole. The actual cause of this more rapid ice retreat is not well understood. We need to develop a better understanding of the determinants of the spatial and temporal

distribution of sea ice and its characteristics in the Bering Sea.

b. What is the role of polynyas in productivity (all levels) and brine formation?

Recently, the location and extent of the St. Lawrence Island Polynya (SLIP) have changed, coinciding with changes in productivity. These shifts also may have influenced the amount and distribution of cold salty brine on the northern Bering Sea shelf. Because polynyas are important persistent features in ice-covered seas, it is critical that we have a better understanding of the effects of polynyas and their role in circulation on the shelf, transport through Bering Strait, and productivity in the northern Bering Sea. An observational program integrated with retrospective studies and modeling is required to understand the complex interaction of sea ice, polynyas, and productivity.

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c. What are the causes and ecological implications of patterns of ice retreat recorded in recent years?

Since 1976, ice retreat or melt-back has occurred in three different patterns in the Bering Sea: from east to west; from south to north along the east side of the Bering Shelf; and from south to north on the west side of the Bering Sea shelf. These different patterns may reflect changes in the oceanic currents and/or atmospheric forcing in different ice seasons and may alter the potential for ice edge production and support of other trophic levels at northern latitudes. A comprehensive study of the nature of sea ice retreat is needed to understand the potential ecosystem impacts of these different patterns of melt-back.

d. How does the role of sea ice differ from north to south over the shelf?

The rate of sea ice formation is greater in the northern regions of the Bering Sea than in the south. While melting occurs throughout the sea, it predominates in the south because of the southward advection of ice and constant melting at the southern edge. In the north, the progression of ice melt varies from west to east. Understanding the variability of the seasonal progression of sea ice freeze and melt and the coincident ecosystem responses is essential for forecasting how warming of the Bering Sea may affect key ecosystem processes.

e. How do variations in sea ice relate to changes in the location and timing of biological productivity?

Sea ice is critical in the onset of spring productivity in the Bering Sea. In recent years, spring has occurred earlier in the region, changing the timing of the phytoplankton bloom and possibly controlling the entire structure of the ecosystem, favoring benthic or pelagic organisms depending on the circumstances of the spring bloom. What would be the long-term effects of a permanent shift to one regime or the other, and will the effects of such changes be similar in the northern and southeastern Bering Sea continental shelves?

f. How does the variability in condition, extent, and structure of sea ice affect the distribution and condition of marine mammals and sea birds?

Because marine mammals and seabirds are important components of the eastern Bering Sea ecosystem, we need more information about how these animals change their location and behavior in response to changes in the sea ice. We need to understand how marine mammals and

seabirds respond to variability in sea ice, and to determine the ecological factors that constrain their habitat selection, seasonal movements, and abundance in the Bering Sea.

g. How does the variability in the extent, timing and structure of sea ice affect the success of subsistence activities?

Sea ice serves as habitat for many marine mammals used by subsistence communities in the Bering Sea, and it provides hunters with a stable platform for transportation to and from hunting grounds. In some cases, coastal hunters wait for the ice to bring mammals within hunting range. In other cases, retreat of the ice brings migrating species to the hunters. Native hunters agree that in recent years they have seen a significant change in the sea ice habitat of the species they normally harvest, generally making them less accessible. They also note that the mammals' health has declined as the ice environment has changed. It is important to understand and incorporate Traditional Environmental Knowledge into studies of the Bering Sea, and to use model results to help assess the impacts of a changing environment on subsistence practices.

h. How can we use traditional ecological knowledge to identify/verify/monitor critical events or changes in the key forcing functions and responses of the Bering Sea?

Communities that depend on the Bering Sea have a direct understanding of the effects of climate change. This knowledge can identify aspects of the Bering Sea important to scientific monitoring but previously overlooked. Traditional knowledge and the health of subsistence communities reflect the ocean ecosystem, offering important information on the abundance,

availability, and quality of food used by Alaska Natives. These potential indices provide windows on change that are important for understanding how ecosystem function is changing and are vital to those who make their livelihoods from the bounty of the Bering Sea.

4.3 How does Water Temperature Affect Ecosystem Structure and Function?

Interannual variability in water temperature may result from a variety of mechanisms, including the formation and melting of sea ice, advection of relatively warm slope waters onto the shelf, or anomalous surface summer heat flux (Overland et al., 2001). Because the rates of physiological processes are sensitive to temperature, as anomalies from the climatological mean change water temperatures, they also affect production, growth and trophic transfer of material through the ecosystem. These changes in rate processes, as well as behavioral responses to temperature by constituent species, can alter species composition and energy flow in both benthic and pelagic ecosystems.

4.3.1 Water Temperatures and Stratification of the Water Column

Changes in wind intensity and heat content of the water column will affect nutrient distribution, altering primary production. The magnitude and effects of such changes on the shelf ecosystem are unknown. 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., in preparation). This stratification inhibits vertical flux of nutri-

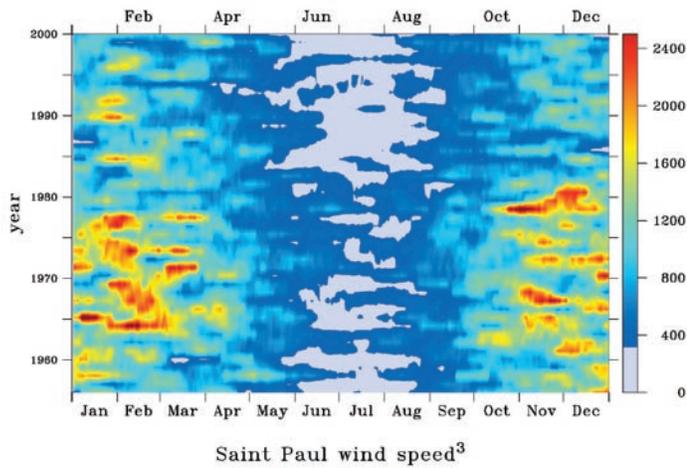


Figure 20. Wind speed cubed, at St. Paul Island, Pribilof Islands. Wind speed cubed is a measure of the ability of winds to mix the upper water column. The light gray color denotes summer winds below the long term mean for winds between June and August. Figure from Pacific Marine Environmental Laboratory.

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ents and limits new production. Nutrients can be replenished when stratification breaks down. 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 promote primary production. 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 (Figure 20). Ladd et al. (in preparation) 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. Weak stratification may result in an early commencement of fall mixing and fall production, thereby increasing the total annual production.

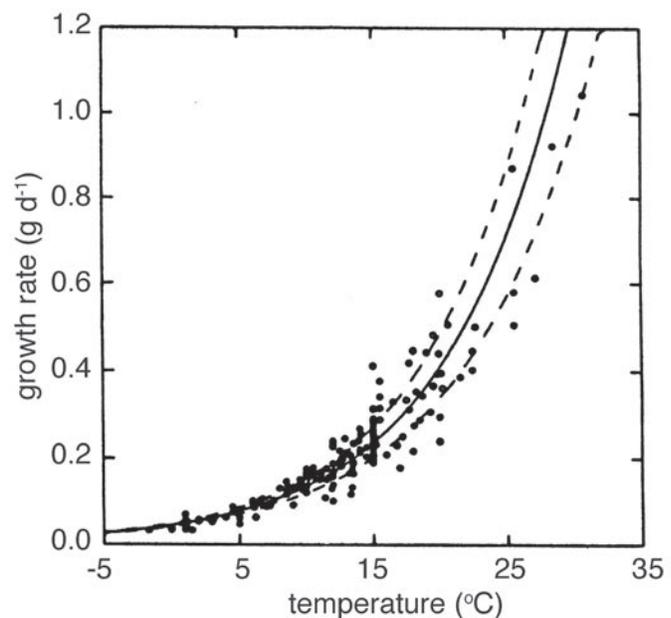
4.3.2 Water Temperature and the Physiological Responses of Organisms

Different species have different physiological responses to temperature change. The magnitude of these responses and their influence on energy flow through the ecosystem are unknown. The rates of physiological processes, such as ingestion, assimilation, growth, and reproduction, generally increase with increasing temperature up to some maximum temperature that varies according to species. At the same temperature, however, the metabolic rate of a cold-adapted species might be considerably higher than that of a warm-adapted species (Huey and Bennett, 1990).

Figure 21. Analysis of 181 published estimates of generation time for 33 species of copepods at environmental temperatures from -1.7 – 30.7°C shows that temperature alone explains more than 90% of variance in growth rate. From Huntley and Lopez, 1992.

Little is known about how species-specific responses to changes in water temperature interact to produce ecosystem-level effects.

Quantitative relationships among temperature, phytoplankton concentration, and zooplankton production are complex and not fully understood. Temperature-driven changes in zooplankton production will alter energy flow and impact higher trophic levels. Zooplankton production can be affected both by the abundance of prey (phytoplankton and microzooplankton), and by the ability of the zooplankton to assimilate food and convert it into biomass. In the southeastern Bering Sea, the available evidence suggests that phytoplankton production during the spring bloom does not limit mesozooplankton grazing rates. Walsh and McRoy (1986) hypothesized that the fate of production in the southeastern Bering Sea is influenced by water temperature, (see also Vidal, 1980; Vidal and Smith, 1986; Townsend et al., 1994a,b). Water temperature exerts a strong influence on the growth rates of zooplankton and may be more important than food availability in limiting the growth rates of small-bodied copepods (Figure 21; 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 hypothesized that zooplankton would capture more of the primary production than in cold years, assuming that phytoplankton growth is less sensitive to water temperature than is zooplankton growth. This assumption has yet to be tested for the phytoplankton and zooplankton of the eastern Bering Sea shelf.

4.3.3 Water Temperature and the Species Composition of Ecological Communities

Changes in water temperature can alter the species composition of primary producers, thus changing food webs. The magnitude and effects of such changes on overall energy flow to apex predators are not known. Because different species are adapted to different temperature optima, the composition of ecological communities may shift with a change in temperature. For example, the species composition of the phytoplankton assemblage will dramatically affect the efficiency of transfer of primary production through the Bering Sea food web. This situation is not unique for cold ecosystems such as the Bering Sea, but it may be exacerbated by the low species diversity of the phytoplankton blooms in high latitude ecosystems. In an example from the southern hemisphere, rapid growth of the haptophyte *Phaeocystis antarctica* in the southcentral Ross Sea polynya (Tagliabue and Arrigo, 2003), coupled with extreme low tempera-

ture (generally $\leq 0.5^{\circ}\text{C}$), resulted in very low direct trophic coupling between phytoplankton production and zooplankton grazing activity during spring and early summer (Caron et al., 2000). Much of the primary production in the Ross Sea sediments rapidly (DiTullio et al., 2000), or is utilized via detrital food webs rather than through direct ingestion of phytoplankton biomass. The coccolithophorid blooms of the 1990s in the Bering Sea (Sukhanova and Flint, 1998; Stockwell et al., 2001) may represent an analogous situation. In contrast, a diatom-dominated phytoplankton may be a more palatable food source for zooplankton. The low and variable species diversity of high-latitude phytoplankton blooms (Sullivan et al., 1993; Arrigo et al., 1999; Sherr et al., 2003), heightens the need to characterize phytoplankton community structure in order to understand the fate of primary production in the Bering Sea.

