Understanding Ecosystem Processes in the Bering Sea
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Learn more at
www.nprb.org/beringseaproject

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Origins and Framework
The Bering Sea lies in the far north, off the coast of Alaska, where the North Pacific Ocean reaches beyond the Aleutian Islands to form one of the world’s largest and most biologically productive semi-enclosed seas. Europeans named this sea for the Danish-born Russian naval officer Vitus Bering, who navigated uncharted waters to the coast of North America, only to perish on the return journey. To most Americans, the Bering Sea remains to this day a remote and mysterious region—but for many of the thousands of coastal residents, the Bering Sea is an everyday part of their existence, and is the fertile garden that provides a bounty of subsistence harvest today, just as it has for centuries past.

The rhythm of seasonal sea ice advance and retreat—moving hundreds of miles south in the winter to retreat in the spring across the broad continental shelf—exerts a powerful influence on the ecology of these waters, and makes the Bering Sea region particularly sensitive to changes in climate. In winter, the combination of geology, latitude, winds and ocean currents produces ice cover extending far into the southern Bering Sea. In the spring and summer, retreating ice, longer daylight hours, and nutrient-rich ocean water flowing onto the shallow continental shelf result in high marine productivity that is vital to both sea life and people. The timing and extent of the seasonal ice play an essential role in the timing of this productivity and in the structuring of the ecosystem.

The turbulent waters of the Bering Sea are home to a rich variety of biological resources, including hundreds of species of fishes and crustaceans. Vast populations of phytoplankton and zooplankton—individually tiny, but collectively forming enormously important biomass—peak and wane with the seasonal cycles in this subarctic sea. Drawn by this bounty of ocean life, tens of millions of individual seabirds (the majority of the seabird population in United States waters) and large numbers of two dozen species of whales, walrus, seals, and other marine mammals live in or visit these cold waters. Diverse and highly productive, the Bering Sea also gives rise to the world’s largest salmon fishery and one of the world’s largest single species fisheries—walleye pollock.

Bering Sea fisheries provide about 40% of the total US commercial catch, with an annual value exceeding $3 billion. After processing, the Bering Sea provides more than half of the wild-caught seafood consumed in the US. And at a more local scale, the Bering Sea provides an estimated three-quarters of the subsistence harvest that supports 55,000 Alaska Native people and others living in more than 30 coastal communities. Many of these communities have existed around the Bering Sea for centuries with important cultural links to this dynamic ecosystem.

Climate scientists predict a major reduction in ice cover over the southern Bering Sea in coming decades, with potential ecological consequences intensifying concern about the future. To better understand and predict the large-scale ecological changes that could have major economic and cultural implications in the Bering Sea and elsewhere, nearly 100 principal investigators from scientific disciplines spanning climate, oceanography, fish and fisheries, seabirds, marine mammals, economics, anthropology, and ethnography joined forces in the Bering Sea Project. Over the course of this complex, seven-year integrated study of the Bering Sea, these principal investigators—together with their many colleagues, technicians, students, ship officers and crews, and other field and laboratory teammates—delved into everything from physics to fish and beyond (Figure 1). Their stories and findings fill the pages that follow.

**FIGURE 1** An illustration of the eastern Bering Sea shelf shows the predominant currents and species, research platforms, ice extent and the location of the cold pool, and also focal coastal communities and their primary subsistence diet. Biophysical moorings are noted as M2-M8. The seven-year “Bering Sea Project” focused on US waters across the entire eastern Bering Sea shelf, slope, and basin, extending south from the Bering Strait and north from the Alaska Peninsula and eastern Aleutian Islands.
Ecosystem-scale Research

The Bering Sea Project was a multi-agency, integrated ecosystem study, aimed at delivering new knowledge and understanding of how climate change and changing sea ice cover will affect the eastern Bering Sea marine ecosystem. The project linked research on climate, physical and biological oceanography, phytoplankton, zooplankton, fishes, seabirds, marine mammals, humans, traditional knowledge, and economic outcomes to investigate the mechanisms that sustain this highly productive region.

A major scientific effort was required to work at the scale of the entire ecosystem in this vast and complex region. The continental shelf area of the eastern Bering Sea is over 1,200 kilometers in length and 500 kilometers in width—roughly the size of California, and close to half of the overall Bering Sea extent of ~2.3 million square kilometers. To meet the need of major resource investment, the seven-year Bering Sea Project received over $30 million in direct funding from a partnership of the National Science Foundation (NSF) and North Pacific Research Board (NPRB). Additionally, there were significant in-kind contributions from the National Oceanic and Atmospheric Administration’s (NOAA) Alaska Fisheries Science Center and Pacific Marine Environmental Laboratory, and from the US Fish & Wildlife Service—bringing the total investment to over $50 million. The Bering Sea Project assembled monetary and ship resources that would have been beyond the reach of any one agency or organization, and has supported 43 collaborative research projects, nearly 100 principal investigators, and a small army of postdoctoral scholars, graduate students, technicians, and vessel crews.

STANDING ON THE SHOULDERS OF GIANTS: A BRIEF HISTORY

Despite being the source of tremendous subsistence and cultural importance and of some of the largest and most lucrative fisheries in the United States, the eastern Bering Sea has received surprisingly little integrated oceanographic study prior to the Bering Sea Project. Earlier projects included the Outer Continental Shelf Environmental Assessment Program (OCSEAP) and Processes and Resources of the Eastern Bering Sea Shelf (PROBES) in the 1970s and early 1980s; the Inner Shelf Transfer and Recycling (ISHTAR) program in the 1980s; and the NOAA-funded Coastal Ocean Program Fisheries Oceanography Coordinated Investigations (FOCI) and NSF-funded Inner Front Project in the late 1990s and early 2000s.

After the conclusion of the ISHTAR program, most eastern Bering Sea programs were relatively small, resource-limited, and focused at a regional level within the eastern Bering Sea. However, these programs were important precursors to the Bering Sea Project because they were interdisciplinary in nature, involved collaborations among NOAA scientists and academic scientists, and, in many cases, involved significant sharing of resources.

More recently, several NOAA programs have made important contributions to the eastern Bering Sea knowledge base:

• The North Pacific Climate Regimes and Productivity (NPCREP) collaborated with the Bering Sea Project by providing important data from times of the year and areas not covered in the other studies.
• The US portion of the Bering-Aleutian Salmon International Survey (BASIS), begun in 2000, has been continued and expanded by the Alaska Fisheries Science Center, providing coverage of Bering Sea shelf ecosystems in late summer and early fall—times not otherwise sampled in the Bering Sea Project.
• The NOAA/PMEL biophysical moorings in the Bering Sea, in place since 1996, supplied a broad range of fundamental data that informed the Bering Sea Project prior to and during the project.

These partnership programs proved to be especially important over the course of the Bering Sea Project, since they included coverage during the warm years of 2000–2005 and were therefore crucial points of comparison to the relatively cold 2007-2010 field years of the Bering Sea Project.
Constructing the Bering Sea Project

In early 2001, a group of scientists led by George Hunt submitted a draft manuscript to NSF that described a potential conceptual model of how climate variability could influence the flow of energy to fish, seabirds, and marine mammals in the southeastern Bering Sea. Subsequent discussion resulted in NSF support for an international planning workshop to review available data and provide advice on the feasibility and value of proceeding with a large interdisciplinary study of the Bering Sea. Workshop participants included oceanographers working in the North Atlantic Ocean, the western North Pacific Ocean, and the Bering Sea. Both Neil Swanberg, NSF Arctic Natural Sciences Program Manager at that time, and Clarence Pautzke, the newly appointed Executive Director of the NPRB, attended the workshop and identified the potential value of collaboration between NSF and NPRB in developing integrated ecosystem studies in the Bering Sea. In March 2003, a second planning workshop convened in Seattle, Washington, and resulted in the development of the 2004 Bering Ecosystem Study (BEST) Science Plan.

Contemporaneous with development of the BEST Science Plan, a long-term science plan for NPRB was drafted, incorporating guidance from a National Research Council panel tasked with developing a plan for guiding the NPRB funding program. The resulting NPRB Science Plan emphasized the importance of large-scale integrated studies of the marine ecosystems of the eastern North Pacific. Following major efforts by NPRB staff, panels, and Board of Directors, the NPRB was consequently poised to launch its first Integrated Ecosystem Research Program in the Bering Sea (named the "Bering Sea IERP", or "BSIERP"). While the BEST program was also being launched, could the two organizations—NSF and NPRB—with different cultures and goals collaborate, or would their programs compete for ship time and scientific manpower?

NSF and NPRB agreed to collaborate in bringing the BEST and BSIERP programs together to form a unified project, and

GUIDING HYPOTHESES

During the planning phase of the Bering Sea Project, researchers from many disciplines came together with people from Bering Sea communities—ranging from ice-free communities in the Aleutians to the seasonally ice-covered waters of St. Lawrence Island. Over the course of many months, they conceived a program of research that would become 43 linked components focused on key species, processes, and selected coastal communities, forming a highly integrated program structured around five core hypotheses:

A. Climate-driven changes in the physical components that control the Bering Sea (e.g., temperature, wind, sea-ice, and currents) modify the availability and allocation of food for all species.

B. Climate and ocean conditions influencing water temperature, ocean currents, and ecological boundaries impact fish reproduction, survival, and distribution, the intensity of predator-prey relationships, and the location of zoogeographic provinces.

C. Warming temperatures and subsequent earlier spring sea-ice retreat result in later spring phytoplankton blooms, thereby leading to increased abundance of piscivorous fish (e.g., walleye pollock, Pacific cod, and arrowtooth flounder) and a food web controlled by predators.

D. Climate and ocean conditions influencing water temperature, ocean currents, and ecological boundaries affect the distribution, frequency, and persistence of oceanographic fronts and other prey-concentrating features, and thus control the foraging success of marine birds and mammals.

E. Changes in climate and ocean conditions will affect the abundance and distribution of commercial fisheries and subsistence harvests.
planned to issue calls for proposals for fieldwork commencing in 2008. Building coordination at this scale between the two organizations required the good will and support of the leadership at NSF and NPRB, in particular Bill Wiseman, NSF Program Director in the Arctic Natural Sciences Program, and Clarence Pautzke, former NPRB Executive Director. They formed an agreement to partition the work, with NSF funding studies of climate, ocean physics, and lower trophic levels through zooplankton in the BEST program, and the NPRB funding studies of large zooplankton through fish, seabirds, and fisheries in the BSIERP program. The agreement included major commitments to ecosystem modeling and to research on subsistence harvest, local and traditional knowledge, and ethnography.

NOAA scientists also threw their full weight behind the new integrated Bering Sea Project, seeing its potential value for enhancing understanding of the mechanisms affecting fish stocks in the Bering Sea. With strong support from the management and staff at the Alaska Fisheries Science Center and also the Pacific Marine Environmental Laboratory, NOAA scheduled extra surveys in the Bering Sea and supported enhancement of planned surveys, complementing the work funded by NSF and NPRB. The result was the support of scientific cruises to the Bering Sea from early spring—when moorings were put out by NOAA scientists, accompanied by others taking hydrographic, chemical, and biological samples—to major broad-scale sampling of the eastern shelf in late August and September.

Launch of the Bering Sea Project

The combined efforts of NSF, NPRB, and NOAA—with additional in-kind support from the USFWS, ADF&G, and others—resulted in the integrated BEST-BSIERP program. This program became known more simply as the “Bering Sea Project”, with the first shelf-wide scientific coverage of the eastern Bering Sea and the first nearly continuous seasonal coverage from early March through mid-September. The stage was set to gather an unprecedented quantity of data, and to do it in a fashion that supported the development of comprehensive climate-to-fish and fisheries models that would provide an integration of the immense and complicated dataset to be gathered. Crucially, a set of core hypotheses (see Feature) and questions were developed to structure and guide the program, evolving from earlier science planning efforts.

A unified project management plan laid out key elements, including responsibilities of the project office, a data management approach, a communications and outreach plan, and a science steering committee. An Ecosystem Modeling Committee was established, consisting of external scientists who were charged with advising the development of the modeling program. Working in collaboration with NSF and NPRB staff, and with coordination among NOAA staff and other in-kind participants, a full-time program manager operated the project office based at NPRB in Anchorage, Alaska, and supported the work of the science steering committee.

The science steering committee, named the Science Advisory Board (SAB), proved essential for the success of the Bering Sea Project. Peers elected six scientists representing the various areas of the science program to serve on the committee—three supported by NSF and three by NPRB. The initial members of the SAB were Mike Sigler and Rodger Harvey (co-chairs), Phyllis Stabeno, Carin Ashjian, Kerim Aydin, and Rolf Gradinger. After two years, Aydin and Gradinger withdrew and were replaced by Jeff Napp and Mike Lomas; the six-member group of Sigler, Harvey, Stabeno, Ashjian, Napp and Lomas served as the SAB for the remaining duration of the project, from 2010-2015. SAB members worked closely with NSF and NPRB staff to help build integration among the individual scientists through monthly conference calls and planning and facilitation of annual principal investigator meetings, and through promotion of program hypotheses and synthesis. SAB members also worked to resolve large-scale logistics issues such as cruise schedules, and partnered with the funding organizations in cases where objectives of individual projects needed to be realigned due to field conditions or other unanticipated factors.

Four Field Years

Initial fieldwork began in 2007 with a limited subset of the participating teams, and in 2008 the Bering Sea Project was fully in motion with the first of three comprehensive field seasons. Our past understanding of the Bering Sea ecosystem had been limited by the difficulty in gathering data, especially in the ice-covered north during wintertime. In a concerted push of major new research activity, field scientists participating in the Bering Sea Project sampled the eastern Bering Sea in every month of the year (except December). The skilled crews of icebreakers operated by the US Coast Guard and UNOLS (University-National Oceanographic Laboratory System) vessels gave researchers access to the region around St. Lawrence Island and the northern shelf, powering through the ice-choked waters of late winter and spring. Enhanced sampling by NOAA survey ships in the April through October period further contributed to a far more detailed view of the ecosystem than was previously available.
FOUR FIELD YEARS  A Illustrating the laboratory-based side of fieldwork, Rolf Gradinger works with ice algae samples in the ship’s wet lab while at sea in late winter. B Pat Kelly (left) and Katrin Iken (right) deploy an under-ice “sediment trap” from the USCGC Healy during a spring research cruise in the northern Bering Sea. The sediment trap measures the transfer of organic matter from the melting ice and upper ocean to the seafloor. C Using a “noose pole”, fieldworker Vijay Patil stretches to capture a thick-billed murre from its cliffside nesting site on St. Paul Island; captured birds are held briefly to enable temporary attachment of research instruments. D Bering Sea Project scientists Chad Jay and Tony Fischbach stealthily approach a group of resting walruses on the sea ice south of St. Lawrence Island, preparing to attach “daily diary” satellite-linked radio tags using a crossbow. The tags remain attached to the walrus for several weeks, allowing the research team to collect data on walrus activity, location, and behavior. E Working in the eastern Bering Sea in the summer of 2008, Gigi Engel (left) and Tracy Shaw (right) extract live zooplankton specimens from a concentrated sample of seawater, using a highly technical piece of scientific equipment—Chinese soup spoons. F A sieved sample of benthic animals living in the upper few inches of mud and sediment on the Bering Sea shelf seafloor, collected using a “Van Veen grab.”
Managing data for accessibility across disciplines and for future research is as critical as the initial data collection out in the field, especially for complex studies like the Bering Sea Project involving hundreds of scientists.

Recognizing this, NSF and NPRB supported the development and maintenance of the Bering Sea Project Data Archive (http://beringsea.eol.ucar.edu) at the National Center for Atmospheric Research’s Earth Observing Laboratory (EOL), the single source for all data from this collaborative effort (Figure 2).