The Bering Sea shelf environment sustains a number of distinct zooplankton communities. Temperature changes are likely to affect different communities differently and in unknown ways. Zooplankton on the Bering Sea shelf consists of both oceanic and neritic species. On the southeastern Bering Sea shelf, the oceanic zooplankton taxa (calanoid copepods *Neocalanus* species, *Eucalanus bungii*, and *Metridia pacifica*, and the euphausiid *Thysanoessa inermis*) are confined primarily to the outer domain, from the shelf break to the 100 m isobath (Cooney and Coyle, 1982; Smith and Vidal, 1986; Vidal and Smith, 1986). Neritic species (calanoid copepods *Pseudocalanus* spp., *Calanus marshallae*, and *Acartia* spp., and the euphausiid *Thysanoessa raschii*) are dominant in the middle and inner domains. In contrast to the southeast Bering Sea, the zooplankton community in the shallow northern Bering Sea is composed of both oceanic and neritic species (Springer and Roseneau, 1985; Springer et al., 1989;



Species of the genus *Neocalanus* are the most abundant copepods in the North Pacific. Photo from NOAA Ocean Explorer page.

Variable	Year		
	1997	1998	1999
Onset of Bloom	Mid - April	Early May	Late March
Upper Mixed Layer Temperature during June (° C)	5.53	3.79	0.45*
<i>Acartia</i> spp.	961	711	64*
<i>Pseudocalanus</i> spp.	1168	893	240*
<i>Calanus marshallae</i>	34	72	3.7*
Calanoid nauplii	616	626	322*
<i>Oithona similis</i>	99	219*	28

Pinchuk, 1993). The oceanic zooplankton is advected onto the shelf and into the northern Bering Sea by the Anadyr Current (Springer et al., 1989; Stabeno et al., 1999a). Zooplankton in the Alaska Coastal Current consists primarily of neritic species.

Ecological models of carbon flow on the Bering Sea shelf do not adequately account for the potential effects of changes in temperature and plankton species composition on carbon flow through shelf ecosystems. Ecological models currently predict that roughly 40% of the annual carbon production in the outer domain of the southeastern Bering Sea is consumed by zooplankton in contrast to about 20% in the middle domain (Walsh and McRoy, 1986). The differences in energy flow in the outer and middle domains are attributed to differences in zooplankton species composition as outlined above. The model does not include a microzooplankton component, which may markedly influence energy flow in the pelagic food web (Olson and Strom, 2002). Microzooplankton are also a potential source of grazing mortality of the spring phytoplankton, as is the case in other high latitude oceans (e.g., Hansen et al., 1996; Strom et al., 2001; Levinsen and Nielsen, 2002). No measurements of microzooplankton biomass or grazing have been made on the Bering Sea Shelf in the spring. In addition, recent evidence suggests that ice cover during cold springs can substantially reduce the overall zooplankton abundance and energy flow

Table 1. 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. * = difference significant at $p < 0.05$. Data from Coyle and Pinchuk (2002b) and Hunt et al. (2002a).

through the pelagic ecosystem (Coyle and Pinchuk, 2002b; see also Coyle & Cooney, 1988). It remains to be demonstrated for both the microzooplankton and mesozooplankton whether or not low temperature, low grazer biomass, or a combination of the two is responsible for lower water column utilization of new production during the spring, including when ice is present.

While low temperatures in spring can markedly lower the abundance and production of copepod populations on the Bering Sea shelf, it is unclear how lower spring copepod production affects the annual carbon budget on the shelf. The abundance of mesozooplankton on the southeastern Bering Sea shelf is sensitive to integrated water temperatures and shows considerable species-specific interannual variability. Two studies show that the abundance of small shelf species of copepods in spring varies with sea temperature. In 1980, the upper layer of the middle and outer shelves of the southeastern Bering Sea warmed slowly compared with 1981 (Smith and Vidal, 1986). In May 1981, small copepods of the middle shelf were more abundant than in 1980, and *Calanus marshallae* was observed to go through two generations in 1981, rather than the expected one (Smith and Vidal, 1986). In the 1990s, a very cold year (1999) can be compared with two during which water temperatures were high (1997, 1998). In June 1999, the abundance of small copepods over the inner and middle shelf areas was reduced by up to 90% compared with the two warmer years (Table 1; 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 that chaetognaths were responsible for the declines in copepod abundance observed in 1999 (Coyle and Pinchuk 2002b). However, these data provide compelling evidence

that, even on a station-by-station basis, the numbers of copepods present were related to integrated water temperatures. As a result, secondary production of calanoids in spring 1999 was about 3–4% that which occurred in the warm years of 1997 and 1998. Interestingly, by August–September, no consistent significant differences were found in the biomass of small copepods between 1999 and the two warmer years (Coyle and Pinchuk, 2002b).

Temperature changes can alter the life cycles of poikilotherms, thus altering trophic relationships and energy flow through marine food webs. The magnitudes of such changes are not known.

Changes in temperature may affect the timing of zooplankton life cycles as well as the animals' abundance. The effect of temperature on euphausiids appears to be the inverse of its effect on copepods; in 1999 (a cold year), the acoustically measured biomass of adult euphausiids on the inner and middle shelf was significantly higher than in 1997–1998 (warm years; Coyle and Pinchuk, 2002a). Coyle and Pinchuk point out, however, that this difference may be related to a delay in euphausiid breeding in cold water, so that more adults remain in the water column through June, than in warm years when most adults may have spawned and died by June. Coyle and Pinchuk (2002a) noted significantly higher densities of euphausiid eggs and larvae in 1999 (a cold year) compared to the warm years of 1997 and 1998. If euphausiid spawn-

ing is completed in early spring, reducing availability of late spawning adults in summer, this could have a negative impact on predators, such as sockeye salmon (*Onchorhynchus nerka*) or short-tailed shearwaters, that depend on euphausiids for a significant portion of their diets (Nishiyama, 1974; Baduini et al., 2001, 2002; Hunt et al., 2002b).

Since the 1970s, gelatinous zooplankton, in particular large scyphomedusae, have gone through a remarkable increase in biomass in the Bering Sea and a subsequent decline (Figure 4; Brodeur et al., 1999, 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., 1999). The reason for the subsequent crash has yet to be determined.

Although trawl surveys have documented substantial changes in groundfish stocks in the Bering Sea, the effects of such shifts on the benthic invertebrate community are not known.

Retrospective analysis of National Marine Fisheries Service bottom trawl surveys indicate substantial increases in the density of several groundfish species since the late 1970s (Connors et al., 2002). Changes in the groundfish abundance and distribution on the shelf were attributed to changes in temperature related to the climate regime shift in the late 1970s. Increases in groundfish stocks may have impacted benthic community structure in the southeastern Bering Sea. Detailed studies of benthic community structure were conducted in the 1970s (Haflinger, 1978; Jewett and Feder, 1981; Stoker, 1981), with additional information available in a number of reports (Roland, 1973; Stoker, 1978; Feder et al., 1976; Feder & Jewett, 1977). These data help assess groundfish abundance during the 1980s and 1990s in conjunction with the regime shifts. Thus, a reassessment of the benthic infauna of the southeastern



The scyphozoan *Chrysaora melanaster* is the most common jellyfish species in the eastern Bering Sea. Photo by Kevin Raskoff, Monterey Bay Aquarium Research Institute.

Bering Sea shelf would be valuable in understanding the ecological effects of climate change in the Bering Sea.

4.3.4 Water Temperature and the Fate of Primary Production

Water temperature affects the abundance of zooplankton (see above) and the period over which primary production occurs, either compressing or extending the duration of the spring bloom, and tuning the match or mismatch between abundance of phytoplankton and grazers (micro- and mesozooplankton; Napp et al., 2000). When water temperatures during the spring bloom are low ($< 2^{\circ}\text{C}$), as during an ice-edge bloom, zooplankton reproduction and population growth will be retarded, and the spring phytoplankton bloom will be less vulnerable to zooplankton grazing (Napp et al., 2000, 2002; Coyle and Pinchuk, 2002a,b). Under these circumstances, most of the primary production is predicted to sink to the benthos (Alexander et al., 1996; Walsh and McRoy, 1986). Walsh and McRoy (1986) thus interpret a sub-surface chlorophyll maximum in the middle domain as evidence of transfer of phytoplankton to the benthos and a lack of tight coupling between primary production and copepod grazing. In contrast, high zooplankton production is associated with late blooms in warm water, and most of the energy in the food web appears to remain in the water column (Walsh and McRoy, 1986; Niebauer et al., 1990; Hunt et al., 2002a; Hunt and Stabenro, 2002). This scenario resembles conditions in the Barents Sea, where zooplankton are able to graze more of the primary production in years when water temperatures are relatively high (Loeng, 1989). Thus, two different mechanisms responsible for bloom initiation (ice melt vs. solar radiation) are hypothesized to set up two distinct energy pathways for the ecosystem: benthic versus pelagic (Walsh and

McRoy, 1986; Hunt et al., 2002a). Although there appears to be little direct evidence to confirm the hypothesized switch between a benthic and pelagic fate for production in the Bering Sea, it is well documented from the Ross Sea polynya, Antarctica (Smith and Dunbar, 1998; Ditullio et al., 2000).

In the northern Bering Sea, ice remains sufficiently late in the year that most spring blooms are likely associated with the melting ice edge. However, it is unclear whether there is a relationship between the timing of ice retreat and the type of bloom that occurs in the central region of the eastern shelf. We do not understand the potential influences of these two bloom types in relation to the length of growing seasons available at different latitudes and sea temperatures in the Bering Sea. In an ice-free Bering Sea, would the northern blooms occur late in the season, and would there then be a sufficiently long and warm growing season for populations of shelf zooplankton to grow and graze the bloom? Further work is necessary to understand the under-ice and in-ice community structure, and the cascading effects of long-lasting changes, such as a warming spring, on the ecosystem as a whole.

It is hypothesized that a shift from a coldwater, ice-associated bloom to a warm-water bloom will promote development of the plankton at the expense of the benthos in the northern and central Bering Sea, but research on this important topic is lacking. In the northern Bering Sea, where the spring bloom is usually ice-associated and integrated water temperatures remain low through most of the summer, one would expect minimal mesozooplankton grazing due to cold water temperatures. Studies in the northern Bering Sea, utilizing sediment metabolism experiments as well as sediment tracer studies (e.g., chlorophyll and radioisotope content), indicate enhanced

carbon flux of material during and after the spring bloom (Grebmeier and Cooper, 1995; Cooper et al., 2002). This enriched environment supports high populations of benthic macro-fauna (e.g., bivalves, amphipods), the prey of diving seabirds and marine mammals. For example, north of St. Lawrence Island, the benthic community in the Chirikov Basin is one of the most productive ever recorded (Highsmith and Coyle, 1990). The amphipod biomass there, however, is apparently declining (Highsmith and Coyle, 1992). It remains to be determined whether this decline is the result of a reduced supply of nutrients and resultant reduction of primary production (Schell, 2000) or because of increased zooplankton grazing. The hypothesis that a trade-off between fluxes to the pelagic and benthic communities in the southeastern central and northeastern Bering Sea depends on water temperature needs to be tested.

A similar decline in bivalve populations south of St. Lawrence Island (the prey source for the diving spectacled eider), is indicative that a decline in hydrographic forcing and nutrient supply may be limiting primary production in the region (Grebmeier and Dunton, 2000; Grebmeier and Cooper, 2002, in press; Lovvorn et al., 2003). The apparent reduction of carbon supply to the benthos in the region over the past 15 years may have had a direct impact on benthic biomass and ultimately may be responsible for the observed decline in higher trophic consumers (Grebmeier and Dunton, 2000; Lovvorn et al., 2003).

4.3.5 Temperature Effects on Geographic Distributions

Changes in temperature are likely to alter the distribution of major fish predators on the Bering Sea shelf. The effects of such changes are poorly understood, and they could severely impact mammal

populations on the northern Bering Sea shelf. The Chirikov Basin, for example, is a major feeding ground for the California gray whale, the only cetacean known to feed primarily on benthic infaunal invertebrates (Rice and Wolman, 1971). The dominant food species are tube-dwelling amphipods of the family Ampeliscidae (Blokhin and Vladimirov, 1981; Nerini, 1984), which account for about 70% of the amphipod biomass and production in the ampeliscid beds of the northern Bering Sea (Highsmith and Coyle, 1992). The benthic community in the Chirikov Basin has been able to sustain intense whale predation because of its high productivity (Highsmith and Coyle, 1990), which is fueled by high primary production generated in the nutrient-rich Anadyr water mass (Coyle and Highsmith, 1994). In addition to its high productivity, the benthic amphipod community is apparently able to sustain high whale predation because many groundfish predators, which also consume benthic amphipods, are excluded from the northern Bering Sea by the low temperatures of bottom water there. The disappearance of cold bottom water from the northern Bering Sea could permit southern groundfish to extend their range northward, altering energy pathways and threatening marine mammal food resources. In recent surveys during warm years, both juvenile and adult pollock were caught in the northern Bering and Chukchi Seas (Wyllie-Echeverria, 1995), as predicted by Strickland and Sibley (1984). The growing gray whale population is showing signs of food stress (Moore et al., 2001, 2003; Perryman et al., 2002), and additional predator pressure on the Chirikov amphipod beds will exacerbate the problem. Thus, even if climate change does not lower the overall production in the Chirikov Basin, warming of the region could severely impact whale populations by permitting a greater percentage of the overall benthic production to flow

through a fish-dominated food web.

South of St. Lawrence Island, the Central Shelf Region is a transition zone between the southeastern shelf, where epibenthic and demersal fish dominate, and the northeastern shelf system, where fish are a minor component of the system and benthic-pelagic coupling dominates the ecosystem. This region has a large and persistent cold pool, which is the result of ice melt. This central portion of the shelf is likely very sensitive to environmental change and warrants a careful examination.

Although fish distributions are affected by changes in the extent of the cold pool, the larger implications for the shelf ecosystems are not well understood.

Unfavorable water temperatures can limit the distributions of fish and other marine organisms. For example, survival of pollock eggs and larvae is negatively affected by low water temperatures (Blood, 2002). Juvenile walleye pollock prefer to avoid waters $< 2^{\circ}\text{C}$ (Wyllie-Echeverria, 1996), and there is a positive relationship between pollock recruitment and ocean temperature (Quinn and Niebauer, 1995). When the size of the southern cold pool is reduced, 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 more vulnerable to cannibalism by adult pollock living in these waters (Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1995, 1996; Wyllie-Echeverria and Wooster, 1998; Wyllie-Echeverria and Ohtani, 1999). Understanding both the potential impact of climate-related shifts in the distribution of fish and the effects of these changes on the structure of the shelf ecosystems will require additional research.

4.4 Questions Related to the Ecological Role of Water Temperature

a. How does temperature affect the magnitude, and timing of primary production and its trophic coupling to grazers?

Ice-associated blooms tend to be short and intense and to occur in cold water, whereas later spring blooms in open, warm water may last longer. We need to know if these two types of bloom are similar in magnitude, and how the different physical settings in which they occur affect the fate of production and the tightness of its coupling to grazers. How does water temperature affect the coupling to different classes of grazers, including mesozooplankton and microzooplankton? Does the effect of low temperature on phytoplankton growth rates surpass the effects on metabolism and grazing activity of microzooplankton or mesozooplankton grazers? How do the species composition of phytoplankton and grazers in affecting the fate of production? How does interannual variability in relative over-wintering abundance of phytoplankton and grazers affect the fate of production?

b. Is the flux of phytoplankton production to the benthos in the southeastern Bering Sea greater in cold years (at -1°C) when the spring bloom occurs early than in warm years (at $>2^{\circ}\text{C}$) when the bloom occurs later?

This is the basic prediction of the hypothesis of Walsh and McRoy (1986), which remains to be tested in the Bering Sea. We do not know the implications for ecosystem structure if there is a long run of warm or cold years. Despite a long period of predominantly warm springs, benthic

biomass has been increasing. Does this indicate that the biggest interannual differences involve the flux to the pelagic food web, rather than an “alternation” of fates? Do the spring blooms in the northern Bering Sea always occur in association with the ice edge, and what would be the fate of an open water bloom there? Earlier warming in the north causes ice melt and expands polynyas, thus likely enhancing primary production, not suppressing it.

c. How does community structure affect trophic efficiencies in the ecosystem?

Trophic efficiencies can be quite high in the northern Bering Sea (up to 50%; Grebmeier et al., 1989), thus the historically tight levels of pelagic-benthic coupling have supported high benthic standing stocks. If the seawater begins to warm regularly, the species composition of phytoplankton will likely change, thus shifting carbon recycling efficiencies. Smaller microplankton contain less energy for grazers than large species, and a change to smaller phytoplankton species could change the zooplankton community structure and thus the prey base for planktivorous seabirds and some whales.

d. As a potential means of understanding effects of climate on benthic-pelagic coupling, compare the responses of the southeastern and northeastern Bering Sea shelf ecosystems to climate variability.

The southeastern Bering Sea and northern Bering Sea shelves provide a natural comparison of potential climate change impacts on two productive ecosystems. The northern Bering Sea has a tightly coupled pelagic and benthic system under the influence of the nutrient-rich Anadyr water. In comparison, the southeastern Bering Sea shelf during ice-free, warm

springs has a delayed spring bloom and mesozooplankton species thrive. How do these differences affect the structure and productivity of the benthic communities in the two regions?

e. How will changes in the distribution and temperature of cold bottom water on the shelf impact benthic and epibenthic communities on the eastern Bering Sea shelf?

Warming in the Bering Sea is likely to result in a decline in the duration and geographical extent of cold bottom water generated by ice cover during winter. As bottom temperatures warm, the ranges of fish and invertebrate predators, previously limited by low temperatures, are likely to expand northward, consuming or displacing indigenous species. How do the benthic communities where cold bottom water is present or absent differ? How rapidly do communities change once the cold bottom water disappears? What are the differences in predator populations where cold bottom water is present and where it is absent? What are the differences in zooplankton abundance, biomass, and species composition where cold bottom water is present compared to those where it is absent? How do these differences impact carbon flow to the benthos and plankton?

f. How does variability in community structure in specific oceanographic domains on the northern and southern shelves affect the coupling of primary production and mesozooplankton grazers?

The mesozooplankton communities of the southeastern Bering Sea vary spatially, with oceanic species predominating in the outer domain and neritic species in the

middle and inner domains. With remarkably different life histories, these species may be differently affected by water temperatures in spring. The zooplankton community of the northern Bering Sea is dominated by zooplankton advected from the oceanic domain. How does the origin of northern zooplankton influence the strength and timing of their grazing of the spring bloom? Do spring water temperatures in the north influence coupling of these grazers to primary production?

How will climate change affect the ecosystems of the Bering Sea? Recent advances in observational and mathematical modeling capability make ecosystem prediction a realistic goal.

5.1 Introduction

BEST will benefit society by contributing to the ability to predict how climate change will affect the ecosystems of the eastern Bering Sea. For example, if climate change alters the relationship between spawner biomass and recruitment for commercially harvested populations, or the interannual survival rates of post-recruitment individuals, knowledge of the new relationships will be essential for managing a sustainable harvest of marine resources. Predicting ecosystem response given a particular future climate scenario will not be easy, but neither was the development of long-range weather forecasting. Recent advances in observational and mathematical modeling capability make ecosystem prediction a realistic goal (see section 5.3).

One of the largest challenges hampering our ability to develop predictive tools useful for forecasting is the current lack of knowledge about basic ecological interactions such as predation and competition (see section 5.2). Some of the organism-level linkages in the Bering Sea food web will be more susceptible to climate change than others. Without detailed knowledge at the level of food web and competitive interactions, it will be difficult to predict how changes in the physical environment might cascade through entire Bering Sea ecosystems.

Another difficult challenge in developing a predictive capability is accomplishing cross-disciplinary integration and synthesis (see section 5.3). Scientific disciplines relevant to the BEST program cover a variety of temporal and spatial scales, from that of regional climate change at decadal scales or longer, to physiological processes or activities of microorganisms that occur in milliseconds over minute distances. The challenge is to scale down from climate events to the impact of physical aspects of the environment on the survival and reproduction of single organisms, and to scale up from organism-level processes to the responses of populations and ecosystems.

A key objective of BEST must be to develop an end-to-end strategy for the integration of Bering Sea research. The end product must incorporate data from field programs and model simulations, include traditional environmental knowledge, provide for analysis of these data to higher-level products, and then disseminate the results to the user community as both scientific and resource management information. To accomplish this, we must understand existing biological and physical models, identify critical space and time scales, identify missing data of importance, and provide data assimilation and analysis strategies. It is also essential that

we understand how changes in the Bering Sea will impact adjacent ecosystems (see section 5.4), as well as understand how changes in adjacent ecosystems may affect the Bering Sea. Examination of similar polar marine systems may provide insight into how the Bering Sea ecosystem functions (see section 5.5).