The comprehensive data management support strategy for the Bering Sea Project involved engaging with the science team early on to determine their requirements and establish priorities based on available resources. It also included implementation of a Project Field Catalog for use aboard the research cruises, and allowed the science teams to upload real-time documentation of data collection. This gave researchers on those vessels real-time displays of current ship track and position, and all ship-based sampling stations for the current and previous cruises, critical in the repeat location sampling strategy used during the project. They also had access to any operational products, such as satellite sea-ice data, used for real-time cruise track selection.

EOL also worked closely with local and traditional knowledge investigators to develop a Geographic Information System tool for displaying detailed data and information collected during the Nelson Island Project (see Feature on page 62), connecting place names to stories and photos.

EOL and partners at NPRB, NSF, and USGS provided clear specifications for “metadata”—the high-level information that describes the gathered information and other documentation that accompanies all datasets. Both metadata and data are housed in a comprehensive accessible database open to the public, which cross-references each unique investigator dataset and can be perused through a search tool or displayed in tables by cruise, subject category, or investigator’s name.

This data archive assures consistent access for both ongoing and future analyses. With data collection now in the past, the over 350 datasets contained in the data archive will be a powerful legacy of the Bering Sea Project.

**FIGURE 2** Snapshot of the Bering Sea Project data archive. It is possible to search over 350 combined BEST and BSIERP datasets by project, cruise and science subject. The resulting table provides a direct link to the dataset and to metadata documentation for easy download and access.
Major ship operations, under often-difficult conditions, allowed scientists to undertake interdisciplinary sampling at higher frequency and across broader spatial scales than ever before attempted in this region. Other field teams spread out across the Bering Sea shelf in smaller vessels, on island and coastal field camps, and in villages and local communities. Combined with the use of novel field and lab technologies, researchers developed a more detailed and insightful description of the seasonal cycle of the ecosystem, and of people who live and work in the ecosystem, than could be gained from the work of individual scientists or smaller teams.

Coastal Communities and Fisheries

The relationships of local people and the commercial fishing community with the Bering Sea ecosystem played an important role in the Bering Sea Project. Abundant pollock, cod, flatfish, halibut, crab, and salmon in the Bering Sea support a powerful economic engine for the state of Alaska and the nation. Particularly in the eastern Bering Sea, subsistence communities coexist with commercial interests, and much of the livelihood of these communities depends upon the condition and health of the ocean. Ultimately, the same processes that affect seabirds and marine mammals and other top-level predators also impact the people and communities who use the Bering Sea ecosystem as a resource.

To get a better sense of the effort involved in Bering Sea Project fieldwork, we did a back-of-the-envelope calculation of fieldwork “person-days.” This is a useful way to measure total effort across many different types of fieldwork—for example, if ten scientists work on a ship for ten days, that’s 100 person-days. Tallying up the research cruises, summer-long camps at seabird colonies and marine mammal rookeries, ethnographic and subsistence harvest research in coastal communities, and all other facets of fieldwork in the Bering Sea Project, resulted in a massive total of over 24,000 person-days. And that number doesn’t include the vital efforts and commitment of the many officers and crew of US Coast Guard, NOAA, USFWS, UNOLS, and charter vessels, helicopter pilots, logistics specialists, and other support team members who enabled hundreds of sea days and fieldwork in all kinds of weather conditions!

Ecosystem Modeling

To weave together existing and new information at the ecosystem level, the Bering Sea Project invested in an ambitious numerical modeling effort anchored in physical oceanography. The models explored both “bottom-up” (resource-limiting) mechanisms, such as climate and physics, as well as “top-down” (predation) forces, such as fisheries and management strategies. In the most ambitious effort, researchers linked a ten-kilometer resolution Regional Ocean Modeling System (ROMS) model of the Bering Sea with a Nutrient-Phytoplankton-Zooplankton (NPZ) model that also included organisms living on the ocean floor. This ROMS-NPZ model was then connected via two-way coupling to an energy flow model of prey fields for commercially important fish species, intended to explore scenarios of changing predation, losses to commercial fishing as defined through economic models, and interactions between ecosystem dynamics and management strategies. Finally, a series of parallel modeling efforts determined how a detailed, vertically-integrated model compares to other approaches.

Wrap-up and Synthesis

After multiple years of planning, from 2002–2006, followed by four field years of sampling, from 2007–2010, and several years of data analysis, synthesis, laboratory studies and extensive modeling work, the Bering Sea Project drew to a close in 2015. As a one-stop-shopping, integrated mechanism for communicating Bering Sea Project results, three ‘special issues’ of Deep-Sea Research Part II, a peer-reviewed scientific journal, have been published so far, and a fourth is in production—see Feature in the “Reviewing Progress” section for more information on the special issues. Many other papers, book chapters, theses, and dissertations have stemmed from the project—a total of over 165 peer-reviewed publications have been published to date, complemented by hundreds of conference presentations and other avenues of communication. Further analyses and syntheses of the information and insights gathered during the Bering Sea Project will produce results and influence further research and policy for years to come.

Welcome to this ‘Magazine’

In the following pages, we present selected new insights into the structure and function of the eastern Bering Sea marine ecosystem, based largely on ‘headlines’ stories that were authored by participating scientists. Topics are grouped by theme within the “Bering Sea” section immediately following this introduction, and ‘further reading’ references guide you to source material in the full “Headlines” references on pages 66-67. The “Reviewing Progress” section draws from the project’s series of special journal issues to provide a summary of bigger-picture insights and synthesis to date. Finally, a “People of the Bering Sea Project” section invites you meet a representative sample of the community of dynamic and hard-working individuals who powered this project to completion. You’ll also find “Feature” stories embedded as boxes within the main text, and informal explanations of technical terms are highlighted throughout the text.
The Bering Sea in a Changing Climate
The eastern Bering Sea ecosystem is structured in part by seasonal ice, advancing in the late autumn and retreating in the spring. The extent of sea ice is controlled by local and regional weather—wind and cold combine with currents and other oceanographic features to shape the formation, extent, and duration of ice. Understanding the mechanics of how a warming climate will affect weather and ice was among the major objectives of the Bering Sea Project.
Few outside of Alaska and the commercial fishing and research communities are aware of the unique nature of the Bering Sea and its seasonal ice cover. The reality TV series Deadliest Catch, characterized by fishermen braving high winds and rough seas to make their living in the commercial crab fishery, has brought global attention to the Bering Sea, but the region and its dramatic weather and ice remain remote to most Americans. Extremes in temperature, ice, and weather patterns influence people’s lives on a regular basis in this cold and stormy region—and those same unforgiving weather conditions interact with the waters of the Bering Sea to result in a bountiful abundance of marine organisms that sustains coastal people and livelihoods.

Ice Shapes the Ecosystem

Even during the summer, surface water temperatures in the ice-free Bering Sea are quite chilly. Maximum temperatures during 2007–2010 averaged around 10 °C, or 50°F. By December, Bering Sea water cools to between 3°C and -1.8°C (37°F to 29°F) and sea ice begins to form along the coast. As the winter season deepens in December, January, and February, sea ice can form offshore in the northern Bering Sea, and strong winds out of the north push the ice southward up to 1,000 kilometers, covering much of the shelf. The extent of sea ice and its arrival and retreat in any given year vary greatly, sometimes by hundreds of kilometers and many weeks (Figure 3).

The patterns of sea ice arrival and retreat illustrate that there is always ice on the northern Bering Sea shelf during the dark winter and much of spring (north of 60°N), and that the variation in extent occurs predominantly in the south. This geographic difference is important, because most of the commercial fisheries for pollock, cod, salmon and red king crab, among others, occur in the southeastern Bering Sea. The pattern also led scientists to categorize the weather on the southern shelf into “warm” years, characterized by little ice after mid-March, and “cold” years, when ice persisted in the south for many weeks into late April.

The presence or absence of sea ice plays an important role in the physics and biology of the entire eastern Bering Sea shelf system. It affects the timing of maximum primary production, including the abundance, distribution, and species composition of phytoplankton, which form the core of the food web that supports the rest of the ecosystem and eventually the people who inhabit the coastlines.

This dynamic weather and ice over the southern shelf further affects zooplankton (Figures 4 and 5), creating dramatic differences in species composition, abundance, and distribution patterns. As the primary food source for many species, fluctuations in small crustacean zooplankton populations impact fish species that feed on them, including pollock, salmon, and other fishes of importance to subsistence and commercial activities.

These fluctuations also affect large baleen whales and millions of seabirds, including short-tailed shearwaters, and crested and least auklets.

Zooplankton

Zooplankton are tiny marine animals that eat other plankton. Some zooplankton are larval or very immature stages of larger animals, including mollusks (like snails and squid), crustaceans (like crabs and lobsters), fish, jellyfish, sea cucumbers, and sea stars. Some zooplankton are single-celled animals, like foraminifera and radiolarians. Other zooplankton are tiny crustaceans, like copepods and the group of euphausiid species known as “krill.”
The Importance of Being Warm or Cold

Historically, the southeastern Bering Sea experienced large interannual variability in temperature and sea-ice extent and duration. Beginning in February 2000, the region entered an almost six-year period of little ice and relatively warm conditions. Following a transition year in 2006, extensive sea ice made a dramatic return to the southern shelf and remained through 2013 (Figure 6).

Over the next several decades, climate models predict that the southern Bering Sea will more frequently experience these warm years with reduced sea ice. This fits with an overall prediction for a warmer planet, resulting from increased concentrations of greenhouse gases such as carbon dioxide and methane. Significant changes can be expected if the warm period observed between 2000 and 2005 is representative of how this ecosystem will respond to warming.

**FIGURE 6** The daily, depth-averaged water temperature from a mooring on the southeastern Bering Sea shelf known as M2 (see Figure 1) is shown in the top panel. Differences from the mean annual temperature are shown in the bottom panel, and ovals indicate the percent of sea ice coverage around the M2 mooring in March and April.

**FIGURE 5** Euphausiids, or “krill,” are an important type of zooplankton in the Bering Sea.
Colder ocean temperatures in the spring, for example, result in an early phytoplankton bloom associated with sea ice, a less saline water column, and a summer with a “cold pool” (see feature) in the bottom water layers where temperatures remain below 2 °C through most of the summer. During warm years, the bloom is delayed until late May and a smaller cold pool occurs which is primarily limited to the northern Bering Sea (e.g., Figure 7).

Scientists originally hypothesized that warmer conditions would favor walleye pollock and other fishes that prefer temperatures above 2 °C (36 °F) and postulated that most of the fishery would move northward as the Bering Sea warms. Researchers revised this original hypothesis after more data became available during the Bering Sea Project. They found that even as the south warmed during 2001 – 2005, the northern Bering Sea remained cold and ice-covered in winter (Figure 3). In the warmer southern waters, scientists observed a sharp decrease in the availability of key prey for young-of-the-year pollock, including krill and large copepods. The reduced numbers of these prey limited the survival of fish during their first winter, and multiple consecutive warm years ultimately resulted in low recruitment to adult pollock populations.

Seasonal sea ice on the eastern Bering Sea shelf impacts the entire marine ecosystem throughout the year, as it leaves behind a footprint of cold bottom water, called the “cold pool,” after the ice retreats back north in the spring (Figure 7). The extent of this cold pool determines not only the population sizes of some species but also their distribution patterns in any given year. Most species, such as pollock or euphausiids, have preferred temperature ranges within which they attain higher growth, survival, and reproduction. Given that pollock and other fish species impacted by the cold pool are of commercial significance, scientists closely watch the cold pool with an emphasis on understanding its dynamics and predictability.

The location and duration of the cold pool depends on atmospheric conditions (temperature and wind) combined with oceanic and sea-ice conditions during the previous winter; these conditions interact in complicated ways and change from year to year. Bering Sea Project researchers developed a mathematical coupled ice-ocean model called BESTMAS (Bering Ecosystem Study ice–ocean Modeling and Assimilation System), which not only successfully replicated observed patterns for past years, but also predicts the future cold pool location and extent months in advance. This effort further revealed that the simulated field of bottom water temperature on the shelf at the end of May is a good predictor of the distribution and extent of the cold pool throughout late spring and summer, thus resulting in a potentially powerful tool for fisheries management and other applications.

**YOUNG-OF-THE-YEAR**
Young-of-the-year refers to fish in their first year of life. This is one of the most vulnerable times in the life cycle of fish, and their survival depends upon many factors, including currents, temperature, available prey, and predation.

**RECRUITMENT**
Fisheries scientists use the term “recruitment” to refer to the proportion of young fish that survive to the age at which they can be caught in a fishery.

**FIGURE 7** Extent of the summer cold pool on the eastern Bering Sea shelf during a cold year (top panel; 2007) and warm year (bottom panel; 2003). The cold pool is indicated by blue colors, below 2°C. The 50 m, 100 m and 200 m depth contours are shown.
A Crystal Ball for the Bering Sea?

In 2014, US temperatures were the warmest on record, and temperatures exceeded the 20th-century average for the eighteenth consecutive year. While global climate models provide consistent global scale predictions of warming over the next few decades, they differ significantly in their predictions on regional scales. Through a series of statistical analyses, a Bering Sea Project research team chose those global models that best fit the data for the region and coupled them to regional physical and biological models. The team concluded that it’s a safe bet the future will include a warmer Bering Sea. But it is uncertain exactly how climate change will be manifested, and in particular, how fast the Bering Sea will warm in summer versus winter, and in the north versus the south. These details in the climate forcing are key in terms of their impacts on plankton community structure and distributions and, ultimately, the entire marine ecosystem, including people.

The research team addressed the formidable problem of how climate change is liable to impact lower-trophic levels, i.e. the base of the food web, using groundbreaking methods and massive computing resources. Their approach featured high-resolution ocean model simulations using the Regional Ocean Modeling System (ROMS) for the Bering Sea and surrounding waters. This model includes interactions among physical water properties, nutrient concentrations, and the growth and consumption of groups of plankton crucial to fish, sea birds, and marine mammals. The regional simulations were embedded in large-scale atmospheric and oceanic conditions from global climate model predictions. ROMS is much more realistic than the global models in representing smaller-scale effects of bottom topography on the currents and temperature (Figure 8).

The climate model forecasts that have been produced are mostly similar in terms of their projections of global means, but they predict different future climates from a regional perspective (Figure 9). There is little justification for selecting one of these models over others to specify the large-scale future climate forcing of the Bering Sea. It is therefore prudent to take a multiple-model approach, and focus on the range of probable outcomes.

An illustration of this range is provided by a set of ROMS projections of euphausiid distributions in August (Figure 10). Euphausiids represent key prey for a number of species, including young walleye pollock. There is consensus from the ROMS model projections that euphausiid populations are likely to decline on the eastern Bering Sea shelf. On the other hand, there is conflicting evidence from the model with respect to the sense of the expected changes in euphausiid populations over the deep basin of the Bering Sea.

In the big picture, the climate research team concluded that their crystal ball needs more work before it’s fully functional—but they do know that climate models are calling for varying amounts of warming, and that their research provides insights for effective monitoring of the Bering Sea ecosystem and the development of improved forecast models.

**FURTHER READING**

See these “headlines” for more information:
* Bond et al., Bering Sea climate futures
* Guy et al., north-south shelf differences
* Stabeno et al., warm and cold years
* Zhang & Woodgate, modeling the cold pool

---

**GLOBAL CLIMATE MODELS**

A type of computer-driven model for weather forecasting, understanding climate, and projecting climate change. There are over a dozen such models, often used together (as an “ensemble”) in an effort to compare different predictions. As different models have somewhat different structures and make different assumptions, the idea behind model comparisons is to increase confidence in model results in instances where all, or the majority, predict similar changes.
FIGURE 9 Change in mean August surface temperatures between “present” (2003-2012) and “future” (2031-2040) conditions, using downscaling ROMS simulations driven by the CCCMA climate model (left) vs. the MIROC climate model (right). Red colors indicate a net warming over the 30-year period; blue colors indicate a net cooling.

FIGURE 10 Near-surface concentrations of euphausiids in August from ROMS projections using the present climate forcing (upper left panel), using the climate forcing of the 2030s from the CCCMA climate model (upper right), using the ECHO-G (ECHAM4+HOPE-G) climate model (lower left), and using the MIROC (Model for Interdisciplinary Research on Climate) climate model (lower right). Color bar scale units for all four panels are milligrams of carbon per cubic meter.
Oceanography: Controlling Forces

A range of fundamental oceanographic processes influence life in the eastern Bering Sea. “Oceanography” encompasses the study of physical, biological, chemical, and geological processes and conditions, which are variable by nature, and also subject to climate changes and to changes driven by their own interactions. At the same time, they control much of the rhythm and change in nutrient availability, plankton populations, etc. These ‘bottom-up’ processes consequently influence fish, birds, and mammals, making them key topics of study in the Bering Sea Project.
The southeastern Bering Sea consists of an extensive continental shelf area and a deep oceanic region with a maximum depth of 3,500 meters. The Bering Sea shelf region is shallow and very large—it is less than 180 meters deep, 500 kilometers broad, and extends over an area roughly the size of California. The shelf break, beginning at approximately 180 meters depth, extends northwestward from Unimak Pass. The shelf has historically been divided into three “domains:” the coastal domain less than 50 meters deep; the middle domain from 50-100 meters deep; and an outer domain 100-180 meters deep. Besides depth, each domain is characterized by differences in how strongly the overlying horizontal water layers are stratified, as well as by different habitats and biota.

**STRATIFICATION**
Stratification refers to the vertical structure of water density, which is dependent upon both water temperature and salinity, with colder, saline water having a greater mass density than warmer, less-saline water. The stronger the vertical gradient in density, the more stable the stratification. Weakly stratified water is easily mixed by winds and tides, resulting in the vertical exchange of heat, salt, and momentum.

The Alaska Coastal Current (Figure 1) enters predominantly through Unimak Pass, introducing heat and zooplankton onto the Bering Sea shelf. The oceanic (basin) region is influenced by the Alaskan Stream flowing through Amchitka and Amukta passes, producing the Aleutian North Slope Current. This current turns northwestward forming the Bering Slope Current, which is a broad current interspersed with meanders and eddies. Both currents are important because they transport heat, nutrients, and the fish eggs and larvae of Greenland and Pacific halibut, arrowtooth and Kamchatka flounder, and other fishes from the oceanic and slope region to the Outer Shelf Domain, where the habitat is more suitable for survival.

**Taking the Ocean’s Pulse**
The Bering Sea shelf covers a vast territory, with weather that challenges even the most experienced seafarers, hunters, and fishermen. While ships provide scientists with the most versatile platform for making ocean measurements, they are expensive, and those ships capable of operating in sea ice—ice breakers—cost the most. Since 1995, anchored oceanographic instruments and biophysical moorings (Figure 11) capable of collecting physical, chemical, and biological information have let NOAA scientists track the status of the Bering Sea shelf year-round. These long-term measurements provide a foundation for understanding the mechanisms that drive this productive region. They also gave the Bering Sea Project the chance to address targeted ecosystem questions about the physical, chemical, and biological changes in climate and ocean conditions in the context of these datasets.

**FIGURE 11** Diagram of a biophysical mooring including surface buoy (used in ice-free seasons), illustrating how instruments are arranged along the length of the mooring. This is a schematic diagram – the actual mooring has instruments every three meters.
Each of the four long-term biophysical moorings in the Bering Sea highlighted in Figure 1 hosts instruments that make hourly measurements of temperature, salinity, nitrate, chlorophyll (fluorescence), currents, and sea ice year-round. Data are stored until the mooring is retrieved and redeployed each spring and fall, weather and ice permitting. The M2 mooring also hosts acoustic instruments that record zooplankton size and abundance as well as marine mammal vocalizations, and sends some of its data to shore via satellite daily.

**CHLOROPHYLL**
Chlorophyll is the green pigment found in cyanobacteria and the chloroplasts of algae and plants. Chlorophyll is used in oxygenic photosynthesis, in which plants take up carbon dioxide and release oxygen to the atmosphere.

In addition to biophysical moorings, Bering Sea researchers used a variety of other technologies and datasets to put their focused ecological studies into longer-term context. They drew on data from past research cruises, the US National Snow and Ice Data Center, NOAA satellite imagery (as shown in Figure 12), NOAA fisheries trawl surveys carried out by the Alaska Fisheries Science Center, community surveys, and other long-term studies.

**You Shall Not Pass? A Northern Boundary Line**
Prior to the Bering Sea Project, scientists observed a northward shift in the distribution of marine species within the southeast Bering Sea. They hypothesized that increased ocean warming would allow the center of distribution for many commercially important fish species to expand to the north towards Bering Strait or across the dateline into Russian waters, particularly those species better adapted to sub-arctic waters. Similarly, snow crab and other cold-adapted species would retract their distributions to the north. Such a shift would have ecological implications in terms of predator-prey relationships, and also economic consequences for the fishing fleet based in the main regional fishing port, Dutch Harbor, on Unalaska Island in the southern Bering Sea.

But marine research often confounds expectations, and in this case, the Bering Sea Project revealed that the Bering Sea is divided from north to south by a transition zone at approximately 59°–60°N. This zonal boundary is established during the winter season, but persists through the summer. The northern shelf is characterized by colder bottom temperatures and less saline surface waters when compared to the southern shelf. These differences are a direct result of the presence of sea ice (Figure 13). The ice persists on the northern shelf longer, resulting in colder bottom temperatures. The ice, which has much lower salinity than the surrounding waters, then melts in late spring when winds are relatively weak and vertical mixing is reduced, thus leaving behind a low salinity surface lens of water.
A more complete understanding of the Bering Sea ecosystem requires understanding the behavior and drivers of the continental shelf currents, which transport heat, nutrients, plankton, fish eggs and larvae from one place to another, aggregating prey and promoting phytoplankton blooms. From July 2008 to July 2010, Bering Sea Project scientists deployed eight oceanographic moorings equipped with current meters on the northern Bering Sea shelf. Analysis of the current meter data with the local wind field showed close connections between the strength and direction of winds and the currents (Figure 14) and revealed some previously unknown patterns. Researchers thought that waters on the shelf flowed predominantly northward. This study confirmed that winds blowing from the southeast to the northwest (southeasterlies) tend to promote shelf flow that originates south and east of St. Lawrence Island toward Bering Strait. Researchers also learned that waters in the Gulf of Anadyr are more likely to flow west past Cape Navarin during those conditions. But it turns out that southeasterlies occur less than half of the time. The rest of the time, especially from October through April, scientists observed northwesterly winds, which created upwelling conditions, a southward flow, and an intrusion of nutrients from the Gulf of Anadyr onto the eastern Bering Sea shelf. This phenomenon may help explain how nutrients replenish over the middle and inner domains of the northern shelf during winter.

A 3D-modeling effort to describe this phenomenon proved successful, and when run in hindcast mode, demonstrated how the greater shelf circulation responds to this wind and current reversal in areas far removed from the mooring array (Figure 15).

**FEATURE**

**WINDS OF CHANGE**

**FIGURE 13** Results from the north-south transect line along the 70 meter isobath sampled in September 2008 shows temperature, salinity, chlorophyll a, nitrate, and ammonium. The four vertical lines through each panel indicate the positions of the four moorings. Note the strong break in temperature and salinity near mooring M5 at roughly 60°N. This is the feature that separates the northern and southern portions of the eastern Bering Sea.

Generally speaking, the winds result in a well-mixed surface layer (warmer water), and the tidal forces result in a well-mixed bottom layer (colder water). The tides are weaker on the northern shelf than on the southern shelf. On the southern shelf, the strong tides cause the two layers to abut each other, while on the northern shelf, the weaker tidal mixing results in an interface a few meters thick between the top and bottom layers. Sufficient light penetrates to support a subsurface phytoplankton bloom in this transition layer as shown in Figure 13.

The presence or absence of ice affects the strength and location of the zonal boundary separating the north and south. Predictions of warming indicate a marked decrease of ice on the southern shelf and persistence of ice on the northern shelf. Scientists wanted to understand how these different north-south scenarios would impact species.

**FIGURE 14** The arrows originate from the eight moorings deployed between July 2008 – July 2010. Red arrows show vertically averaged currents during winds with a southeasterly component and blue arrows show currents during winds with a northwesterly component. Depth contours are drawn at 200, 100, 70, 50 and 20 meter depths.

**FIGURE 15** Vertically averaged hindcast current vectors from the 3D-model for a month with strong southeasterly winds (December 2000, top) and strong northwesterly winds (December 1999, bottom). The shelf break (180 meter isobath) is denoted with a black line.

**HINDCAST**

A hindcast (the opposite of ‘forecast’) is a way of testing a mathematical model. Known or closely estimated inputs for past events are entered into the model to see how well the model output matches the measured results. Hindcasting is also known as backtesting.
and which species might be most vulnerable in a rapidly changing ecosystem.

By exploring the temperature preferences of Bering Sea fishes and snow crab, researchers suspect that some species using mainly warmer surface waters, such as juvenile sockeye salmon, might expand their summer range into the northern Bering Sea. Others, such as pink salmon, may increase in abundance, while walleye pollock, arrowtooth flounder, and other species occupying bottom waters are limited by the cold northern boundary line and therefore will not shift their ranges and are unlikely to become common in the north. Interestingly, those species that did expand their distributions northward during the warm years in the early 2000s did not contract their distributions southward during the cold years.

A warmer southern shelf would be less hospitable for snow crab and other Arctic species now dwelling there, restricting them to colder northern waters and potentially having a direct effect on commercial fishing.

**The Nitrogen Cycle: Fertilizing the Sea**

Bioavailable nitrogen (in the form of nitrate, nitrite, and ammonia) is a key nutrient determining the growth of algae in the Bering Sea, the ultimate source of food for all other organisms on the shelf. The Bering shelf becomes nitrogen-limited once phytoplankton consume the bioavailable nitrogen under ample light conditions; if there were more nitrogen, more could be absorbed by the phytoplankton, supporting further growth. Understanding the origins, transformations and ultimate fate of nitrogen on the shelf in a quantitative manner helps scientists understand shelf ecosystem dynamics, and how those dynamics will be affected by climate-induced changes in circulation and ice cover.

By taking water samples at numerous stations in the eastern Bering Sea and conducting detailed chemical analyses for all different forms of nitrogen found in the environment, scientists determined that the annual resupply of nitrogen, in the form of nitrate from the open Bering Sea off the shelf, contributes an important fraction of the “fertilizer” available for the spring bloom upon ice retreat. This was especially important on the outer shelf and on the seaward portion of the middle shelf (Figure 16). Shoreward on the middle and inner shelf, however, nearly all of the nitrogen in the water column originates from mineralization in situ.

The concentration of nitrogen fertilizer relative to phosphorus, another nutrient, decreases dramatically inshore and northward, because bioavailable nitrogen is converted to unavailable N₂ gas by denitrifying bacteria in the sediment. This nitrogen escapes the system as the gas leaves the water and enters the atmosphere. These so-called “denitrifiers” actually “breathe” nitrate when oxygen runs out in order to decompose organic material.

Project scientists found that phytoplankton collected in ice-covered waters relied on preferential use of nitrogen from ammonium released from sediment, whereas phytoplankton growing in open waters had a greater reliance on nitrate in the water column for their growth.

**MINERALIZATION**

Through the process of mineralization, organic material rich in nitrogen and phosphorus from the previous season’s growth accumulates in sediments on the shallow continental shelf. It decomposes during the dark winter and is released as inorganic nutrients back to the water, fertilizing the spring bloom.

**NITRIFICATION AND DENITRIFICATION**

The process by which bacteria use oxygen to change ammonium derived primarily from dead plant material into nitrates, which plants can then absorb as food, is called nitrification. During denitrification, bacteria convert nitrates into nitrogen gas, which is then released into the atmosphere. This is one of the mechanisms by which sea floor bacteria obtain their energy.
FIGURE 16 The proportion of oxidized nitrogen recycled on the shelf rather than replenished from the North Pacific water off the shelf.

FIGURE 17 Nitrogen (N) productivity, surface nitrate concentrations, and ice extent in the eastern Bering Sea in 2007 (A); 2008 (B); 2009 (C); and 2010 (D). In each panel, the color map represents surface nitrate concentrations (nitrate is the most abundant form of nitrogen for phytoplankton growth). Note that the data in 2010 are from a smaller region of the shelf than in the other years. The vertical bars represent nitrogen productivity (a measure of the rate of phytoplankton growth). For each N-productivity bar, purple represents the amount of nitrate productivity and gray represents the amount of ammonium productivity. The solid line is the 200 m depth. The dashed lines represent the ice extent in March, April, and May in each year, and together with the nitrogen productivity rates show the elevated productivity associated with the ice edge on the western shelf.

Photograph of the ice edge in the Bering Sea. The chunks of ice overturned by the ship’s passage reveal the dense growth of diatoms, coloring the bottom of the ice greenish-brown. The ice releases these algal cells as it melts, and these contribute to dense phytoplankton blooms at the ice edge.
Nitrogen is released from the sediments under the ice and when the ice retreats, there is food and light and the phytoplankton start growing—sounds simple enough! But after studying the ice-edge conditions for several years, scientists found that not all ice edges were created equal. Some ice edges were associated with dense phytoplankton blooms, but others were not. An example was the region of the outer shelf from just north of the Pribilof Islands to beyond Zhemchug Canyon, where fast, heavy growth and large concentrations of phytoplankton occurred in each of the four sampling years, fueled by deep-water nitrogen introduced from off the shelf (Figure 17).

Ironing out the Differences
Understanding the nitrogen-ice-light dynamic in the Bering Sea proved to be important in the Bering Sea Project. But algae also require the trace metal iron for healthy growth, and differences in iron availability seem to determine bloom magnitude even when nitrogen is abundant.

Sea ice can be an important source of iron in the surface of the ocean (Figure 18). As it forms, the ice incorporates iron-rich particles derived from atmospheric deposition, freshwater runoff, and sediment suspension. When the sea ice melts in the spring, the ice releases these iron-rich mineral particles into the water column, and a portion of the particulate iron dissolves. This additional iron source, researchers found, is especially important to the spring bloom, as iron deeper in the water can no longer reach the surface due to the strong stratification brought about by the relatively fresher water on the surface as the ice melts.

The difference in the iron content of sea ice in different locations affects the intensity of plankton blooms. In the absence of sea ice iron input, diatom productivity over the outer shelf and shelf break in the spring eventually becomes limited. Bering Sea Project scientists believe that the variability in sea ice extent in the future is likely to translate into a varying supply of dissolved iron to the Bering Sea outer shelf and shelf break in early spring, contributing to changes in the timing and community composition of the spring phytoplankton bloom.

**FURTHER READING**
See these “headlines” for more information:
- Cokelet, inferred Bering Sea circulation
- Danielson et al., Bering Sea circulation
- Granger et al., origin and fate of nitrogen
- Guy et al., biophysical moorings
- Guy et al., north-south shelf differences
- Panteleev et al., model data assimilation
- Sambrotto & Sigman, ice edge phytoplankton
- Stabeno et al., warm and cold years
- Wu et al., ice, iron, and the spring bloom
Only a very few marine regions have seasonal ice cover as extensive as in the Bering Sea. Winter and spring ice exerts a powerful influence on the structure of the marine waters, which can drive the extent and timing of primary production, and forms an important physical habitat for many species including walrus, eiders, and seals. The tremendous regional importance of ice and ice-related ecology led directly to several sea ice studies in the Bering Sea Project.