5.2 Organism–organism Interactions

Section 4 dealt with interactions between organisms and the physical environment. Understanding these processes is necessary, but not sufficient, for forecasting ecosystem-level responses to climate change. To do this, we must understand how changes in one trophic level can initiate a trophic cascade that impacts many different levels. For instance, sustained high levels of fishing and whaling in the Bering Sea in the mid-20th century may have influenced production at lower levels through a trophic cascade effect. This may have led to increases in the abundance of pollock and other predatory fishes and decreases in forage fishes, shrimps, and crabs (National Research Council, 1996). This cascade of effects may have been exacerbated by climate-driven regime changes in the late 1970s. Thus, a regime-specific view of predation may be necessary to assess the ultimate role of predators in marine ecosystems. Adjacent trophic levels may interact in a number of ways, but predation provides the most basic level of interaction. Two major current ecological theories characterize trophic interactions via predator-prey relationships. These are the concepts of “bottom-up and top-down control” and “match-mismatch” (Cushing, 1995).

5.2.1 Bottom-up and Top-down Control

Bottom-up control characterizes an ecosystem in which a population’s size is limited by the availability of prey; this may occur when a population is stable or in decline because of insufficient food for maximum growth or reproduction. Top-down control occurs when a population is limited by predation. Although a large portion of variability in fish year-class strength is attributed to environmental factors influencing early life history survival, predators can reduce prey abundance at juvenile and later stages. For example, cannibalism by walleye pollock in the eastern Bering Sea explains at least part of the density-dependent recruitment patterns seen at large adult pollock spawning stock sizes (Springer, 1992; Livingston and Methot, 1998; Aydin et al., 2002). Multi-species modeling of predation on walleye pollock indicates that mortality due to predation on juvenile pollock varies across time and depends on the population levels of their predators (Livingston and Jurado-Molina, 2000). Hunt et al. (2002a) hypothesized that, in the Bering Sea, top-down control of pollock recruitment may occur periodically when the number of adults is sufficiently large that cannibalism of juveniles limits recruitment.

There is a strong possibility that the degree of top-down versus bottom-up control in marine ecosystems is situational; in times of increasing food supply (warm conditions), top-down control may dominate, but in times of decreasing food supply (cold conditions) bottom-up control may dominate (Figure 22; Hunt et al., 2002a). Seen on the time scale of regimes, the presence of predators may control the peaks and troughs of this alternating cycle even if, at any given moment, control may be primarily top-down or bottom-up. Predators are often long-lived species, so that in the context of climate change/eco-

Oscillating Control Hypothesis

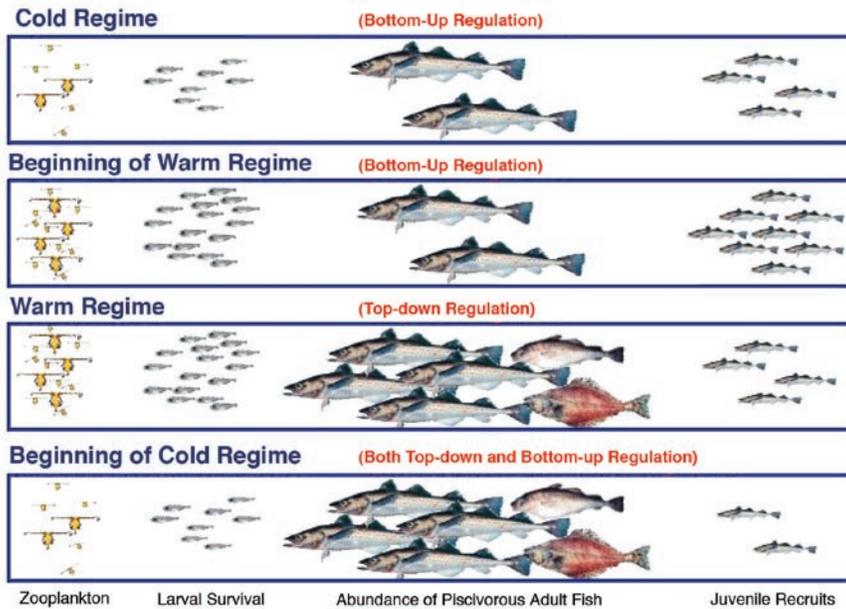


Figure 22. When the water is cold, fish recruitment is limited by the availability of forage for larval or juvenile stages. At the beginning of a warm period, forage for larval and juvenile fish is abundant, cannibalistic adults are few, and so recruitment is strong. During a warm period, abundant predatory adults reduce recruitment despite plentiful forage for young fish. At the start of a cold period, recruitment is negatively affected by both a lack of forage and by predation. Figure from Hunt et al., 2002a.

system response, they introduce an internal time lag or memory in the system with a corresponding filtering effect for several years.

There are conflicting opinions about the importance of top-down control in food webs. Polis and Strong (1996) conclude that trophic cascades and community regulation are relatively uncommon in nature, but that top-down effects are more likely when consumers in a particular food chain are subsidized from energy outside that food chain. This subsidy allows consumer population and biomass to increase and potentially depress the resources available to them inside the central food chain. This subsidy effect might be an important consideration in marine food webs with migratory species and on-shelf transport of alternative prey species. Density-dependence in the functional response of predators may be a stabilizing force in food webs (Murdoch and Oaten, 1975), and competition between predators may play the same role. A relatively constant amount of piscivory, but alternation in the dominant predators in the system has been noted in the northeast Atlantic (Link and Garrison, 2002). Changes in the piscivore populations of the eastern Bering Sea may be occurring, but without synoptic diet data and understanding of

predator functional responses, it is difficult to assess the degree of predator control in the system.

5.2.2 Match–Mismatch

Match–mismatch is a statement of hierarchy theory that maximum energy exchange will occur when there is a match of temporal and spatial scales. For example, transfer of energy from the atmosphere to the ocean is sub-optimal because while both cover large spatial scales, the temporal scale for the maximum energy content of the atmosphere is much shorter than that for the ocean (Cushing, 1995). In biological oceanography, a mismatch typically occurs when one process that depends on another is separated from that process in time such that some essential transfer of energy fails to take place. A significant example for the Bering Sea is between the spring bloom of phytoplankton and zooplankton. If sea ice remains into April it will cause an early phytoplankton bloom and a mismatch with the developing zooplankton. There is a better match in years when the bloom occurs in May, after solar heating has stabilized the water column (Hunt et al., 2002a). This mismatch between phytoplankton and zooplankton has consequences up the trophic ladder: in

very cold years, first feeding pollock may not have sufficient zooplankton prey for growth and survival (Napp et al., 2000). Similarly, shifts in the distribution and abundance of zooplankton can create severe shortages for planktivorous seabirds, thereby affecting their reproductive success (Bertram et al., 2001).

5.2.3 Organisms as Indices

It will be imperative to identify species that may serve as indicators of ecosystem change. In the long term, it will be impossible to monitor all aspects of the physical and biological environment of the eastern Bering Sea. Patterns of flow may provide point sources of information on variability in the system. Likewise, species that are characteristic of particular water masses or temperature regimes can be monitored to detect change. Parameters such as the condition and location of mammals that use sea ice and changes in migratory routes of marine birds and mammals may also indicate changes to the ecosystem. Where aspects of reproductive ecology can be monitored, marine birds provide an inexpensive and immediate index of the availability of their prey (Cairns, 1987, 1992; Hamer et al., 1993; Montevecchi, 1993; Ainley et al., 1995, 1996; Hunt et al., 1996a,b; Sydeman et al., 2001; Gill et al., 2002). The strength of these relationships is the basis of their use as monitors of krill populations in the Southern Ocean (Croxall et al., 1988). These same responses have also proved indicative of the effects of climate change on marine systems (Montevecchi and Myers, 1997; Gjerdrum et al., 2003). In other cases, the survival of marine birds has been tied to decadal-scale climate variability (Veit et al., 1996, 1997; Thompson and Ollason, 2001; Jones et al., 2002). For example, in the western Aleutians, there is

now evidence that annual adult survival of least auklets (*Aethia pusilla*) varies with large scale climatic conditions in the North Pacific (Figure 23; Jones et al., 2002). During the course of an extended field program, use should be made of the opportunity to identify and calibrate the responses of sentinel species or processes. The provision of indices and variables that managers could use to develop ecosystem-based management of fishery resources would greatly advance stewardship of the Bering Sea.

Physiological approaches may also provide valuable indicators of stress within an ecosystem. Kitaysky and colleagues (1999a,b, 2000, 2001a,b) demonstrated that a limited food supply can result in elevated levels of stress hormones (e.g., corticosterone) in breeding seabirds. Elevated levels of corticosterone indicate catabolic metabolism, signaling reliance by seabirds on endogenous energy reserves. Marine mammals and fish may show similarly elevated levels of corticosterone when stressed, and thus measurement of this hormone in upper trophic level species can provide an index of the stress that organisms are experiencing. It will be valuable to examine this and other potential quantitative indices as indicators of ecosystem stress.

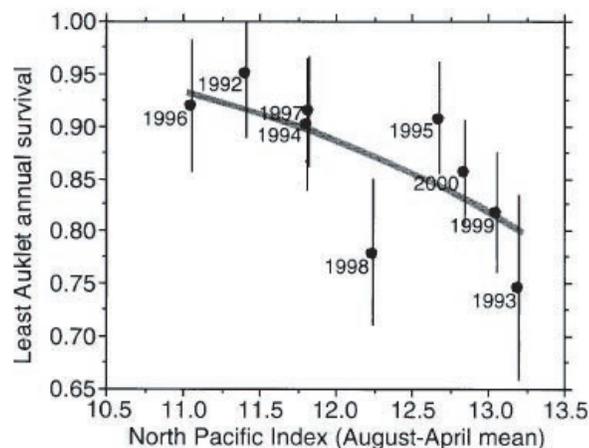


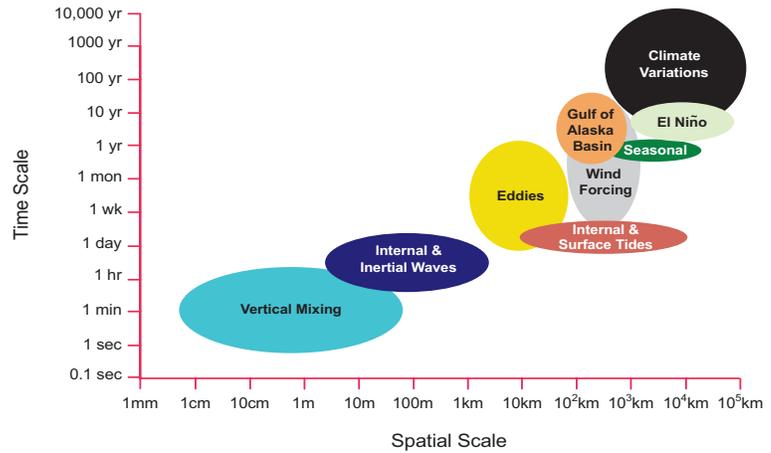
Figure 23. Trends in annual adult survival of Least Auklets (*Aethia pusilla*) at Buldir Island, Alaska 1990–2000 and North Pacific oceanography as indicated by mean annual North Pacific Index (NPI) for the period August–April. Line based on point estimates from model in which survival covaries with NPI. From Jones et al., 2002.