Sea ice structure revealed by the passage of an icebreaker, showing firmly packed snow cover at the surface and some 70 cm of layered ice below, with dense ice algae in the bottom ice layer.
Sea ice is a characteristic and vital part of the Bering Sea marine ecosystem. Given the recent changes in temperature and ice conditions in the Bering Sea, scientists wanted to learn more about the importance of sea ice ecosystems for the broader Bering Sea food web. They also sought to understand how much ice algal biomass forms during spring before the ice melts, and how this production is linked to the biological communities in the water column and on the sea floor.

The Sea Ice Ecosystem

Sea ice serves as breeding and migration grounds for marine mammals (including walrus, seals, and polar bears), resting areas for birds and walrus, and as a realm for hundreds of different species ranging from microscopic, one-celled plants to larger animals. To find out exactly what this habitat holds, researchers used a specialized ice corer to sample hundreds of different ice floes during expeditions to various locations each spring in 2008, 2009 and 2010.

Back on the ship, scientists melted the ice cores and analyzed them for concentrations of algal pigments, mainly chlorophyll a. They then compared these data to the algal development below the sea ice.

They found that each spring, vast amounts of highly concentrated sea ice algae accumulate at the bottom of sea ice floes, exceeding water column phytoplankton volumetric concentrations by a factor of 100 to more than 1,000 from mid-March to the end of June. The total amount of plant biomass within the bottom ten centimeters of the ice was about the same as that for all of the phytoplankton present in the upper twenty meters of the water column.

SEA ICE

Sea ice is frozen seawater that forms in the ocean. Sea ice forms during the winter months and melts during the summer months, but some sea ice remains all year in certain regions of the Arctic Ocean.

About 15% of the world’s oceans are covered by sea ice during part of the year. Even though sea ice occurs primarily in the polar regions, it influences our global climate. Sea ice has a bright surface—much of the sunlight that strikes it is reflected back into the atmosphere. As a result, areas covered by sea ice don’t absorb much solar energy, and temperatures in the polar regions remain relatively cool. If gradually warming air and water temperatures melt sea ice over time, fewer bright surfaces are available to reflect sunlight back into space, more solar energy is absorbed at the surface, and temperatures rise. This is known as a ‘positive feedback loop’ and is one of the reasons that arctic regions will experience a greater rate of change in times of climate warming than more temperate regions.

Sea ice also affects the movement of ocean waters. When sea ice forms, most of the salt dissolved in seawater is forced into the ocean water below the ice, although some salt is trapped in small pockets between ice crystals. Water immediately below the sea ice therefore acquires a higher concentration of salt, becoming more dense than surrounding ocean water, and so it sinks.

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Ice algae are the only concentrated food available during late winter—as a result, copepods and krill, previously thought to depend mostly on phytoplankton in the water, seem to depend upon this large ice-associated biomass in the winter and early spring. For example, the abundance of the copepod *Calanus glacialis*, an important prey species for juvenile fishes, seabirds and whales, fluctuates widely between years, but is more abundant in the southeastern Bering Sea in years with spring sea ice than in years without ice. The availability of food controls reproduction and growth, and if these copepods are abundant in the spring, researchers assume that they are somehow obtaining sufficient food under the ice to grow and reproduce, most likely ice algae.

Using DNA extracted from the guts of copepods in the spring to determine the identity of individual prey species, researchers found that most of their stomachs were full of ice-algal species. Not surprisingly, further analysis revealed that more extensive ice cover, persisting longer in the spring in colder years, appears to favor the growth of copepods, and results in greater abundance in late spring. This critical finding suggests that the dependence of copepods on ice increases the vulnerability of this important prey species to climate change.

Bering Sea Project researchers now know that the southern extent of sea ice, as well the timing of its retreat northward as it melts in the spring, helps to determine the structure and function of the Bering Sea marine ecosystem. The success of this region’s highly productive fisheries, some of the world’s richest, begins with the massive blooms of tiny, single-celled plants that occur each spring when increasing light and abundant nutrients enable ice algae and phytoplankton to grow and flourish both in the ice and in the water.
Sea Ice as a Platform

Sea ice not only provides nutrients to the water and harbors organisms of many sizes and species, but also serves as a platform for marine mammals, seabirds, and people for resting, pupping, feeding, hunting, and traveling. This is especially true in the northern Bering Sea; there, the shelf system is dominated by species living at the bottom of the ocean, compared to the more southerly Bering Sea shelves where open-water fisheries dominate.

Walruses, eiders, gray whales, and other bottom-feeding predators in the north depend upon abundant biological communities whose biomass, distribution, and species composition seem to be dependent on sea-ice cover patterns. In turn, St. Lawrence Island Yupik and mainland Yupik and Iñupiat communities depend indirectly on these dynamics through subsistence harvests of walrus and ice seals (spotted, ringed, bearded, and ribbon seals).

To better understand how dynamic ice cover influences marine waters and the seafloor, Bering Sea Project researchers sampled the ice-covered northern Bering Sea in March to make observations of the water column, marine sediments, and the animals living in this benthic ecosystem (Figure 19). One of their research goals was to determine where walruses and spectacled eiders were feeding on clams on the seafloor, and to match that with the distribution of clams and the shifting sea ice that might impact the ability of air-breathing predators to access their prey on the seafloor and return to the surface of the sea.

Scientists found that ice algae rains down on these benthic communities after the ice melts and supplies many species living on the sea floor with food. Consequently, large numbers of predators, including walrus and endangered spectacled eiders take advantage of these rich communities and use the ice as a platform to feed from and rest on between meals (Figure 20).

For hunters, the presence of ice and this productive benthic ecosystem are critical for the continued presence of walrus through the winter and spring. The Bering Sea Project sought to find out how the ecosystem is changing and what those changes mean, especially for people who depend upon the Bering Sea for food and livelihoods. Combining local and traditional knowledge interviews, daily data on walrus harvests, number of hunting trips, wind speed, wind direction, sea ice concentration, visibility, and some innovative data analysis, a Bering Sea Project research team found that one-quarter to one-third of the variability in the number of hunting trips that were made could be explained by wind and ice conditions.

Yet while other factors—like the skill and experience of the hunters—combine to explain much more of the variability, wind and ice conditions do matter. The analysis also helped explain how they matter—in other words, how a change in wind or ice would affect hunting. For example, higher winds make boating more dangerous and difficult, so hunters tend to stay on shore when it is too windy. Similarly, too much ice makes boat travel difficult, but too little ice can mean there are few walrus since the walrus like to haul out on ice; or too little ice can allow waves to build much higher, again making it dangerous for hunters. So walrus hunters on St. Lawrence Island may indeed be affected by changing ice conditions, but they are accustomed to dealing with variability and are quick to adjust and adapt as needed.

FURTHER READING

See these “headlines” for more information:
• Cooper et al., northern Bering Sea winter
• Gradinger et al., ice in the Bering Sea
• Huntington et al., walrus hunting and weather

Inset: A close-up view of some of the thousands of male (mostly white) and female (brown) eiders gathered in an open ice lead; these sea ducks use the ice to rest upon between feeding bouts, expending less energy by remaining on the ice than by resting in the open water.

Spectacled eiders use openings in the sea ice of the northern Bering Sea to reach clam populations on the sea floor 40-60 meters below.
Plankton and Benthos: The Living Water Column

From top to bottom, the water column and the seafloor in the Bering Sea are alive. Ice algae flourish in association with the seasonal ice covering much of the northern portion of the shelf, and in ice-free areas, ocean circulation and biological processes combine to support open-water phytoplankton blooms that feed vast populations of zooplankton. Organic matter not used in the upper waters eventually falls to the seafloor, where a host of organisms are ready to consume and recycle vital nutrients.

Scientists collect zooplankton using a “bongo” plankton net from the aft deck of the US Coast Guard icebreaker Healy during a late winter research cruise in the Bering Sea.
The intricate connections between ice retreat, intensity of the spring phytoplankton bloom, and the productivity of the Bering Sea motivated researchers to understand the drivers behind the timing and extent of the spring bloom, and to evaluate how plankton populations and life on the sea floor might be altered in a future, warmer Bering Sea.

**THE SPRING BLOOM**
Phytoplankton are microscopic marine plants. Just like terrestrial plants, phytoplankton undergo a dramatic “bloom” or increase in abundance in the springtime. Many of the important zooplankton species, including the large copepod *Calanus glacialis/marshallae*, take advantage of ice algae and the spring phytoplankton blooms to reproduce. Adult females that have survived the food-limited winter respond almost instantly to the increased food supply by producing up to 50 eggs per female per day during the bloom. In turn, the eggs and early developmental stages of copepods become important food for larval fishes. Bering Sea Project researchers set out on a fleet of vessels, including the USCGC Healy, R/V Knorr, and R/V Thomas G. Thompson, to describe and quantify the dynamics of the planktonic ecosystem during spring sea-ice conditions. They collected samples over a large region of the shelf using ice cores, water samplers, and net systems to identify and quantify the biomass of the various planktonic and benthic ecosystem components. They also conducted shipboard experiments to measure processes of primary productivity and zooplankton feeding, growth, and reproductive rates.

**Setting the Table**
Project scientists found the spring ice-associated bloom to be of vital importance to the productivity of the Bering Sea. It not only begins the growth season for phytoplankton, but also supplies a large and dependable food source to which the life cycles of many of the important zooplankton species are timed. Until recently, however, researchers believed that large zooplankton in the Bering Sea, including copepods and krill, fed preferentially on large phytoplankton cells in the water. But shipboard-feeding studies clearly demonstrated that copepods and krill readily feed on ice algae, phytoplankton, and microzooplankton. What exactly they eat ultimately depends on a combination of preference and what is available to them. For example, ice algae can provide an important source of food early in the season before the phytoplankton start to bloom. Then during the spring bloom, zooplankton would likely eat mostly large phytoplankton, while in the summer zooplankton might have a larger part of their diet made up of microzooplankton. This is because the microzooplankton may be preferred and because during summer the phytoplankton are small and less abundant than in the spring.

Researchers documented that as the ice melts, spring phytoplankton blooms...
support a highly diverse zooplankton community awakening from a period of relative inactivity during the long, dark, cold winter. These zooplankton include one-celled microzooplankton, often no larger than the tiny plant cells they consume, and larger, many-celled mesozooplankton dominated by copepods and krill (Figure 21). This zooplankton community dramatically increases in response to the highly productive spring phytoplankton bloom, and in turn becomes an abundant and highly nutritious source of food for seabirds, mammals, and fishes, including commercially valuable species. The Bering Sea Project shed light on the critical ecological roles that some of the tiniest of plankton play in the Bering Sea as grazers, photosynthesizers, and prey for larger species.

Rich Sea Floor

The spring bloom creates a short window of time when so much excess food is available that copepods are able to increase their biomass up to 10-fold between early spring and summer. Even so, the zooplankton community does not fully graze the spring bloom, and the ungrazed portion falls to the sea floor, feeding the “benthos”—the organisms that live on or in the seafloor.

The amount of organic matter that falls to the sea floor (also called carbon “export”) varies across the Bering Shelf, with highest carbon export in the icier northern domain and lower export offshore, except during the brief period in spring when ice melt near the shelf break leads to an ice-edge bloom in the outer domain and a pulse of food exported to the benthos. Over the inner shelf, nearly all organic matter that sinks to the bottom stays there. This is in contrast to the middle and outer domains where up to 30% of the settled organic matter is actually transported into the deep ocean basin by currents. In ice-free water, carbon export does not vary systematically south to north along the shelf. But when ice is present during spring over the northern Bering Sea shelf, higher rates of carbon export were found under the ice due to sea-ice algae sloughing off the underside of the ice. The Bering Sea Project showed that once this material hits the bottom, microbes and
The biochemical processes termed “mineralization” that break down organic matter are complicated and interesting. Bacterial communities use a variety of biochemical processes to oxidize the food that hits the bottom. Aerobic respiration is the most energy-efficient mechanism, but in the absence of dissolved oxygen, bacteria use anaerobic respiration with different oxidants to break down organic carbon. The sequence of oxidants that we would expect to observe in Bering Sea sediments in order of decreasing efficiency include oxygen, nitrate, manganese oxide, iron oxide, and sulfate. This efficiency sequence produces vertical gradients in these chemicals within the sediment column, with the most efficient closest to the surface.

The oxidative pathways taken by the organic matter likely vary with the rate of food supply to the sea floor. But, because the quantity of organic matter exported to the bottom of the Bering Sea is in part dependent on the timing of sea-ice melt, researchers wondered whether a warmer climate could reduce the quantity of organic matter reaching the sediment, causing other wide-ranging ecological effects. Researchers collected sediment cores from approximately 125 locations on the Bering Sea shelf, slope, and rise over four years (Figure 22) using a multi-corer. They incubated these cores on the ship at near in situ temperatures, and directly measured the rate of oxygen consumption and nitrogen gas production to quantify denitrification in the sediments.

Using chemical markers to follow the fate of the ice-derived matter in the food web (with oxygen consumed and nitrogen gas produced), they were able to confirm that food supplied from the overlying water takes different oxidative pathways in different regions of the Bering Sea in a manner that is consistent with its variation in supply from the water column (Figure 23). Interestingly, whereas denitrification and iron reduction were among the least important pathways for organic carbon mineralization, they had the largest effect on ecosystem processes by changing the rate of release of nitrogen and iron, nutrients required by phytoplankton.
multi-cellular organisms consume it and they, in turn, support a rich community of organisms, including commercially important king, snow and Tanner crab, and flatfishes such as halibut, sole and plaice. Any longer-term changes in primary productivity related to the melting ice and nutrient inputs onto the shelf will have a direct impact on organic matter export and therefore the richness of the bottom community.

**Surprising Role of Microzooplankton**

The ecological chain connecting nutrients, phytoplankton, zooplankton, fishes, and other predators turns out to involve one more link previously not well understood in the Bering Sea.

Researchers thought that crustacean zooplankton, such as copepods and krill, usually eat diatoms and are then consumed by other predators. However, this concept of a linear food chain gave way to new evidence from the Bering Sea Project that diatoms are also consumed by protists, single-celled predators known as microzooplankton.

Copepods are small, about the size of grains of rice, but microzooplankton protists are even tinier, smaller than poppy seeds. How are such miniscule predators able to feed on diatoms that are often as big, or even bigger, than the protists themselves?

While conducting incubation experiments on the decks of research vessels to measure the feeding rates of microzooplankton, researchers discovered that the most common types of diatom predators were large protistan dinoflagellates with some ingenious ways of feeding.

Common species of marine dinoflagellates make their living by feeding on other organisms, and cannot produce their own food. Abundant *Gyrodinium* dinoflagellates in the Bering Sea surround and engulf large diatom cells and chains (Figure 24). In some cases, the dinoflagellate cell distends so far, to accommodate a long diatom chain, that it appears ready to pop (Figure 24C).

Other types of predatory dinoflagellates are encased in rigid armor plates, called theca. These thecate dinoflagellates cannot change their shape to surround a diatom chain as do their *Gyrodinium* cousins. Instead, they extrude an amoeba-like blob of protoplasm that attaches to a diatom chain. The protoplasm surrounds the diatoms, releases enzymes to digest the algae, and then slurps the food back into the dinoflagellate cell (Figure 24D).

The most curious predators, perhaps, are the shelled amoebae that suck out the protoplasm of centric diatoms (Figure 25A, B). In one shipboard experiment, these amoebae dramatically increased in abundance, which showed that they can grow rapidly on diatom food. Even smaller protists prey on diatoms by attaching to the silica shell and injecting enzymes to digest the cell contents. In summer in the Bering Sea, researchers observed parasitic flagellates preying on centric diatoms, and during a spring study, noted similar flagellates infesting chains of pennate diatoms (Figure 25C).
Bering Sea microzooplankton include planktonic ciliates, such as this rather uncommon (and beautiful) heterotrophic tintinnid species.