Figure 24. Physical oceanographic time and space scales. Adapted from D. Chelton, Oregon State University.

5.3 Integration across Spatial and Temporal Scales

Understanding the ecological consequences of different life-history patterns of organisms contributes to integration across time and space scales. Concepts of scale

are particularly important for developing model frameworks. They define the context for local, regional and large-scale interactions, integration of single species processes into multiple species models, and up-scaling and down-scaling of climate effects. The space and time scales associated with physical (Figure 24) and biological (Figure 25) oceanographic processes in the northern North Pacific Ocean encompass many orders of magnitude. Small organisms, such as viruses, bacteria, and some phytoplankton, can cycle through multiple generations in the time that it takes for a storm to pass through the region; in contrast, cetaceans and some seabirds do not breed until they are ten years of age or older and live for several decades. For these long-lived species, a storm occupies but a tiny fraction of the length of a generation. Population-level responses of organisms to climate change will differ depending on the time-scale of the climate events and inherent life-history characteristics.



5.3.1 Modeling

Models provide a framework for testing scenarios that are not immediately amenable to experimental testing or observation. State-of-the-art models that allow integration and synthesis of observations are now an integral part of most oceanographic observational programs. A number of approaches can be used to bridge the vast temporal and spatial domains that characterize the Bering Sea ecosystem. Numerical modeling provides one approach for integrating across space and time scales and examining system stability (see section 5.3.2). By simplifying the constituents of a system and allowing “manipulation” of key elements in the system, models provide a framework for examining the “what if” of future ecosystem variation. Models can also highlight the parameters and processes to which a system is most sensitive, pointing to elements that must be the focus of experimental or observational studies. They also provide a means of interpolating among scattered and scarce data, and across disparate

time and space scales. The efficacy of the models can be tested through a variety of approaches. BEST will strive to provide the measurements and data types that will be needed to calibrate and verify the modeling system developed for the Bering Sea.

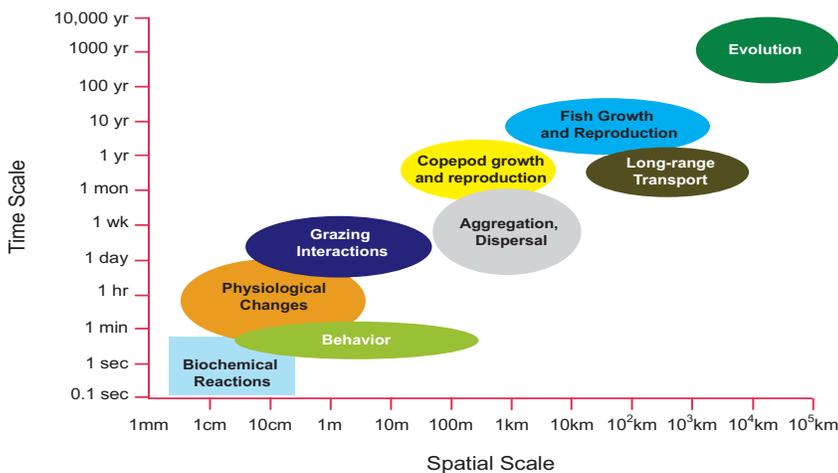


Figure 25. Biological oceanographic time and space scales. From S. Strom, Western Washington University.

One of the ultimate goals of BEST will be to implement a coupled climate-ecosystem model that can be used to understand, predict, and forecast. Such a model would include components for simulating ocean circulation, sea ice conditions, water optical properties, and water mass properties. This in turn would be coupled to models that provide predictive simulations of the lower trophic levels, including primary and secondary productivity, and the linkages of these to the upper trophic levels. Large-scale ocean general circulation models (OGCMs) provide an approach for specifying boundary conditions for regional and local ecosystem models that are configured at finer resolutions. This coupling will allow inclusion of local processes as well as feedbacks with the larger-scale Bering Sea response to climate change. Properly nested models within OGCMs allow downscaling to local ecosystem models, which in turn upscale local information to the larger-scale OGCM. Coupled physical (e.g., sea ice-ocean) models exist and can be further improved to include the physical forcing functions in the Bering Sea, such as sea ice, tides, shelf-basin exchanges, Aleutian and Bering Strait through flows, and freshwater runoff. Likewise, ecosystem models exist that are suitable for application to the Bering Sea; if provided with realistic and high resolution initial conditions and physical forcing, these should yield realistic simulations of food web dynamics and its variability.

A subset of the model will differentiate the effects of fishing from natural variability, thus allowing investigation of how anthropogenic effects might interact with natural variability. Fishing has the potential to influence ecosystems in many ways, one of which is by removing energy. Energy removals, in the form of total catch biomass, from fishing of groundfish, herring, halibut, and shellfish in the eastern Bering Sea have totaled 1.5

to 2 million metric tons annually over the past 20 years. When these amounts are compared with total system biomass, they are less than 1% of the total system energy as determined by a mass-balance model (Queirolo et al., 1995). Although the energy losses due to fishing are small relative to the total, removals of energy concentrated at particular locations or trophic levels may disrupt energy flow patterns in marine food webs. The potential for these energy removals to produce changes in system biomass, respiration, production, or energy cycling that are outside the range of natural variability should be examined further using present-day ecosystem models of the Bering Sea.

It will be important to develop a scientific consensus on model implementation and validation. Basic elements in developing a predictive modeling capability include identifying data gaps and meeting information requirements. Other issues critical to the success of an integrated, predictive modeling effort remain. Agreement on a modeling and validation program will be imperative for evaluating the ability to answer many of the research questions raised in this study. Fortunately, BEST can build on experience from other programs, such as the Global Ocean Ecosystem Dynamics project (GLOBEC), the work sponsored by the North Pacific Research Board (NPRB), and the Gulf Environmental Monitoring Program (GEM). We will also take advantage of the currently available ocean-circulation and sea-ice-community models and will modify these for application to the eastern Bering Sea. These models already contain the capability for data assimilation and for coupling to biological models. Thus, the modeling efforts in BEST will benefit from a large and well-developed ocean modeling community.

5.3.2 System Stability and Non-linear Changes

Unlike subtropical ecosystems, with relatively stable environmental conditions and a wide diversity of species, the Bering Sea is dominated by a few species at each trophic level. The pelagic system is currently dominated by pollock, which is considered the center or nodal species. At present, juvenile pollock are a major source of prey for a number of upper trophic level predators, thus forming a “wasp-waist” food chain. Simple mathematical models demonstrate that this food web structure is generally unstable and can produce large natural swings in biomass. The benthic food web for the Bering Sea shelf, in contrast, has four main prey species in roughly equal biomass, which is, presumably, a more stable structure.

With regard to ecosystem stability, the subarctic Bering Sea responds to high energy atmospheric and oceanographic forcing with seasonal, interannual, and interdecadal variability. Stability for some combinations of duration and position of forcing can be explained reasonably well by conventional ecological theory. For other combinations, particularly forcing at time scales of predator generations on top-down ecosystems, the major dynamics are non-equilibrium, transient conditions, with ecosystems far from their potential carrying capacities (Rice, 2001). Non-equilibrium states cannot be eliminated as a possibility for the Bering Sea.

Most potential change for the Bering Sea is expected to manifest itself through changes in atmospheric circulation rather

than direct thermal forcing (J. Overland, personal communication). This leaves the Bering Sea open for “climate surprises.” Increased atmospheric variability or a shift in the mean state may allow extreme events that are out of the range of past experience. Given the probable non-equilibrium of the Bering Sea ecosystem, these changes could be damped as they propagate through the system, or they could interact with internal ecosystem dynamics to shift the basic structure of the food web in ways that are not easily recoverable. Understanding these effects will require a powerful and viable modeling effort.

5.4 How Changes in the Bering Sea Affect Adjacent Ecosystems

Efforts at integration across spatial scales must include the relationship between the Bering Sea and its adjacent ecosystems. The Bering Sea influences adjacent systems by altering the properties of North Pacific Water before it passes into the Arctic Ocean and through the export of organic material. Organic exports include fish to the freshwater lakes and rivers of western Alaska, the removal of fish by commercial fisheries, and the export of organic material by marine birds and mammals that forage in the Bering Sea during the summer months and then emigrate, in some cases with energy stores needed for the remainder of the year.

Predicting how climate change will influence exports of heat, salt, and organic material is important. Exports of salt, freshwater, and heat influence the hydrographic structure of the Arctic Ocean and its exchanges with the North Atlantic (Aagaard and Carmack, 1994; McLaughlin et al., 1996). Exports of fish, particularly salmon, to the freshwater ecosystems of western Alaska are critical for subsistence



Caught by trawlers, walleye pollock are processed primarily for frozen fish sticks, fast-food fish sandwiches, and imitation crab. Photo courtesy of NOAA Photo Library.

cultures there (M. Pete, personal communication) and provide important nutrients to rivers and adjacent forests (Kline et al., 1993, 1997; Schmidt et al., 1998; Wipfli et al., 1999). Commercial fisheries depend on the Bering Sea for large quantities of fish. Changes in the ability of the Bering Sea to support populations of migrating seabirds and marine mammals may impact the other marine ecosystems they visit during other times. For example, short-tailed shearwaters that forage in the Bering Sea from May to September nest in southeastern Australia and are an important component of that ecosystem from October to April. Likewise, northern fur seals that breed on the Pribilof Islands in summer spend the winter foraging in the North Pacific, in particular in the California Current System (York, 1987). Developing an ability to predict how climate change will affect these exports will allow adjustments in resource management to take advantage of improvements in resource availability and to minimize the impacts of decreases in resource availability.

5.4.1 Export of Salt, Freshwater, Carbon, Heat, and Nutrients to the Arctic Ocean

We need to know how climate change may alter the way the Bering Sea influences the Arctic Ocean. If the Bering Sea warms, less sea ice is likely to be produced in the winter, and thus brine formation will be reduced. If upwelling of nutrients from the deep Bering Sea onto the shelf is reduced due to a reduction of transport through Bering Strait, these salts and nutrients will no longer be available north of the strait. Warming of the northern Bering and Chukchi Seas would likely cause a trophic shift from a benthic- to a pelagic-dominated system, with a rapid impact on trophic levels that feed near the bottom of the food chain. If warm waters from the eastern Bering Sea shelf are exported to the

Arctic Ocean, they might control marginal ice zone dynamics over the Chukchi shelf, as well as sea ice thickness and concentration and the upper water column stratification as far north as the central Beaufort Sea. For example, warm water from the eastern Bering Sea detected by moorings in Bering Strait in 1997–1998 has been hypothesized to be related to the subsurface temperature maximum observed over the Northwind Ridge during the NSF Surface Heat Budget of the Arctic Ocean (SHEBA) project in 1998 (Uttal et al., 2002).

5.4.2 Nutrient Export to Freshwater Systems by Salmon

There is a need to know how changes in eastern Bering Sea ecosystems will affect the abundance of salmon runs. Most salmon growth occurs in marine waters. Under natural conditions, as adult salmon migrate to their natal streams and lakes to reproduce, there is a substantial net export of production in terms of both biomass and nutrients from the marine to freshwater environments. In Alaskan waters where high natural runs have been maintained, millions of fish enter freshwater habitats providing substantial nutrients to oligotrophic systems (Kline et al., 1993, 1997; Schmidt et al., 1998; Wipfli et al., 1999). Nutrient enhancement resulting from decomposing salmon carcasses can lead to phytoplankton blooms and increased growth and abundance of freshwater invertebrate prey of juvenile salmonids. Growth and survival of peak year juveniles are enhanced in response to marine-derived nutrient loading (Wipfli et al., 2003). Estimates of the variation in nutrient subsidies to freshwater due to fishing or climate change, similar to those made for Pacific Northwest salmon (Gresh et al., 2000), have not been calculated for the Bering Sea.

Fishery management strives to harvest sufficient numbers of returning



Spawning sockeye salmon (*Oncorhynchus nerka*).
U.S. Fish and Wildlife Service photo.

adult salmon to maintain intermediate escapement (spawner) levels, theoretically leading to optimal levels of progeny (recruits). Large sockeye salmon escapements, however, have been shown to improve production in Karluk Lake (Kodiak Island), and commercial fishing may have negatively affected overall production in that system over time (Schmidt et al., 1998). Although commercial fishing removes 50–60% of the Bristol Bay sockeye run each year, it is not clear whether this strategy has compromised nutrient loading and salmon productivity in any of the rearing lakes.

5.4.3 Use of Fish by People

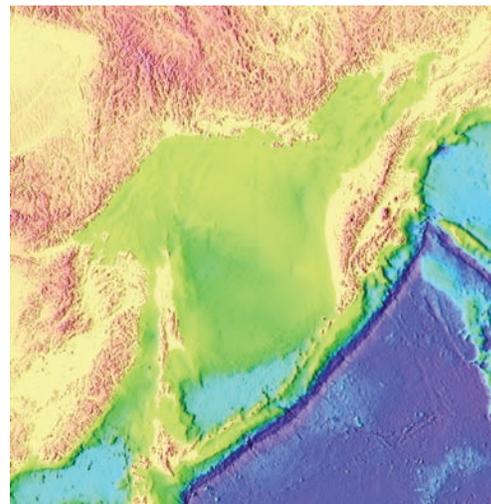
There is a need to know how changes in the ecosystems of the eastern Bering Sea will affect the availability of fish for use by people. As mentioned earlier, migrating North Pacific salmon species support not only a major commercial fishery, primarily in Bristol Bay, but also are of major importance to subsistence and sport fisheries in western Alaska. Likewise, groundfish and crabs support some of the largest and most lucrative fisheries in United States' waters. Changes in the species composition, abundance, quality, or distribution of these fish and shellfish have major economic and social impacts, particularly in the coastal communities of western Alaska. Climate change may favor increases in some species and decreases in others. If BEST can provide managers and planners with the tools to predict how climate change will impact important resource species, then appropriate adjustments in human behavior and investment may be possible.

The Sea of Okhotsk.
Bathymetric map from the U.S. Geological Survey
Coastal and Marine Geology Program.

5.5 Comparative Studies

Comparisons with other polar marine ecosystems may provide key insights into how the Bering Sea ecosystem responds to climate change. Five systems, the Okhotsk Sea, the Labrador Sea, the East Greenland Sea, the Barents Sea, and the Southern Ocean, are likely to yield considerable insight into Bering Sea ecosystem variability. All are high latitude seas with seasonal ice cover, and all are undergoing rapid change, likely due to climate forcing (IPCC, 2001). Of these areas, the Sea of Okhotsk and the Barents Sea offer the most direct comparisons. The Southern Ocean may provide opportunities to investigate how primary and secondary production associated with sea ice affects overwintering strategies for food web components, and how changes in environmental structure ramify through the food web to top predators.

The **Okhotsk Sea** is a semi-enclosed, subarctic sea where Northern Hemisphere sea ice reaches its southernmost extent, and the scales of interannual and seasonal variation in sea ice cover are similar to those in the Bering Sea. Recent satellite studies have revealed a dichotomy between sea ice edge and open water blooms similar to that found in the Bering Sea (Matsumoto et al., submitted). There is also evidence that the sea ice cover in the two regions is out of phase; heavy sea ice cover in the Bering Sea coincides with light sea ice in the Okhotsk Sea (Honda et



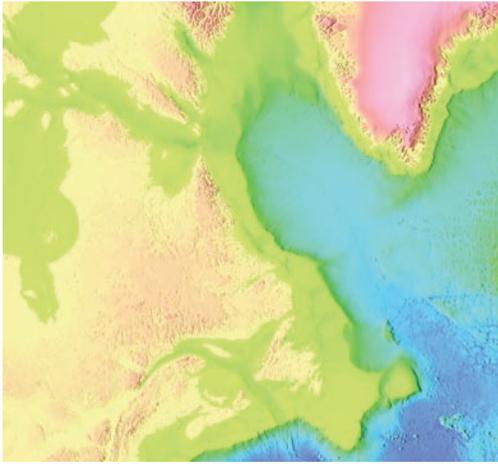
al, 1999). Understanding this relationship may help in defining larger scale physical forcings for both regions. A comparative study with the Okhotsk Sea might provide insight into the relationship between primary productivity near the ice edge and the effects of an earlier spring on ecosystem productivity and function (Oscillating Control Hypothesis, Hunt et al., 2002a). An ongoing Japanese research program in the Okhotsk Sea offers opportunities for collaborative study.

The **Barents Sea** is an open arctic-boreal shelf-sea with an area of about 1.4 million km² and an average depth of 230 m (Sakshaug et al., 1992). Although located from about 70°N to nearly 80°N, sea temperatures are considerably higher than those at similar latitudes in the western Atlantic or Bering Sea due to inflow of relatively warm Atlantic water masses from the southwest. This inflow also strongly influences year-to-year variability in temperature in the highly productive southern part (Loeng, 1991; Ingvaldsen et al., in press), as does regional heat exchange with the atmosphere (Ådlandsvik and Loeng, 1991; Loeng et al., 1992). Variability of Atlantic inflow to the Barents Sea is discussed by Ingvaldsen et al. (2002) and Ingvaldsen et al. (2003). The dynamics among the three commercial and economically valuable fish stocks: cod, capelin, and herring are particularly important (Bogstad and Gjørseter, 1994; Gjørseter and Bogstad, 1998; Hamre and Hatlebakk, 1998). The calanoid copepod



Calanus finmarchicus, marine mammals (including ringed and harp seals, and minke and fin whales), and sea birds are also abundant and prominent in the region's food web. Even if the Barents Sea ecosystem is relatively simple, large-scale climate fluctuations may influence population dynamics and community structure through a number of different mechanisms (Ottersen et al., 2001; Stenseth et al., 2002). **Regional climate-change predictions for the Barents Sea indicate a further increase in sea temperatures over the coming 50–100 years. These scenarios are uncertain, however, and the ecological effects even more so.**

Although located much farther south than the other regions, the subarctic **Labrador–Newfoundland Shelf** (43°N–60°N) is influenced by waters emanating from the Arctic. These waters come through Fram Strait, carried via the East and West Greenland Currents to the Labrador Shelf (Smith et al., 1937), and through the Arctic Archipelago via Baffin Bay (Jones and Rudels, 2002). Seasonal sea ice coverage on the Labrador–Newfoundland Shelf affects heat exchanges with the atmosphere, influences the annual salinity cycle (Myers et al., 1990; Petrie et al., 1991) and is thought to determine the timing of the spring bloom. Like the Bering Sea, the system is strongly advective due to the presence of the Labrador Current. Approximately 20% of the transport in the Current occurs over the shelf, and 80% is at the shelf edge (Lazier and Wright, 1993). Interannual variability in winds, air and sea temperatures, and sea ice extent and transport is strongly linked to changes in the North Atlantic Oscillation (NAO; Colbourne et al., 1994; Myers et al., 1994; Drinkwater, 1996). The once-thriving fishery on this shelf crashed in the late 1980s and early 1990s, leaving an altered ecosystem, collapse of the subsistence lifestyle, and massive unemployment. For over 500 years,



The Labrador-Newfoundland Shelf. Bathymetric map from the U.S. Geological Survey Coastal and Marine Geology Program.

cod (*Gadus morhua*) was the dominant fish species in the region, but by 1992 the stocks declined to such low levels that a moratorium on cod fishing was imposed. Although some attribute the collapse of northern cod only to over-fishing (Hutchings and Myers, 1994; Myers et al., 1996), climate also appeared to have significant effect (Taggart et al., 1994; Rose et al., 2000; Drinkwater, 2002). Coincident with the cod decline, the NAO increased to very high levels, with cold air and sea temperatures and severe ice conditions prevailing. At the same time, other changes were occurring within the marine ecosystem including a southward shift in the distribution of many fish species, an increase in invertebrate stocks such as snow crab and shrimp, and poor growth, delayed spawning, and reduced recruitment of finfish stocks. In the intervening decade, in spite of the moratorium largely remaining in place, the cod have not recovered. Recent modeling studies of the calanoid copepod *Calanus finmarchicus*, an important component of the zooplankton and the major food source for larval cod, suggest that the cold conditions in the late 1980s and early 1990s could have reduced the zooplankton stocks by upwards of 30–40% (B. deYoung, Memorial University, St. John's, Newfoundland, personal communication).