Return of the Zooplankton

During the recent warm years in the Bering Sea, from 2000 to 2005, large zooplankton populations declined (Figure 26). At the same time, fewer juvenile pollock survived, causing concern about the walleye pollock fishery and about other fish species, including salmon, herring, and capelin that depend on large zooplankton for food. Without large zooplankton to eat, larger age-0 pollock turned to consuming smaller age-0 pollock and small zooplankton, thus further lowering pollock survival and recruitment. As the recruitment of young fish declined, the abundance of adult fish subsequently declined due to natural and fishing mortality. The North Pacific Fishery Management Council consequently reduced the number of fish that could be harvested during that period to preserve the fishery.

As temperatures started cooling in 2006, Bering Sea Project researchers found the cooling brought with it a recovery of the large zooplankton populations, and also noted the occurrence of large Arctic zooplankton species that had not been seen in the Bering Sea since the 1970s.

Through more shipboard experiments, researchers discovered additional significant ecological roles that microzooplankton play. They found an abundance of microzooplankton, especially in summer; at times their biomass was greater than the phytoplankton on the middle and inner shelf. Many of these were “green” ciliate protozoans—part animal, part plant, able to graze on small phytoplankton, but also able to photosynthesize, sometimes contributing over 50% of the chlorophyll in the system!

Microzooplankton clearly play a multitude of critical roles in Bering Sea ecology. These tiny organisms produce energy; graze heavily on phytoplankton, consuming almost all of the daily summertime phytoplankton production on the middle and inner shelf; and become the dominant food of larger zooplankton in summer.

This prompted questions about how the dynamics of ice, nutrients, and phytoplankton influence zooplankton populations, and what these changes might mean for fish, seabirds, marine mammals, and humans. Researchers wondered if the earlier decline of large zooplankton was due to insufficient numbers of phytoplankton and tiny microzooplankton during the warm years—a ‘bottom-up’ influence—or if hungry fishes and species preying on zooplankton exerted a ‘top-down’ influence. And how are such changes in the food web linked to changes in climate and ocean circulation?

To answer these questions, researchers looked more closely at the links between the base of the marine food web and larger animals. They analyzed a decade of data, including information on climate, physics, and phytoplankton and microzooplankton production and predation to examine how large zooplankton production results from the interplay between bottom-up (food supply) and top-down (predation by fish) controls under varying climate scenarios. Scientists also sampled zooplankton, environmental variables, and predators almost year-round.

FIGURE 26 During warm periods (up to 2005), large zooplankton densities were low, and small zooplankton densities were high. This relationship reversed when the Bering Sea switched to a run of multiple cold years during the Bering Sea Project study period.
for three years, taking into account the vertical migration of the large-bodied oceanic zooplankton.

While some zooplankton reside on the shelf, other species overwinter in deeper waters and move onto the shelf in spring (see Feature on next page). Modeling results using the data suggested that on-shelf pathways of offshore zooplankton from the deeper waters, where they spend the winter at depth in a semi-dormant state, is enhanced in the vicinity of canyons. This three-dimensional simulation model further suggested that, once in the upper, wind-mixed layer of the ocean, wind speed and direction take over as the primary factors driving on-shelf pathways. However, the success of oceanic zooplankton once on the outer shelf will also depend on other environmental conditions, most notably the amount of food they find and how heavily others prey on them. The interactions between both the physical and biological conditions end up determining the biomass of oceanic zooplankton over the outer shelf.

For krill, their spatial distribution differed between warm and cold years (Figure 27), with greater abundance over the shelf during cold periods (Figure 28).

Researchers speculate that the difference between cold and warm years may be the result of changes in wind and associated ocean circulation, as more southward flow during cold years brought ice and colder water over the southern shelf, creating an extensive cold pool. This cold pool, in turn, excluded some predators such as walleye pollock from large areas of the shelf.

Additional studies showed that phytoplankton and ice algae are the main food source for these large zooplankton in the spring, but in summer, phytoplankton are smaller and microzooplankton become the major food source. Thus, the energy flow through the ecosystem differs between warm to cold conditions (Figure 29).

In warm years, sea ice and ice algae were less extensive over the southeastern shelf and the phytoplankton bloom occurred later. In cold years, algae growing on the bottom of the ice and earlier ice-edge blooms gave the large zooplankton an early bounty of food, helping to sustain egg production and the survival of juveniles. Combining all of these mechanisms may partially explain the return of large zooplankton in recent cold years, and help us to understand the dynamic of their predators (fishes, birds, seals, and whales), which depend upon the presence of zooplankton for their survival.

**FURTHER READING**

See these “headlines” for more information:

- Bi et al., krill demography and dynamics
- Campbell et al., spring bloom importance
- Durbin, copepod populations and feeding
- Gibson et al., zooplankton transport
- Harvey et al., diets of Bering Sea krill
- Moran et al., changes in carbon export
- Mordy et al., zooplankton population change
- Pinchuk & Coyle, zooplankton populations
- Sherr et al., protists prey on phytoplankton
- Shull et al., organic matter mineralization
- Stoecker et al., role of microzooplankton

**FIGURE 27** In cold years, krill were more abundant and more widely distributed across the shelf compared to warm years as determined by acoustic surveys of krill biomass (kg per hectare, wet weight).

**FIGURE 28** With a change from warm conditions in 2000-2005 to cold conditions in 2007-2010, researchers found an increase in the number of *Calanus* copepods and krill on the eastern Bering Sea shelf. Vertical bars represent the standard deviation of the data.

**FIGURE 29** Cartoon illustrating the relationships among the timing of ice retreat, the bloom, and the production of copepods of different size classes. When there is an early ice retreat, the bloom occurs late in relatively warm water. These conditions favor small neritic copepods over mid- to large-sized *Calanus glacialis/marshallae*. When the ice retreats late, the bloom occurs early, in association with the ice, and *C. glacialis/marshallae* constitutes a major portion of the copepod biomass produced. Figure from Hunt et al., 2011, ICES Journal of Marine Science 68: 1230–1243.
Three major species of krill (known collectively as euphausiids) thrive in the Bering Sea, each occupying a different habitat. Researchers found *Thysanoessa raschii* in abundance in the middle and inner domains. They documented *T. inermis* more abundantly in the outer domain and *T. longipes* dominated through the outer domain and beyond the shelf-break (Figure 30).

To examine the relationship between growth, survival, and demographic structure of these different krill populations, researchers deployed a Multiple Opening and Closing Net with an Environmental Sensing System (MOCNESS) to collect krill samples. They used some samples to determine krill ages through a biochemical approach focused on the eye pigments, while preserving and sorting others to determine the species. Afterwards, scientists developed an individual-based mathematical model to determine krill growth-rate estimates for spring and summer of 2008 and 2009.

They found that krill longevity is as much as 2 to 3 years, and that ages varied among different krill species. In general, most *T. raschii* and *T. inermis* were 3-9 months old. In spring 2009, however, older individuals tended to be most abundant for both krill species. Also, the growth of *T. inermis* and *T. raschii* tended to be faster in 2008 than in 2009, whereas the growth of *T. longipes* was similar between years. The difference in growth could be explained by age structure and survival rates, in which populations with higher numbers of young individuals grow faster, and populations with older individuals grow slower, but have higher survival rates.

**FIGURE 30** Distribution of different krill species: *T. raschii* (red; TR), *T. inermis* (yellow; TI) and *T. longipes* (blue; TL) in 2008, 2009, and 2010. Three black lines indicate 50 meter, 100 meter and 200 meter isobaths.
Fish play a range of starring roles in the year-round drama that is the Bering Sea, from prey for a host of marine creatures during their drifting ichthyoplankton stage to voracious predators in adult form—even cannibalizing their own. And the ecological importance of fish is matched by their importance to subsistence harvests and to the regional economy, with tens of thousands of jobs and several billion dollars annually tied to Bering Sea fisheries.
Among the starring roles played by fish in the Bering Sea ecology, economy, subsistence harvest, and cultural life, walleye pollock could be considered the superstar. Walleye pollock—*Gadus chalcogrammus*, or simply ‘pollock’—support the world’s largest single-species fishery, and one of the world’s most commercially valuable fisheries with a first-sale value in excess of $1B in recent years. As a result, fishermen, biologists, resource managers, and economists focus intently on all of the factors influencing this species during every stage of their life cycle. This also led to the choice of pollock as one of the three focal fish species in the Bering Sea Project, along with Pacific cod and arrowtooth flounder. With the ultimate goal of better understanding the biological and physical processes controlling the population dynamics of these species, and how they may respond during changing climatic conditions, researchers conducted field collections, laboratory studies, and modeling.

Pollock larvae hatch relatively underdeveloped. During this early stage as fish plankton (ichthyoplankton), they are at the mercy of predominant ocean currents and are extremely vulnerable to predators. Shifting wind patterns that alter ocean flow, combined with temperature-driven changes in adult spawning areas, deliver larvae to different habitats during warm and cold periods, potentially affecting the type and densities of prey these developing larvae will encounter. They need enough prey to grow and survive during this important phase of growth that leads to recruitment to the next phase of life critical for the fishery. Shifts in the timing of larval production can cause mismatches in space or time between fish larvae and prey, resulting in lower growth rates, lower rates of survival, and fewer larvae available to recruit to the juvenile stage.

A single female pollock can produce millions of eggs in her lifetime. If even three of her millions of potential offspring survive to adulthood, the female has not only replaced herself and her mate, but she has added one more to the overall population. In this case, population growth is positive. However, numerous factors act to reduce the number of young that survive, and current evidence suggests that eastern Bering Sea pollock populations had low recruitment during recent warm years. And despite some population rebound during the more recent cold years, there is mounting evidence to predict gradually warmer and more frequent warm years in the Bering Sea, a major spawning area for pollock.

**FIGURE 31** Peak abundance of pollock eggs and larvae occur a month earlier during warm periods (red line and shaded area) compared to cold (blue line and shaded area), suggesting that spawning of walleye pollock adults is accelerated when ocean temperatures are warmer than average.

Researchers in the field sampled fish eggs and larvae using small-mesh plankton “bongo” nets during spring onboard the NOAA Ship *Oscar Dyson*. 
Some Like It Hot

As part of the Bering Sea Project, scientists were interested in determining if warming conditions affect the survival, distribution, and growth of young pollock. To find out, they compiled data collected with small-mesh nets in the eastern Bering Sea from 1988 to 2010 as part of NOAA’s Fisheries Oceanography and Coordinated Investigations (FOCI) program.

Information about pollock eggs, larvae, and juveniles in cold and warm years during this time period was used to calculate the respective mean geographic centers-of-distribution over the continental shelf during warm periods and cold periods, and to determine if there have been shifts in the timing of peak egg production.

The results were revealing—scientists found evidence of up to a 30-day shift in the timing of spawning of adult pollock from warm to cold years (Figure 31), and an eastward shift from the outer to the middle domain during warm years (Figure 32).

Warmth Takes A Toll

Researchers also looked at the impact of ocean temperatures on growth and survival of larvae and juveniles and found that these shifts in time and space resulted, on average, in increased growth and reduced mortality in warm years. This would suggest that a warming ocean is a good thing for pollock populations, but this early advantage does not translate into larger, fishable adult populations. After a certain threshold, high temperatures decrease recruitment. This decline can be partially explained by lower prey availability, changes in predation by arrowtooth flounder and adult pollock, in particular (Figure 33), and in part by the way young pollock allocate energy between growth and storage (Figure 34).

Effects of Temperature on Energy

Animals generally put surplus energy either towards growth or storage. Juvenile pollock can grow larger and avoid predation, or store energy to avoid starving over the winter. Using a laboratory process called “bomb calorimetry” to measure the number of calories in fish and their prey (see Feature on page 41), researchers compared data collected between 2003 and 2012 in the context of cold and warm years to reveal yet another piece of the puzzle that contributes to our understanding of the many factors that control fish survival. They found that fish and their prey were leaner, with less fat, in warmer years compared to those in cooler years that had stored more energy as fat (Figure 35).

Combining this information with survival to recruitment age showed that the years that produced big, fat juveniles were the same that produced more fish for the fishery (Figure 34). In cold years, even though there are fewer fish in the fall, this stored energy allowed those fish to survive winter better. This mechanism explained how climate cycles between 2001 through 2014 first caused a 40% decline in the nation’s largest fishery, and then led to its recovery.
The same pattern was true for euphausiids and other prey of juvenile pollock. When sea ice lasted longer, and the Bering Sea was cooler, fatter prey became more abundant than in warmer years and the fat content of prey was higher, as well.

This suggests that if the Bering Sea gets too warm, it will produce fewer pollock. These observations were consistent with an overall understanding that the Bering Sea fish that people depend on, such as pollock, have evolved life history strategies that rely on the presence of ice in spring. As the Bering Sea warms and ice retreats earlier, juvenile forms of species important to commercial and subsistence fisheries may find it increasingly difficult to survive.

**Ferocious Flatfish**

A shift in distribution in time or space, such as the one described for the early stages of pollock, can also alter the overlap between predators and prey and potentially influence the dynamics of prey populations. Given that the abundance of marine fishes, birds, and mammals in the Bering Sea depends upon finding plentiful, nutritious prey, it is critical to understand the mechanisms that influence the strength of species overlap. Such knowledge can improve our ability to anticipate shifts in predator-prey relationships, such as pollock becoming prey to a growing population of arrowtooth flounder. Knowing how these mechanisms affect the Bering Sea as the climate changes can increase our understanding of the magnitude and variability of natural mortality and survival to fishery size, and lead to better forecasts of ecosystem-level effects of changing environmental conditions.

Arrowtooth flounder are known to be voracious predators of juvenile walleye pollock. In the Bering Sea, the potential impact on pollock population dynamics of a growing flounder population has become a real concern. Increased predation by arrowtooth flounder on juvenile stages, in particular, combined with other top-down and bottom-up pressures on the survival of pollock during their early life stages, could have important ecological and economic consequences.
Using data collected by NOAA’s Alaska Fisheries Science Center during intensive surveys aimed at estimating species abundance, distribution, and predator-prey interactions, researchers characterized pollock and flounder distribution. They then predicted the species overlap relative to even greater potential increases of flounder biomass and warming ocean temperatures.

The analysis showed an increase in the geographic overlap between arrowtooth flounder and juvenile pollock at higher ocean temperatures during years of high flounder biomass. Given that flounder like warmer water and their abundance has increased eight-fold over the past three decades, prompting increased movement and expansion of their habitat, this overlap is not a surprise. This increase in the overlap between juvenile pollock and one of their main predators may place further pressure on pollock in the future.

Forage Fishes
Pollock are not the only fish of interest in the Bering Sea, nor are juvenile pollock the only forage fish available. Forage fish are small fishes such as capelin, sand lance, herring, and the young life stages of walleye pollock and Pacific cod, which become food for many ecologically and commercially important fishes, birds, and marine mammals throughout the world. Evidence suggests that forage fish distributions, just as for zooplankton described earlier, can change from year to year, vertically within the water column and horizontally across the Bering Sea.

Researchers don’t yet fully understand the mechanisms that control this variability, however. As part of the Bering Sea Project, scientists conducted a comprehensive analysis of physical, biological, and climate factors to investigate what affects forage fish distributions to predict how climate change may affect their populations and that of the predators that count on them as prey.

Researchers used echosounder data—in conjunction with the Bering Aleutian Salmon International Survey (BASIS) and ground-truthed with surface and mid-water trawls—to reveal a series of interesting patterns (Figures 36-38).

When scientists examined the influence of physical, biological and climate factors on forage fish distributions, they found that temperature, bottom depth and/or zooplankton prey were important predictors of forage fish presence and density. For example, the highest densities of age-0 pollock were found in the southern regions of the middle domain waters (50–100 meter depth) in waters warmer than approximately 1˚C. By contrast, age-1 pollock were observed near the seafloor over the middle domain and in midwater in the northern outer domain in cold years, and were more broadly dispersed across the middle and outer domain in warm years. Capelin were found in the inner domain in all years (Figure 38), but age-1 pollock and capelin seldom co-existed in the middle domain where age-1 pollock were most abundant. But in regards to climate, these species overlapped in almost twice as many stations in cold years than warm years. Interestingly, broad-scale factors such as the relative amount of sea ice or storminess were sometimes as important (or more important) than local conditions at the sample stations. Understanding these factors became critical in determining the link between forage fishes and the distribution and abundance of other fishes, birds, and mammals.

FURTHER READING
See these “headlines” for more information:
• Ciannelli et al., pollock spawning
• Duffy-Anderson et al., fate of pollock larvae
• Heintz & Siddon, fish bioenergetics
• Hunsicker et al., fish predator-prey overlap
• Parker-Stetter et al., forage fish distribution
• Petrik et al., pollock eggs and larvae
• Uchiyama et al., groundfish interaction model

Sorting the catch of age-0 walleye pollock and Pacific cod.
Capelin, a key forage fish in Bering Sea waters, shown schooling in the shallows.

**FIGURE 36** Acoustic echograms show differences in vertical distribution of age-0 pollock in 2008, 2009, and 2010. Depth ranges are not to scale.

**FIGURE 37** Distribution of age-0 pollock in the surface (left) and midwater (right) in 2009. Larger dots show higher densities. Bottom temperature (°C) was an important predictor of midwater pollock density and is shown on the midwater figure (red is warmest). Although there were few age-0 pollock in the surface zone in 2009, there were regions of high densities in the midwater zone.

**FIGURE 38** Spatial distribution and co-occurrence of age-1 pollock and capelin from NMFS bottom trawl survey in July 2004–2009. Contour lines identify the inner front (50 m depth), the middle front (100 m depth), and the shelf break (200 m depth).
Seabirds and Marine Mammals: A Changing Environment

Seabirds and marine mammals are the roaming predators of the Bering Sea, with huge numbers raising their young in the eastern Bering Sea and Aleutian Islands, and millions more visiting the region as a vital feeding area. As the most visible parts of the Bering Sea ecosystem, and as important subsistence and cultural resources, marine mammals and seabirds and their complex ecology were focal topics of study in the Bering Sea Project.

Seabird nesting cliffs at St. George Island.
The important role young wall-eye pollock and other forage species play in the marine ecosystem becomes very evident when looking at the response of fishes, seabirds and marine mammals to shifts in forage species abundance and distribution. Researchers aim to use the health or reproductive success of fish-eating (piscivorous) seabirds and marine mammals as indicators of forage fish abundance and distribution, since the forage fish themselves can be difficult to assess directly. In the breeding season, many seabirds carry whole small fish or a slurry of fish and krill back to their chicks, giving researchers an opportunity to count and identify what the birds have caught.

For the chicks to survive, adult seabirds must return to the nest within a certain period of time to feed them. During this phase of their lives, adult seabirds can only forage for food within a certain radius of their colony, earning them the name ‘central place foragers’ because they always return to this central place. The same holds true for fur seals that also raise their young on land; in contrast, newly-born whales move with their mothers in finding prey. Among other topics, the Bering Sea Project looked at the mechanisms linking both central place and more mobile foragers with their prey.

**Location is Everything**

The Bering Sea is home to millions of seabirds that breed on islands and coasts, and also supports visiting species like shearwaters and albatross that arrive from New Zealand, Hawaii, Japan, or other parts of the Pacific to forage during their non-breeding season.

The Pribilof Islands (St. Paul and St. George) lie near the edge of the Bering Sea shelf (Figure 39), and are home to a number of seabird species, including the thick-billed murre (Uria lomvia) and black-legged kittiwake (Rissa tridactyla). Fish-eating seabirds on these islands experienced dramatic population declines after 1976, when researchers documented a large shift in ocean conditions from a cold to a warm period.

Despite their close proximity to one another, seabird populations on St. Paul continued to decline, whereas those on St. George recently stabilized, puzzling seabird researchers. Compared to St. George Island, St. Paul Island is three times farther from the shelf edge and the more oceanic habitat. Scientists wondered whether this difference in location, and possibly prey availability, could be the reason for the seabird population differences; proximity to shelf could provide easier access to pelagic energy-rich species such as lanternfish (myctophids). If so, this might also suggest that birds will have trouble compensating for effects of persistent warming, even if they spend more time foraging or consuming more lower-quality prey.

**FIGURE 39** Spatial distribution of chick-rearing black-legged kittiwakes (Top, n = 133 birds) and thick-billed murres (Bottom, n = 80 birds) nesting at the Pribilof Islands (St. Paul and St. George) during 2008, 2009 and 2010.
As part of the Bering Sea Project, a study was designed to answer these questions. It tracked surface-feeding black-legged kittiwakes and deep-diving thick-billed murres as they raised chicks on St. Paul Island and St. George Island during the years 2008-2010. Researchers tracked birds by simultaneously attaching two types of data loggers, a Global Positioning System (GPS) and Time Depth Recorder (TDR), providing information about feeding location and behavior. Seabird scientists collaborated with forage fish researchers to relate seabird diets and the use of marine habitats by birds to biomass and distribution of forage fish prey in the surrounding waters. They assessed the costs and benefits of the foraging strategies with at-colony measures of chick-feeding rates, fledging success and nutritional stress of adults.

Researchers found that seabirds from St. Paul Island, which is located farther from oceanic basin waters and where the seabird populations are declining, spent more time feeding in closer but more food-limited shelf regions than birds nesting on St. George. Kittiwakes from St. George fed in the oceanic basin, where food was more abundant, and murres fed in the waters above the shelf slope (Figure 40).

The researchers studying prey found low biomass and patchy distribution of juvenile pollock on the shelf in 2008 and 2009. Both seabird species consumed less juvenile pollock and other shelf species, such as Pacific sand lance (Ammodytes hexapterus), compared to previous years (Figures 40 & 41).

The year 2010 marked a very poor year for shelf prey. To compensate for the lack of food near their colony, kittiwakes from St. Paul made extremely long trips to the basin to access lipid-rich lanternfish. Murres from St. Paul flew farther and dove deeper than their counterparts on St. George, foraging on the shelf during the day when they were feeding their chicks. The murres on St. George also fed on oceanic squid overnight. By increasing their foraging effort, St. Paul birds buffered their chicks from the lack of nearby prey, resulting in the same number of chick meals and the same success rate for chicks fledged at each colony. This increased effort, however, showed up as higher nutritional stress measured by the levels of stress hormones in their blood. Higher stress levels were detected in kittiwakes in 2010 and in murres in 2008 and 2009 on St. Paul compared to St. George (Figure 42).

Murres in a Warming Sea

Seabirds generally lay only one or two eggs each year, and live a long time, with some species surviving up to 30 years or longer. If, in some years, environmental conditions seem unfavorable, seabirds may forego breeding until the next year, thus maximizing the chances of survival for both their chicks, and themselves. Regulating their reproduction is one way to buffer themselves from anthropogenic and climate-induced changes in their environment.

FIGURE 40 Biomass and distribution of age-1 and age-0 pollock in 2008 and 2009 around the Pribilof Islands. The black bars in the lower right-hand plot represent the number of foraging trips in different directions away from the island and indicate the preferred northwest trip direction of kittiwakes from St. Paul Island in 2009, overlapping with the location of age-1 pollock.

FIGURE 41 Diets of black-legged kittiwake and thick-billed murres nesting on St. Paul and St. George Islands, 2008-2010.
To better understand the impacts of changes in the environment on the demographics of thick-billed murres, researchers applied a new technique, measuring the length of “telomeres”—a DNA marker believed to be an indicator of age. By collecting and analyzing data from three murre colonies that reflect contrasting environmental conditions and population trajectories in the southeastern Bering Sea, researchers demonstrated that where environmental conditions are favorable, such as on Bogoslof Island, or on the relatively stable St. George Island, older birds have higher stress levels than young birds, likely due to the effects of aging. In contrast, older birds have lower stress levels than young birds when conditions are poor (as on St. Paul Island). Scientists concluded that even though older birds are more experienced, prior experience in finding food is less important when food is plentiful. Thus, younger birds, being physiologically fitter, do better. But as conditions worsen and birds become food-limited, older birds outperform the younger ones as their experience in finding food and weathering tough years becomes more important than their aging physiology (Figure 43).

Over the long term, these results seem to indicate that too many years with poor prey availability, which occurs during warm years in the Bering Sea, may lead not only to a decrease in population size because chick survival decreases, but also to an aging population as older individuals may have higher survival than young individuals.
If seabirds live for 30 years or more, and we want to truly understand the impact of environmental conditions on their populations, we must also take a long-term perspective.

From 2008 to 2010, cold ocean temperatures and extensive ice characterized the three years of Bering Sea Project seabird field work. The reproductive success of black-legged kittiwake was well below average in 2008-2009 and slightly above average in 2010. But how much impact do years like that have on populations overall?

Thanks to a comprehensive and long-term seabird monitoring program conducted by the US Fish and Wildlife Service in Alaska, researchers had access to a 35-year record of seabird diet and reproductive success. They found that kittiwake diet was correlated with some broad-scale climate variables, such as the Arctic Oscillation (an index of sea-level pressure variations north of 20°N latitude) and regional summer sea surface temperatures, but not with local physical variables.

When they separated reproductive success into its sequential components, such as the number of eggs laid, number of eggs hatched, and number of chicks fledged, they found that timing was an important predictor of laying success for kittiwakes. Success in earlier parts of the nesting cycle and the previous year were more important predictors of overall productivity than any climate variables. These findings suggest a cascade effect, in which adult conditions carry over from the previous year and play a large role in subsequent reproductive success.
Distribution of Marine Mammals as the Climate Changes

Whales and porpoises (or “cetaceans”) found in the Bering Sea cover vast areas in search of the optimal balance between concentrations of their preferred prey and the environmental conditions that best suit their needs. Fluctuations in cetacean abundance and distribution are therefore more likely an indication of broad-scale rather than local changes.

Since variations in ocean conditions also affect the distribution and abundance of important prey species on a large scale, researchers wondered how cetaceans react to these changes and were also curious about the long-term implications.

Combining sighting surveys conducted by NOAA in 2002 with surveys carried out in 2008 and 2010 as part of the Bering Sea Project, scientists collected information on the location, species, and the number of individual whales and porpoises seen throughout the eastern Bering Sea shelf and examined this information to determine long-term trends.

The study revealed that the abundance and distribution of cetaceans changed with temperature. In colder years, when other facets of the Bering Sea Project showed more abundant and fattier prey at the base of the food web, researchers noted more whales (particularly those that consume plankton) and fewer porpoises, which eat fish (Figure 44). Humpback whale (Megaptera novaeangliae) and fin whale (Balaenoptera physalus) distributions were similar, regardless of temperature, but minke whales (B. acutorostrata), Dall’s porpoise (Phocoenoides dalli) and harbor porpoises (Phocoena phocoena) seemed to shift toward deeper waters in colder years. Overall, the abundance of porpoises decreased between 2002 and 2010, but researchers do not yet fully understand this decrease.

**FIGURE 44** Sightings of the five cetacean species in the study area, by year; red dots for 2002, blue for 2008, green for 2010.
**Hot Spots for Seabirds and Whales**

Scientists assume that the abundance and quality of their prey drives the distribution of seabirds and whales. These ocean predators often exploit places where small fishes and zooplankton persist in large patches. For an animal hunting food in the cold and stormy Bering Sea, finding predictably dense patches, or “persistent hot spots” of favorite prey saves time and energy, and may make the difference between survival and starvation. But what happens if changes in the ocean make the location of these “hot spots” less predictable during a time when seabirds, seals, and sea lions have to regularly return to the place where they nurture their young? Would the change matter for migratory whales that can move freely about to take advantage of the Bering Sea’s summer bounty?

Bering Sea Project researchers wanted to explore whether the way these predators hunt, and whether they are tied to a breeding site, affect their ability to respond to these dense patches of prey and their changes.

Using available data between 2004 and 2010, researchers examined the distributions of surface-feeding black-legged kittiwakes and pursuit-diving thick-billed murres during their summer nesting period, when their foraging range was limited. They also looked at free-ranging humpback and fin whales. They studied the distribution of all four species of seabirds and whales in relation to two of their key prey: age-1 walleye pollock and euphausiids. Researchers then compared the seabird and whale foraging locations with age-1 pollock and euphausiid concentrations, and analyzed data on the basis of how long these concentrations were present in time and space on an annual basis.

This analysis revealed several patterns. Euphausiids were ubiquitous, with persistent hot spots within specific 37 square kilometer blocks (Figure 45). Age-1 pollock were patchier and their hot spots persisted only on scales greater than 37 square kilometers, as shown in Figure 45. Both kittiwakes and murres, despite the difference in their feeding style, were consistently associated with age-1 pollock, but not consistently with ‘hotspots’ of euphausiids, even though the euphausiid hotspots were more persistent than those of the small fish (Figure 46). The diving thick-billed murres, which have greater travel costs than kittiwakes, foraged on prey concentrations nearer to their island colonies than did the surface-feeding black-legged kittiwakes, which foraged widely. Humpback whales, not tied to a central place, were found only where euphausiids were concentrated and where these concentrations were persistent, whereas fin whales were found where age-1 pollock were more likely to occur, similar to black-legged kittiwakes and thick-billed murres. So for mammals and seabirds, location matters, but so does the ability to find prey over a large and dynamic area.

**FURTHER READING**

See these “headlines” for more information:
- Friday et al., whales and porpoise
- Kuletz et al., seabirds and their prey
- Kuletz et al., albatross distribution changes
- Mangel et al., kittiwake behavior modeling
- Renner et al., seabird diet and reproduction
- Sigler et al., ‘hotspots’ of prey
- Young et al., stress and age in seabirds

**FIGURE 45** Persistence in distribution of prey species on the Bering Sea shelf, with primary “hotspots” (locations where concentrations were consistently found year after year) circled in red. The color scale shows the proportion of study years (2004-2010) that euphausiids (left panel) and pollock (right panel) were especially concentrated in each 37 x 37 km block—i.e. how persistent of a hotspot the block was.
FIGURE 46 Persistence in distribution of predator species on the Bering Sea shelf, with primary “hotspots” (locations where concentrations were consistently found year after year) circled in red. The color scale shows the proportion of study years (2004-2010) during which predator species were especially concentrated in each 37 x 37 km block.
Commercial Fisheries: Economic Engine of the Bering Sea

Bering Sea commercial fishing is very important in Alaska and the nation, supporting tens of thousands of jobs, contributing billions of dollars to the state’s economic output, and accounting for half of the total US seafood industry. Alaskan fisheries are regarded as well-managed, but the Bering Sea Project tackled some key questions: How will ecological impacts of a warming Bering Sea affect fisheries? Can we better understand complex interactions among species and fisheries? Can predictions be improved?
The Bering Sea Project focused on climate and the ultimate implications of change for Bering Sea inhabitants, including people. The economic part of this story was a vital component of the Bering Sea Project, and also takes us back to those elusive forage species, such as krill and young fishes, whose response to different climate conditions and cascading effects on the food web are key building blocks to understanding population growth, feeding grounds, and “hot spots” for species of interest to commercial fishers.