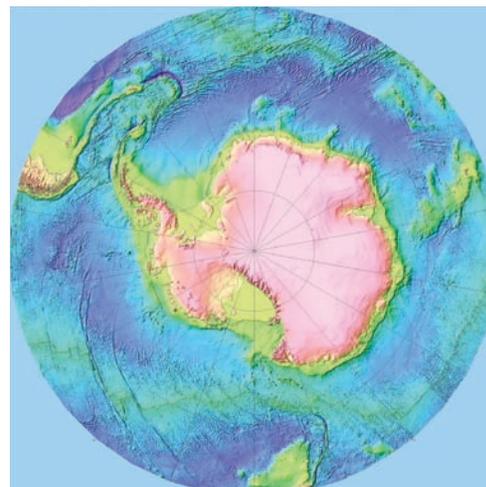
Significant work has been done in the Labrador Sea, including development of an historical database and an observational program integrated with descriptive and predictive modeling. Partnerships with Canadian researchers working in

the Labrador would bring considerable first-hand experience to the problem of investigating natural versus anthropogenic forcing on the Bering Sea ecosystem.

In studies of the Bering Sea, the ecological significance of the distribution, timing, and duration of sea ice in the Marginal Ice Zone (MIZ) between an arctic and a sub-arctic environment can be compared and contrasted with processes and studies in similar environments in the Southern Hemisphere.

Do these two systems behave similarly, or does the presence of a broad, shallow shelf in the Bering Sea mean that benthic-pelagic coupling is sufficiently strong that the two systems are fundamentally different? There is an excellent opportunity for comparison with results from the Southern Ocean GLOBEC program, the Committee for Conservation of Antarctic Marine Living Resources (CCAMLR) Environmental Monitoring and Management (EMM) program, the Antarctic Pack Ice Seals (APIS) program, and the Research on Ocean-Atmospheric Variability and Ecosystem Response in the Ross Sea (ROAVERRS) program.

There is also potential to use the great north-south extent of the eastern Bering Sea continental shelf for comparative studies of the northern and southeastern shelves. Currently the northern shelf is driven more by the Arctic Oscillation, and thus is tied to atmospheric processes north of Bering Strait. By comparison, the southeastern Bering Sea is more directly



The Southern Ocean. Bathymetric map from the U.S. Geological Survey Coastal and Marine Geology Program.



Differences in water temperature in the currents of the Bering Sea are reflected in the cloud forms condensing above. Photo taken from Space Shuttle *Challenger*, October 1984, courtesy Lunar and Planetary Institute.

5.6 Questions Related to Integration across Spatial and Temporal Scales

a. How do changes in forcing functions impact the shelf ecosystem, including production, community composition and trophic linkages?

This is the key over-arching question in BEST. To answer it, we must determine the important linkages within the ecosystem in both the physical and biological domains, including trophic, intra-, and inter-specific relationships. We must also address issues of spatial and temporal scales, how the life-history characteristics of species affect their connections with the ecosystem (match-mismatch issues), and how regulation of the ecosystems may switch from bottom-up to top-down. Modeling will be necessary to determine how these changes affect the productivity of the eastern Bering Sea fisheries, and whether there are bifurcation points at which further forcing will cause the systems to shift to alternative “stable” states (e.g., Scheffer et al., 2001).

b. What are the key spatial and temporal scales that characterize the Bering Sea ecosystem? How can we define these scales and cross-link them (down-scaling and up-scaling)?

To develop useful models of external forcing of ecosystem function in the eastern Bering Sea, it will be necessary to identify the key spatial and temporal scales at which the components of the system function. It will be important to develop techniques for downscaling from global to regional processes and thence to the

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tion tied to the Pacific Decadal Oscillation, the Aleutian Low, and Pacific Ocean transport conditions. A warming of waters in the Bering Sea would dramatically impact the extent and duration of the annual ice sheet covering the area, which is intimately tied to ecosystem function in the two regions. If transport is reduced through Bering Strait, the shelf-basin exchange processes providing nutrients onto the Bering Sea shelf could change, with a reduction in nutrient on-welling causing an overall decline in water column production. A stoppage of the flow through Bering Strait would also mean that less heat would be advected northward from the North Pacific Ocean, and there could be considerable cooling of the eastern Bering Sea region, with unknown effects. Alternatively, if warming occurred, this could enhance micro- and mesozooplankton grazing on the available carbon, thus reducing carbon supply to the benthos and limiting benthic standing stocks in the area.

reactions of individual organisms to physical forcing functions. If the impacts of regional forcing functions on the physiology and behavior of individuals can be coupled, it then will be necessary to scale up to the level of population and ecosystem response. It will be important to take into account individual species' life history characteristics (generation time, age at first breeding, fecundity), because these can affect a population's responses to different frequencies and amplitudes of environmental change (life cycle relative to event scale). These issues are central to understanding match–mismatch interactions.

c. Are there lessons to be learned from studies of other marginal seas?

Other sub-arctic and high latitude seas have been studied intensively and for longer than the eastern Bering Sea. In some of these other systems one or more cycles of decadal-scale climate variability have been observed. Thus, examination of these data sets, forcing functions, and ecosystem responses may provide useful insights as to the most important components or mechanisms to investigate in the Bering Sea. Since there are also important differences between the Bering Sea and other regions (e.g., water depth, advection, latitude, and hence seasonal light regime), it will also be important to examine how the eastern Bering Sea differs from other regions in its responses to climate fluctuations.

d. Can we develop a predictive modeling capability?

With sufficient understanding of forcing functions and individual and ecosystem response, it should be possible to develop models to predict how the eastern Bering Sea will respond to climate change. Such

studies are now underway for other systems, and BEST will be able to draw upon these results and models. With models developed for the Bering Sea, it may be possible to separate the impacts of climate from those of direct anthropogenic forcing (fisheries takes, pollution), and to determine how these different forces interact. Answers to the issues of interaction are particularly important if they result in non-linear ecosystem responses and alternative stable states that are undesirable. These modeling efforts should reveal the dominant forcing mechanisms producing variability at different time scales in recruitment responses of fish. Modeling efforts may also help in identifying the influences of top-level predators on the structure and functions of shelf ecosystems.

e. Are there regions, processes, or species that are unusually sensitive to changes in the forcing functions and that might serve as sentinels of change?

It is likely that some locations, processes, or species are more sensitive to climate change than others. They thus could serve as sentinels of impending change. If the responses of sentinels can be identified and quantified, the response variables may then be incorporated in management models. The development of a suite of quantitative indices may also improve our ability to address broader issues of management of ecosystems as a whole.

f. How do changes in the ecosystem impact the quality, quantity, and availability of Bering Sea resources for commercial and subsistence harvests?

The resources of the eastern Bering Sea are critical for the survival, and the social and economic well-being of people, par-

ticularly those living in western Alaska. The ability to foresee how climate change will affect resource availability could be of great benefit in planning the societal responses to ecological change. Whether it is the future availability of salmon to villagers on the Yukon/Kuskokwim Delta, or the abundance of pollock available for commercial harvest, knowledge of potential change in resource availability can improve planning decisions. A prime goal of BEST must be to contribute to our ability to manage the marine resources of the eastern Bering Sea sustainably and to provide managers and planners with the knowledge of ecosystem response to climate change.

The goal of BEST is to develop an ability to predict the effects of climate change on the ecosystems and resources of the eastern Bering Sea, and their ability to support sustainable commercial and subsistence harvests.

The BEST Science Plan provides the scientific background and rationale for a series of questions designed to elucidate mechanisms connecting regional climate forcing to the responses of ecosystems and their constituent species. The investigations necessary to answer these questions will form the backbone of a multi-year, multi-platform research program in the eastern Bering Sea. Elements of the program include study of the connections between climate variability and flows through the Aleutian Archipelago and into and across the eastern and northern shelves, the roles of sea ice and water temperature in controlling the timing, amount, and fate of

primary production, and the interactions among species that control the ultimate structure of the region's ecosystems and their ability to support sustainable fisheries. BEST provides an excellent opportunity to integrate basic oceanographic research and the emerging requirement for ecosystem-based management of fisheries. Because the eastern Bering Sea supports some of the nation's largest and most lucrative fisheries, and its ecosystems are already showing signs of response to climate variability and change, BEST is timely and will fill an important societal need for knowledge and sound, science-based management.

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Appendix 1

Members of the International Planning Workshop held in Laguna Beach, California, 4 –6 September 2002.

Richard Beamish
Fisheries and Oceans Canada
Pacific Biological Station
3190 Hammond Street
Nanaimo, B.C. V9T 6N7
Canada
Phone: 250-756-7029
Fax: 250-756-7141
BeamishR@pac.dfo-mpo.gc.ca

Ken Drinkwater
Fisheries and Oceans Canada
Bedford Institute of
Oceanography
P.O. Box 1006
Dartmouth, N.S. B2Y 4A2
Canada
Phone: 902-426-2650
Fax: 902-426-6927
DrinkwaterK@mar.dfo-mpo.
gc.ca

Mikhail Vladimirovich Flint
P. P. Shirshov Institute of
Oceanology
Russian Academy of Sciences
Nakhimovskiy prospekt 36
Moscow, 17851
Russia
m_flint@orc.ru

Jackie Grebmeier
Department of Ecology and
Evolutionary Biology
University of Tennessee
Knoxville, TN 37996
Phone: 865-974-2592
jgrebmei@utk.edu

Roger Harris
Plymouth Marine Laboratory
Prospect Place
Plymouth, PL1 3DH
United Kingdom
Direct Phone: 44-0-1752-633400
Switchboard: 44-0-1752-633100
Fax: 44-0-1752-633101
rph@pml.ac.uk

George L. Hunt, Jr.
Department of Ecology and
Evolutionary Biology
University of California, Irvine
Irvine, CA 92697-2525
Phone: 949-824-6322
Fax: 949-824-2181
glhunt@uci.edu

Nina Karnovsky
Department of Ecology and
Evolutionary Biology
University of California, Irvine
Irvine, CA 92697
Phone: 949-824-4747
Fax: 949-824-2181
nkarnovs@uci.edu

Harald Loeng
Havforskningsinstituttet
Institute of Marine Research
PO Box 1870 Nordnes
Bergen, N-5817
Norway
Phone: 47-5523-8466
Fax: 47-5523-8584
harald.loeng@imr.no

James Morison
Polar Science Center
Applied Physics Laboratory
University of Washington
1013 NE 40th Street
Seattle, WA 98105
Phone: 206-543-1394
Fax: 206-616-3142
morison@apl.washington.edu

Jeff Napp
Alaska Fisheries Science Center
National Oceanic and
Atmospheric Administration
7600 Sand Point Way NE
Seattle, WA 98115
Phone: 206-526-4148
Fax: 206-526-6723
Jeff.Napp@noaa.gov

Brenda L. Norcross
Institute of Marine Science
University of Alaska, Fairbanks
P.O. Box 757720
Fairbanks, Alaska 99775-7220
Phone: 907-474-7990
Fax: 907-474-1943
norcross@ims.uaf.edu

Geir Ottersen
Department of Biology
Division of Zoology
University of Oslo
P.O. Box 1050 Blindern
Oslo, N-0316
Norway
Phone: 47-22-85-72-88
Fax: 47-22-85-46-05
geir.ottersen@bio.uio.no

Clarence Pautzke
North Pacific Research Board
441 West 5th Ave, Suite 500
Anchorage, AK 99501-2340
Phone: 907-278-6772
Fax: 907-276-7178
cpautzke@nprb.org

Naonobu Shiga
Marine Biodiversity
Laboratory
Graduate School of Fisheries
Sciences
Hokkaido University
3-1-1 Minato
Hakodate 041-8611
Japan
Phone: 81-138-40-5501
Fax: 81-138-40-5542
nao@fish.hokudai.ac.jp

Phyllis Stabeno
NOAA - Pacific Marine
Environmental Laboratory
7600 Sand Point Way NE Bldg. 3
Seattle, WA 98115
Phone: 206-526-6453
Fax: 206-526-6815
stabeno@pmel.noaa.gov

Neil Swanberg
Office of Polar Programs
National Science Foundation
4201 Wilson Boulevard
Arlington, VA 22230
Phone: 703-292-8029
Fax: 703-292-9081
nswanberg@nsf.gov

Appendix 2

Participants, Advisors and Observers of the Planning Workshop held in Seattle, Washington, 17–19 March 2003.