Landings of pollock, cod, and flatfish in the Bering Sea account for about 40% of all US commercial fishery landings. Based on assessments of their abundance and productivity, annual catch limits are set for each species individually by the North Pacific Fishery Management Council. Yet patterns in fish species abundance are not independent from each other. For example, good years for pollock and cod reproductive success tend to coincide, but reflect patterns opposite those for flatfish. Are these trends a result of interactions between predators and prey, or perhaps due to species’ responses to environmental variations, or a result of commercial fishing?

Trends in Groundfish Populations

The Bering Sea Project sought to develop a deeper understanding of interactions among major groundfish species in the Bering Sea, supporting a management approach that acknowledges ecological interactions of these species and the combined effects of climate and fishing.

To understand the variability of many fish species in the ocean, scientists generally examine four main elements: environmental conditions, predator-prey relationships, multispecies interactions and direct human impact, such as fishing. Often, independent studies allow only partial insight into these complex interactions. The Bering Sea Project, however, looked at all of these elements and used a series of multispecies and ecosystem models to reveal key characteristics that, when combined with climate models, have the potential to complement current Bering Sea conservation and management efforts with more proactive and strategic actions.
Ecological Patterns

One of the ecosystem modeling efforts in the Bering Sea Project integrated NOAA bottom trawl survey data and environmental indices to evaluate shifts in the abundance and distribution of species over time and space. Applying a “random forest” statistical method, researchers evaluated the extent to which environmental variables predict distribution patterns, and quantified species responses to temperature, depth, substrate, stratification, and other physical variables. The research team identified threshold shifts in the composition of the aggregate biological community, and used these to delineate distinct regional boundaries (Figure 47).

Hungry Fish Make a Difference

In addition to finding their preferred ecological region, fish species must find sufficient food to reproduce and survive the harsh winter conditions in the Bering Sea. Project researchers developed an ecosystem model called “FEAST” (Forage and Euphausiid Abundance in Space and Time) that centered on food availability and how it is influenced by climate, with predator response to climate and prey availability also included in the model.

The team used a 3D simulation model for oceanography, nutrients, and plankton (called a Nutrient, Phytoplankton, Zooplankton—or “NPZ”—model), constructed from previous work, and added data for several species of fish at different lengths based on historical databases from the NOAA National Marine Fisheries Service. Rather than assuming zooplankton gets eaten in proportion to their biomass, the team assumed it gets eaten according to fish energy needs or bioenergetics. Different types of zooplankton (such as krill) and fish were assigned energetic values in calories, and fish consumption and growth were then based on how many calories the fish ate and how they expended energy on swimming, living and growing, all of which are affected by temperature. The model was run for the entire eastern Bering Sea, estimating everything from oceanography to plankton dynamics, fish numbers, distribution, length, and weight. This required a lot of calculations and computer time, so the team used a supercomputer, dividing the whole region into smaller cells and sending those cells out to several hundred interlinked computer processors.

Prior to this study, knowledge about fish in the eastern Bering Sea centered on their feeding habits, species abundance, and distribution in summer and early fall. Little was known about them during the rest of the year, including their interactions with climate, winds, currents, or zooplankton, such as krill. Many
fishes feed on krill, but there is only so much krill biomass to go around. Every year, krill abundance peaks in late spring and early summer, bottoming out at the end of winter.

Migrations and movement of predators are tuned to the seasons, but what happens when the Bering Sea experiences an overall change in krill abundance driven by fluctuations in ocean temperature?

Both field observations and the FEAST model revealed that krill abundance is higher during cold years and lower during warm years. But rather than assuming that krill consumption by predators is directly related to their abundance (Figure 48), the model showed that the amount of energy fish need to grow also changes with temperature. To grow the same amount, fish require less energy in cold temperatures and more in warm temperatures because of an increased metabolism. So fish eat less krill in cold years, when krill is more abundant, and need more in warm years, when krill is less abundant.

This combination creates large areas where krill are depleted in warm years, but not in cold years, impacting krill predators such as forage fishes, seabirds, and marine mammals (Figure 49).

**An Alternative Approach**

To understand variability of multiple species in the ocean, scientists often develop whole ecosystem models that attempt to explain the flow of energy from phytoplankton throughout the marine ecosystem—like the NPZ-FEAST model described above. Such ecosystem models tend to be very complicated, require large quantities of data, and make multiple assumptions. As an alternative approach, one Bering Sea Project team developed simpler multispecies models, informed by routinely collected assessment and ecological data, to better understand patterns and trends of the most commercially important fish species in the eastern Bering Sea.

Knowing that fish predators interact with one another, even eating each other when they can, the research team developed multispecies fish models for the eastern Bering Sea that considered the interactions among walleye pollock, Pacific cod, arrowtooth flounder and a small-mouth flatfish group, comprised of yellowfin sole, flathead sole, northern rock sole and Alaska plaice (Figure 50). The models were based on many years of fish stomach samples collected by the National Marine Fisheries Service, Alaska Fisheries Science Center. Once the predator-prey interactions were worked out, the team used their models to examine the effects of fishing and environmental factors on these groundfish species based on findings from companion studies.
FIGURE 52 Schematic diagrams showing alternative hypotheses on how cold climate may affect distribution of fish on the eastern Bering Sea shelf and predation on young pollock. The cold pool (blue) is a pool of cold water (< 2°C) on the Bering Sea shelf formed by melting sea ice. In cold years, the cold pool covers a large portion of the middle shelf region. Most fish species are driven to the outer shelf region by the cold water, where predation is intensified by increased prey and predator density (A). However, there is some evidence that young pollock (major prey for other fish, including adult pollock) are more tolerant to cold water, in which they are protected from predators (B). If this is the case, predation on young pollock would decline under cold climate and increase under warm climate.

The Economic Implications of Fish Movement

While some other global scale research has suggested that a warming climate will propel marine species northward, work carried out as part of the Bering Sea Project has demonstrated that, for the biggest fisheries in the Bering Sea, this has not occurred as expected. For pollock between 1999 and 2009, the fishery did in fact move northward in the summer—but this occurred in cold years more than warm years (Figure 53). Similarly, for Pacific cod, a larger cold pool (where bottom water temperatures are below 2°C) in cold years has led to fish—and the fishing vessels that pursue them—being more concentrated in northern areas.

The model successfully reproduced observed changes in populations of pollock, cod, and flatfish in the eastern Bering Sea since the 1980s. From the model, researchers learned that, in warm years, juvenile pollock were more heavily eaten by arrowtooth flounder and cannibalized by adult pollock, whereas temperature appeared to have no or little effect on juvenile predation by cod or by small flatfish (Figure 51). Scientists inferred that these different temperature responses likely reflect different thermal preferences by species, which may change with life stage. For instance, a lingering pool of cold bottom water after cold winters is avoided by adult pollock, but may provide refuge for juvenile pollock and reduce cannibalism by adult pollock. Because of the dominant abundance of pollock, the net effect of warmer temperatures is increased juvenile mortality, resulting in fewer survivors to grow to adults to support future fisheries (Figures 52).

These bioenergetics, multispecies and ecosystem models are just beginning to reveal the wealth of information and understanding from this study. Researchers continue to further explore how environmental conditions alter environment-species and species-species relationships, and to evaluate their implications for fishery management and expected future fishery yields.
As part of this project, marine resource economists looked to identify the mechanisms by which climate impacts fisheries. They collected information on fishing locations, fish and fuel prices, and how those factors interact with biological survey information and environmental data. After collecting those data and talking to fishermen, the research team used a variety of statistical methods to see how management, changing prices, and changing biological and environmental factors have impacted the fisheries (Figure 54).

They found that abundance and environmental conditions both directly impact where the fisheries occur. Fishermen are the apex predators of the Bering Sea ecosystem, and better understanding their spatial behavior—as undertaken by this Bering Sea Project team of researchers—can tell us a great deal about the way in which fish populations are shifting under changing climate conditions. After controlling for other factors, how has variation in climate conditions affected the spatial extent of Bering Sea fisheries? How do we expect predicted changes in future climate to impact fisheries and fishing communities? Informing decision-makers on how climate and fisheries are interacting is essential to the effective management of marine resources in the future. The decisions that managers make now will impact the welfare of fishermen, communities, the nation, and the ecosystem over the next century.

**FURTHER READING**

See these “headlines” for more information:
- Haynie & Pfeiffer, fisheries and climate
- Hollowed & Baker, ecological regions
- Ortiz et al., climate and ecosystem modeling
- Uchiyama et al., groundfish interaction model

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**FIGURE 53** The eastern Bering Sea and the fishing areas of the pollock catcher–processor fleet. Points represent the catch-weighted mean center of the distribution of fishing hauls by season. This shows the large distinction in the northward movement of the fishery during cold years that occurs in the summer fishery (B Season) as well as the lack of movement between cold and warm years in the winter fishery (A Season), driven by the location of more valuable roe-bearing fish.

**FIGURE 54** A conceptual model of how the environment affects the distribution of fishing effort. Arrows represent the direction of causality, and dotted lines represent mechanisms that may occur on a non-contemporaneous time scale (TAC = Total Allowable Catch; CPUE = Catch per Unit Effort; E = expectation, P = price, Q = quantity).
A wide range of communities rely on the Bering Sea for sustenance and cultural life, with some almost wholly connected to the marine waters. Research in local communities was a priority from the outset. Ethnography, anthropology, and subsistence research all had a place in the Bering Sea Project, with more quantitative science operating hand-in-hand with traditional ecological knowledge and the study of natural and cultural history.
The same factors that affect the physical and biological aspects of the Bering Sea are important to people as well. For many centuries, coastal and island communities of Alaska Native peoples have depended on the natural resources of the Bering Sea, and in more modern times Native peoples and other residents continue to rely on the bounty of the Bering Sea. This reliance links directly to the availability of fish and wildlife, effective harvest technologies, and detailed environmental knowledge accumulated across generations and applied through direct experience. Now, in the early 21st century, livelihoods in these communities are based on a mixed subsistence and cash economy that blends harvest and use of traditional foods with adaptations to a rapidly changing, interconnected world.

Five communities participated in the local and traditional knowledge (LTK) and subsistence harvest component of the Bering Sea Project (Figure 55). Selected communities included those with subsistence harvest data from earlier studies, and represented a range of associations with sea ice, from none to ice-covered waters. These communities also represent linguistic and cultural diversity, with two Aleut, also known as “Unangan” communities – Akutan and St. Paul; two Central Yup’ik communities – Togiak and Emmonak; and a Siberian Yupik community – Savoonga on St. Lawrence Island. In addition, several Central Yup’ik communities of Nelson Island (Toksook Bay, Tununak, Newtok, Chefornak, and Nightmute) participated and provided local and traditional knowledge about changing ocean conditions, weather and climate alongside a wealth of information on place names, traditional hunting and fishing practices, oral histories, and traditional tales (see Feature on page 62).

**Subsistence Harvests in Five Bering Sea Communities**

Using standard harvest survey methods developed by the Alaska Department of Fish and Game, *subsistence* harvests were documented in Akutan, Togiak, Emmonak and Savoonga, recording the harvest of all species of mammals, fishes, birds, invertebrates, and plants during a calendar year. In St. Paul, researchers elected to monitor the harvest during the year, rather than conducting recall interviews the following year. This continued a harvest monitoring effort that had been underway for some time on the island, and tracked the harvest of northern fur seals, Steller sea lions, and reindeer.

**SUBSISTENCE**

“Subsistence” is the term used to refer to the gathering of wild resources (usually food) for personal necessities. Alaskan and Federal law define subsistence similarly, as the “customary and traditional uses” of wild resources for food, clothing, fuel, transportation, construction, art, crafts, sharing, and customary trade.

The results of the household surveys showed the continuing importance of wild resource harvests in the study communities. Virtually all households used wild foods in the study year, and large percentages participated in and shared resource harvests. These harvests were diverse, consisting of a variety of fishes, most notably salmon, land mammals, marine mammals, marine invertebrates, birds, eggs, and wild plants (Figure 56).

Comparisons of harvest data across study years, combined with key respondents’ observations, suggest that subsistence harvest patterns have changed in the study communities over the last several decades. These changes were not uniform across communities. Akutan saw lower harvest quantities and diversity in 2008 than in 1990, the only previous year for which comprehensive survey data were available. In contrast, Togiak recorded higher harvests and greater diversity of uses in 2008 than in the previous study year of 1999 (Figure 56).
Shifts in harvest composition have also occurred. Compared to previous surveys, Emmonak harvested more moose and fewer non-salmon fish, and more bearded seals but fewer ringed seals. Togiak harvested fewer moose and caribou and more salmon, and Akutan’s harvests of marine mammals dropped, while salmon harvests increased. On St. Paul, where multiple years of data are available for fur seals, sea lions, and halibut, subsistence harvests for these three key resources declined since the early 1990s.

Survey respondents offered a range of personal, economic, and environmental explanations for changes they have experienced. Personal and economic factors dominated their explanations of changes in 2008 compared to other recent years. However, interviews with key respondents, perhaps because of the greater time depth and broader experience applied to their observations, identified other factors that are shaping trends over a longer time frame.

These explanations are complex and multifaceted. For example, at Akutan, respondents cited the effects of persistent storms and shifting winds that restrict travel and reduce the predictability of the locations of key resources. Emmonak respondents also experienced shifting winds and persistent storms, as well as unpredictable and unstable sea ice. They cited a combination of environmental and resource management factors, including salmon bycatch—a particular concern, considering that salmon remains their most important subsistence and commercial resource.

Overall, the study found that subsistence hunting, fishing, and gathering remain nutritionally, economically, culturally, and spiritually essential to individual and community well-being in the five study communities. Residents of the study communities continue to demonstrate considerable flexibility in their subsistence activities on an annual and long-term basis—key respondents observed that change itself is not remarkable, but constant.

**Subsistence Patterns Follow Ecological Patterns**

When Alaska’s coastal residents hunt and fish, they sample their local environment, and while these activities necessarily rely on what is locally available, researchers were interested if other factors might also affect harvest patterns. They wondered whether those patterns revealed any cultural preferences for certain types of foods, and whether subsistence harvest characteristics could be used as indicators of the condition of the ecosystem.

Extending their work from the information collected during the Bering Sea Project, this research team made use of subsistence harvest survey results compiled by the Alaska Department of Fish and Game, covering 35 communities in the region. Because some communities had more than one year of data, the team had a total of 53 harvest surveys from 1964 to 2009.

Taking a geographic “cluster analysis” approach, the researchers divided the...
villages into six oceanographic regions based on earlier work, and compared the village groupings to one another to see which ones had subsistence harvests that were most closely related (Figure 57). The northern Bering Sea aligned more closely with the Chukchi and Beaufort than with the central and southern Bering Sea. This is not surprising given the migration routes of bowhead whales and walrus, which are popular subsistence resources in the northern Bering Sea as well as along the Chukchi and Beaufort coasts.

**Broad Origins of Subsistence Food**

People eat and harvest what is within their reach, and their hunting success is directly dependent on local conditions. But subsistence harvesters are also indirectly dependent on a multitude of biophysical processes that control the distribution and abundance of the target species. Much attention has been given to subsistence use areas, where people hunt and fish. Coastal residents have a great deal at stake when it comes to ecosystem well-being, and their interest extends across the entire region, not just in the areas where people travel, hunt, and fish.

Inspired by the informal knowledge that subsistence hunters and fishers rely on a vast area of the ocean, a Bering Sea Project research team looked in detail at the extent of the waters that help produce subsistence fish and animals. Using the “watershed” concept, the team coined the term “calorie-shed”—the area that contributes to the food that ends up on people's plates. Using subsistence harvest records to identify important species, they used biological data to establish how far those species range from the community or area where they are harvested. The team did this for Togiak (Figure 58) and Savoonga (Figure 59) using three species for each village. It turns out that the areas are huge!