Organizing Committee members denoted by bold type.

Kevin R. Arrigo
Department of Geophysics
Mitchell Bldg, Room 355
Stanford University
Stanford, CA 94305-2215
Phone: 650-723-3599
Fax: 650-725-7344
arrigo@pangea.stanford.edu

Richard D. Brodeur
Northwest Fisheries Science
Center
National Marine Fisheries
Service
Hatfield Marine Science Center
2030 S. Marine Science Drive
Newport, OR 97365-5296
Phone: 541-867-0336
Fax: 541-867-0336
Rick.Brodeur@noaa.gov

David A. Caron
Department of Biological
Sciences
University of Southern
California
Los Angeles, CA 90089-0371
Phone: 213-740-0203
Fax: 213-740-6720
dcaron@usc.edu

Ken Coyle
Institute of Marine Science
University of Alaska, Fairbanks
P.O. Box 757720
Fairbanks, AK 99775
Phone: 907-474-7705
Fax: 907-474-7204
coyle@ims.uaf.edu

Jackie Grebmeier
Department of Ecology and
Evolutionary Biology
University of Tennessee
Knoxville, TN 37996
Phone: 865-974-2592
Fax: 865-974-3067
jgrebmei@utk.edu

Eileen Hofmann
Center for Coastal Physical
Oceanography
Old Dominion University
768 W. 52nd Street
Norfolk, VA 23529
Phone: 757-683-5334
Fax: 757-683-5550
hofmann@ccpo.odu.edu

George L. Hunt, Jr.
Department of Ecology and
Evolutionary Biology
University of California, Irvine
Irvine, CA 92697-2525
Phone: 949-824-6322
Fax: 949-824-2181
glhunt@uci.edu

Lewis S. Incze
Bioscience Research Institute
University of Southern Maine
96 Falmouth Street
Portland, ME 04104-9300
Phone: 207-228-8070
Fax: 207-228-8057
lincze@usm.maine.edu

Gordon Kruse
School of Fisheries and Ocean
Sciences - Juneau Center
University of Alaska, Fairbanks
11120 Glacier Highway
Juneau, AK 99801
Phone: 907-465-8458
Fax: 907-465-8461
Gordon.Kruse@uaf.edu

Evelyn J. Lessard
School of Oceanography
Box 357940
University of Washington
Seattle, WA 98195
Phone: 206-543-8795
Fax: 206-543-0275
elessard@u.washington.edu

Pat Livingston
Alaska Fisheries Science Center
NOAA - National Marine
Fisheries Service
7600 Sand Point Way NE Bldg. 4
Seattle, WA 98115
Phone: 206-526-4242
Fax: 206-526-6723
Pat.Livingston@noaa.gov

Larry Madin
Woods Hole Oceanographic
Institution
Mailstop 38
Woods Hole, MA 02543
Phone: 508-289-2739
Fax: 508-457-2169
lmadin@whoi.edu

Wieslaw Maslowski
Department of Oceanography
Naval Postgraduate School
833 Dyer Road
Monterey, CA 93943
Phone: 831-656-3162
Fax: 831-656-2712
maslowsk@nps.navy.mil

Lyn McNutt
Geophysical Institute
University of Alaska, Fairbanks
P.O. Box 757320
Fairbanks, AK 99775
Phone: 907-474-6077
Fax: 907-474-7290
lyn@gi.alaska.edu

Jeffery Napp
Alaska Fisheries Science Center
NOAA - National Marine
Fisheries Service
7600 Sand Point Way NE Bldg. 4
Seattle, WA 98115
Phone: 206-526-4148
Fax: 206-526-6723
Jeff.Napp@noaa.gov

James Overland
NOAA - Pacific Marine
Environmental Laboratory
7600 Sand Point Way NE Bldg. 3
Seattle, WA 98115
Phone: 206-526-6795
Fax: 206-526-6485
overland@pmel.noaa.gov

George Owletuck
124 Yukon Avenue
Marshall, AK 99585
Phone: 907-679-6112
George_Owletuck@mail.com

Mary Pete
Division of Subsistence
Alaska Department of Fish and
Game
PO Box 25526
Juneau, AK 99802-4426
Phone: 907-465-4146
Fax: 907-465-2066
mary_pete@fishgame.state.
ak.us

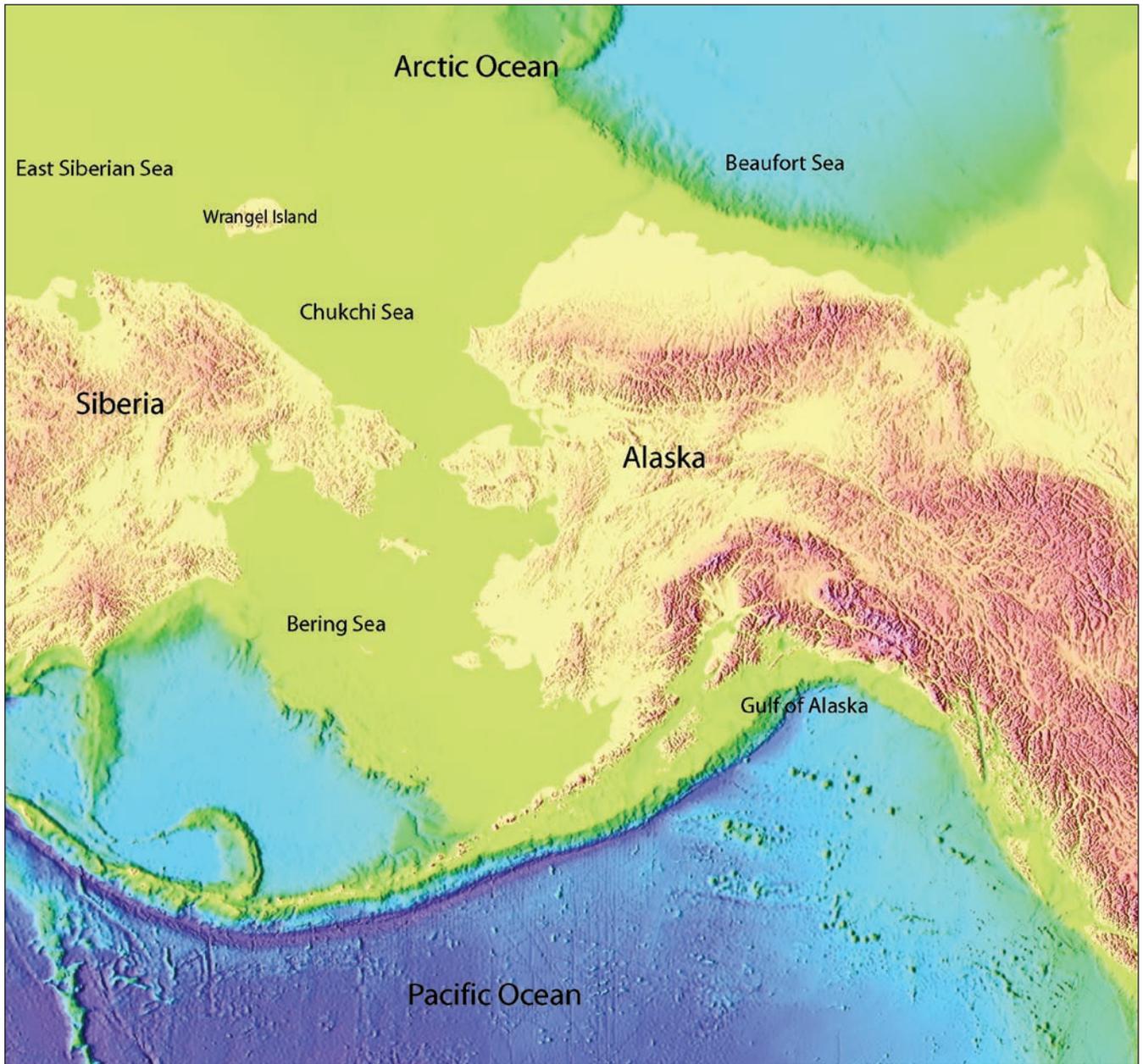
Vladimir I. Radchenko
Sakhalin Research Institute
of Fisheries & Oceanography
(SakhNIRO)
196 Komsomolskaya Street
Yuzhno-Sakhalinsk, 693023
Russia
Phone: 7-4242-456-779
Fax: 7-4242-456-778
vhrad@sakhniro.ru

Sei-ichi Saitoh
Graduate School of Fisheries
Sciences
Hokkaido University
3-1-1 Minato-cho Hakodate
Hokkaido, 041-8611
Japan
Phone: 81-138-40-8843
Fax: 81-138-43-5015
ssaitoh@salmon.fish.hokudai.
ac.jp

Ray Sambrotto
Lamont-Doherty Earth
Observatory
Columbia University
P.O. Box 1000
61 Route 9W
Palisades, NY 10964-1000
Phone: 845-365-8402
Fax: 845-365-8150
sambrott@ldeo.columbia.edu

Phyllis Stabeno
NOAA - Pacific Marine
Environmental Laboratory
7600 Sand Point Way NE Bldg. 3
Seattle, WA 98115
Phone: 206-526-6453
Fax: 206-526-6815
stabeno@pmel.noaa.gov

Luis M. Tupas
Office of Polar Programs
National Science Foundation
4201 Wilson Boulevard
Arlington, VA 22230
Phone: 703-292-7425
Fax: 703-292-9082
ltupas@nsf.gov



The Bering Sea in a regional context. Base map from U.S. Geological Survey Coastal and Marine Geology Program.

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Science Plan

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Phone: 907-474-1600 Fax: 907-474-1604
www.arcus.org info@arcus.org**