By visualizing the full geographic extent of people's interactions with and dependence on the Bering Sea ecosystem, calorie-sheds provide another way of considering how changes in large marine ecosystems may affect the coastal communities in the Bering Sea. By revealing how much of the ecosystem subsistence harvesters draw on, the research team showed why an individual community might be concerned about what is happening far away. Calorie-sheds highlight the connectivity between systems, and the challenges faced by natural resource managers.
As part of the Bering Sea Project, the Calista Elders Council (CEC, the primary heritage organization for southwest Alaska) worked with elders and community members from five Nelson Island communities on the Bering Sea coast to document the natural and cultural history of their homeland.

Between 2006 and 2010, Council staff traveled with elders out on the land to document historic sites and landscape features on and around Nelson Island (Figure 60). Council staff also hosted a number of topic-specific gatherings—two and three-day meetings with elder experts devoted to a single topic—as an effective means of both documenting traditions and addressing contemporary scientific concerns. Unlike interviews, during which elders answer questions posed by those who often do not already hold the knowledge they seek, gatherings (like academic symposia) encourage elders to speak among their peers at the highest level.

This five-year effort resulted in the publication of two books: Ellavut/Our Yup’ik World and Weather: Continuity and Change on the Bering Sea Coast (Fienup-Riordan and Rearden, 2012) and Qaluyaarmiuni Nunamtenek Qanemciput/Our Nelson Island Stories: Meanings of Place on the Bering Sea Coast (Figures 61 and 62).

Some of the more striking results are summarized on the following page:
POPULATION CONCENTRATION
The last sixty years has seen dramatic change in the way Nelson Islanders inhabit their land. Perhaps the most significant is the concentration of people into five permanent villages and the abandonment of hundreds of small camps and settlements still vibrant through the 1940s. These villages—ranging in size from 250 to 600 inhabitants—are small by modern standards but huge compared to the tiny settlements of the past. As people gather closer together on and around Nelson Island, the island’s resources, although still abundant, are more distant. Now men often travel miles, either by gasoline-hungry snowmobile or skiff, to set their nets and traps. People still harvest from the fishing sites their parents used, but at a cost many find difficult to afford.

LINKING LOCAL AND GLOBAL
Work with Nelson Islanders provides a unique, nearshore perspective on the Bering Sea. While oceanographers attempt a comprehensive understanding of the ocean, Yup’ik hunters are most concerned with surface features of the water and ice cover that impact on hunting success and safety of travel. Yet coastal Yup’ik residents also see the ocean as an integral part of ella, a word they translate as weather, world, universe and awareness, depending on context. The emerging question that concerns both Yup’ik and non-Yup’ik ocean observers is: How can we link local observations with large-scale environmental issues?

In the many warnings elders give of a dangerous and unpredictable ocean, they also identify key research problems. One example is connecting the response of the nearshore ice regime to ocean swells and tides. Yup’ik people have many words describing the appearance and response of ice to currents and winds. Using satellite images, meteorologists were able to demonstrate linkages between diminishing Arctic sea ice and changes in the Arctic terrestrial ecosystems, finding that areas in the High Arctic have experienced the largest changes, with some exceptions over land regions along the eastern Bering Sea. In discussions, elders pointed out a decline in tundra berry production, and a change in the timing of the harvest in recent years, which they associate with a decrease in fall rain and snow cover. Winds during the growing season were another factor. These observations point to the need to look at changes in wind and precipitation as well as sea ice cover to explain changes in coastal ecosystems.

STORM SURGES AND COASTAL EROSION
The rise of sea level and related effects of increased fall storm surges are of particular concern, both to ocean scientists and coastal residents. Elders’ long-term observations on these changes are particularly valuable. The village of Newtok, 3 meters (10 feet) above sea level, was established in 1950 on the low-lying tundra north of Nelson Island. Men chose the site because it was accessible to barges bringing in lumber for the new school. Despite Newtok’s marshy location, it doubled in size to its current population of 350. At the same time Newtok was growing, the land was sinking and eroding at an alarming rate. A move to relocate the village to a bedrock site on Nelson Island is already underway.
Local and Traditional Knowledge

As exemplified by the Nelson Island Project, people who live on the shores of the Bering Sea, especially those who spend a lot of time hunting and fishing, have a deep understanding of the environment. In Alaska Native villages, this knowledge has accumulated over many generations, allowing people to hunt and fish successfully and safely. By documenting what Bering Sea residents know about their ecosystem through interviews, in addition to gathering subsistence harvest data, important local details about ecological processes and changes come to light. Researchers can also check what has been learned from other types of studies, by comparing what local residents are seeing with the findings of oceanographers, climatologists, biologists, and others.

Bering Sea Project researchers interviewed experienced hunters and fishermen in five Bering Sea communities: Akutan, St. Paul, Togiak, Emmonak and Savoonga. Many aspects of the Bering Sea ecosystem were discussed, especially those related to the hypotheses driving the entire project. Most of the interviews were open-ended discussions, closer to a conversation than to a poll or a question-and-answer session. After the interviews, what had been written down was reviewed with the hunters and others in the communities.

Comparisons between local knowledge and western science revealed a complex and changing ecosystem, in which scale is a dominant feature, and where no two communities that participated were the same. In the southeast, many species are in decline, but in the north, the ecosystem remains productive with an abundance of fishes, seabirds, and marine mammals. The most rapid changes are occurring at the edge of the sea-ice maximum extent, in the southern Bering Sea, where ice-associated species such as bearded seals are becoming scarce. Ice conditions are also changing in the northern Bering Sea, but hunters reported a thriving ecosystem. Of particular interest were descriptions of “hot spots,” or areas with very high productivity. Around St. Lawrence Island, hunters noted several such locations, all of which are still productive, attracting an abundance of fish, seabirds, and marine mammals (Figure 63).

Overall, the results from the local and traditional knowledge interviews shed light on several aspects of the Bering Sea Project’s research. First, broad differences between the southern and northern Bering Sea were similar in the local and traditional knowledge results and in several other analyses of the ecosystem, giving us confidence in this interpretation. Second, observations about summer storms were contrary to what was anticipated in the hypotheses, but could have been due to the fact that the study period was generally cold in the Bering Sea. Third, changes in abundance and distribution of species did not follow a simple pattern across the Bering Sea, but showed great local variation, reemphasizing that the ecosystem is complex.

FURTHER READING

See these “headlines” for more information:

- Fall et al., subsistence harvest
- Fienup-Riordan et al., Nelson Island ethnography
- Fienup-Riordan et al., knowledge synergies
- Huntington et al., subsistence calorie-sheds
- Huntington et al., local ecosystem knowledge
- Renner & Huntington, subsistence patterns
- Stott et al., data and metadata archive
A carver in the Siberian Yupik village of Savoonga, called the “Walrus Capital of the World”, holds a seal carved from walrus tusk.
Bering Sea Project Headlines

Bering Sea Project “headlines” are a series of two-page, user-friendly summaries of new research findings that formed the basis for this magazine. Project scientists were invited to author headlines, with editing and design help from NPRB and NSF staff and others. Here we list the full authors and title of each headline for cross-reference to the short versions noted in this magazine’s “further reading” sections. Visit the project website to view headlines, and contact authors or peruse the project’s “Scientific Publications” webpage to learn more about the peer-reviewed papers that stand behind each headline.


Reviewing Progress, and Lighting the Way Ahead
The common thread through the Bering Sea Project has been the central hypotheses: (1) Physical forcing and its modification by climate affects food availability; (2) Ocean conditions structure trophic relationships through bottom-up processes; (3) Ecosystem controls are dynamic; (4) Location matters and; (5) Commercial and subsistence fisheries reflect climate. As described in the following pages, in the three special issues published to date—and in the upcoming fourth special issue as well as the many other peer-reviewed papers emerging from the Bering Sea Project—manuscripts begin to explore warm versus cold comparisons through synthesis of other datasets with those generated by the Bering Sea project, or interpreting other datasets (e.g., mooring datasets) in the context of the broader ecology of the Bering Sea. These synthetic activities are focusing within and among trophic levels, providing a basis to understand the ecosystem in a more mechanistic way, and to improve our ability to predict ecosystem responses to a changing climate and sea ice conditions.

The impact on people is especially challenging to predict. History has shown that humans are incredibly adaptable. Coastal communities have persisted in this ever-changing environment over thousands of years, and whereas diets and customs may change, people remain. An open question is whether commerce, subsistence and management practices alike can respond to, mitigate, or anticipate future change quickly enough to sustain a viable system—a system that continues to support people’s livelihoods and well-being.

As highlighted in the preceding pages, the Bering Sea Project has delivered a wealth of new knowledge and understanding of the mechanisms controlling the flow of energy and material through Bering Sea pelagic and benthic food webs, and an enhanced ability to anticipate the inevitable changes that will occur in a warming northern climate. Although we may not be able to assert exactly how climate change will play out in the region at this point, the results from the research conducted in the Bering Sea Project already represent a big step forward in our understanding. The Bering Sea Project has provided the basis towards the development of improved forecast models, as well as insights for effective monitoring and continued sustainable management of this system in the face of ongoing change.

For all of us involved in the origin, management, and execution of the Bering Sea Project, it is our hope that the knowledge gained and partnerships established will continue to pay dividends in the years ahead, as synthesis and writing collaborations continue, and as future new projects build on the Bering Sea Project foundations.
In this ‘magazine’, we have presented headlines and highlights of individual and collaborative research teams, emerging in the participating scientists’ own words. Those same scientists—the nearly 100 principal investigators plus dozens of additional collaborators—typically publish their work as papers in peer-reviewed journals, and they’ve been very busy in the closing years of the Bering Sea Project, with over 165 papers published to date!

Within this broad group of publications, there is a subset of papers that have been the focus of particular attention—“special issue” papers. The Bering Sea Project supported a series of special journal issues, published in Deep-Sea Research Part II. These special issues are a core mechanism for sharing and integrating results, and an opportunity for related research to be brought forward in an easily accessible one-stop-shopping format, facilitating comparisons and connections among the broad scope of topics encompassed by the Bering Sea Project.

To date, the Bering Sea Project has published three special issues of Deep-Sea Research Part II, encompassing a total of 75 papers. Volumes 65–70 were published in 2012, volume 94 was published in 2013, and volume 109 was published in 2014. A fourth and final issue, with 30 papers either already ‘in press’ or in review and revision, should be complete and published by early 2016.

The first two Bering Sea Project special issues primarily present papers that describe new information on this ecosystem and how change will affect individual species, trophic levels, or guilds. Those papers placed new data in their historical context, assessed implications for the future of the Bering Sea ecosystem and generally addressed one or more of the core program hypotheses that guided the field program and ongoing synthesis activities. These hypotheses include: (1) physical forcing, including climate, affects food availability; (2) ocean conditions structure trophic relationships through bottom-up processes; (3) ecosystem controls are dynamic; (4) location matters; and (5) commercial and subsistence fisheries reflect climate. The third special issue continued to address the core hypotheses, but with a greater focus on mid-level synthetic activities, which advance our understanding of the ecosystem as an integrated whole, and our understanding of how the ecosystem may respond to climate-driven changes.
As an introduction to the special issue series—and as an overview of the synthesis of new knowledge gained so far in the Bering Sea Project—here we provide context from the first two special issues and brief summaries of each of the papers appearing in the 3rd Bering Sea Project special issue, grouped by broad topic or trophic level. Citations are provided if you’d like to learn more—visit the special issue page at the Bering Sea Project website (nprb.org/beringseaproject) to view or download individual articles, or download special issues in their entirety.

1. OCEAN PHYSICS

The Bering Sea shelf varies both spatially and temporally. While the most distinct differences in shelf regions are in the cross-shelf domains (coastal, middle and outer), papers in the first special issue documented a division at 59–60°N between the northern and southern shelves (Stabeno et al., 2012a). The northern shelf is colder, with weaker tides and vertical stratification to which temperature and salinity contribute equally; by contrast, the southern shelf is warmer, with stronger tides, and is vertically stratified mainly by temperature. One of the drivers of the differences between the north and south is that ice persists for approximately two months longer on the northern than on the southern shelf (Stabeno et al., 2012b). In the third issue, Sullivan et al. (2014) investigated the impact of melting ice and found that the southern Bering Sea was cooled and freshened by melting ice as it is first advected southward in winter, while the northern Bering Sea is freshened in spring when the ice melts during its retreat. This difference results in the presence of a low-salinity pool on the northern shelf. The presence or absence of sea ice on the southern shelf in March and April determines whether a given year is warmer or colder than the long-term average.

After the first two special issues, an open question remained of how comparable the years defined as “warm” and “cold” in the southern Bering Sea were to those in the north. Panteleev and Luchin (2014) found that there was no correlation between northern and southern cold/warm years. Both papers reinforce the marked differences between the northern and southern shelves.

2. SEA ICE

Winter and spring sea ice is a defining characteristic on the Bering Sea shelf, determining such diverse variables as ocean temperatures through the following summer, the extent of the cold pool, and timing of the spring bloom. Temperature and stratification are key predictors that structure the Bering Sea ecosystem (Baker and Hollowed, 2014). The timing of ice retreat is a primary indicator of the temperature of the southern shelf during the following summer, and thus defines warm and cold years (Stabeno et al., 2012b). While the northern shelf is expected to maintain extensive ice for the foreseeable future, the southern shelf is extremely sensitive to changes in the timing of ice retreat. Cheng et al. (2014) predicts that, as a result of climate change, a northward shift of ice extent by ~2° latitude in the next 40 years is to be expected. This loss of sea ice on the southern shelf will result in a warmer southern shelf.

3. PHYTOPLANKTON AND PRIMARY PRODUCTION

The seasonal presence or absence of sea ice in the south-eastern Bering Sea, just as for physics, appears to have a marked impact on the diversity and function of the lower trophic levels. For example, in an analysis of the mooring chlorophyll fluorescence time-series, Sigler et al. (2014) observed that the timing of the open water spring bloom was dependent upon stratification. This pattern of physical control, tied to the presence or absence of sea ice, leads to a variable time period between the fall blooms in one year and the spring bloom in the subsequent year and is hypothesized to have important implications for the flow of energy to mesozooplankton in the spring (Morales et al., 2014; Sigler et al., 2014) and for ‘refueling’ in the fall. Sigler et al. (2014) also suggest that the presence or absence of sea ice impacts the magnitude of the spring bloom, where ice algal production may reduce the nutrient content of the upper water column by consumption and rapid export to the benthos, thus leading to lower chlorophyll and primary production in the subsequent open-water spring bloom and summer period. The lower chlorophyll values may not necessarily result from lower net primary production, as reductions in the mean cell size of the phytoplankton population and warmer summer temperatures leading to enhanced nutrient recycling may offset reduced total chlorophyll in some regions as observed by Stauffer et al. (2014). A further complication in chlorophyll production is spatial variability in nutrient limitation, which would tend to favor smaller cell size.

Previous papers in the Bering Sea special issue series have highlighted the importance of material exported to the benthos versus retention of that material to be recycled in the upper water column (e.g., Baumann et al., 2013; Moran et al., 2012). In the third special issue, Cross et al. (2014) show that the pattern of benthic-pelagic coupling varies across the shelf, with more material exported horizontally to the deep ocean basin from the outer domains, whereas in the middle domain, most organic matter is locally exported to the benthos. The extensive export of material to the benthos temporarily removes nutrients from the upper water column and can lead to nutrient limitation in the phytoplankton, thus favoring growth of small cells (Goes et al., 2014), with further cumulative effects for both small and large grazing zooplankton and microzooplankton. The retention of organic matter in shelf sediments deprives the upper water column of nutrients, but leads to significant remineralization at depth. This in turn results in an increase in carbon dioxide and the acidification of deep waters as observed by Mathis et al. (2014), which may ultimately have a negative effect on benthic (and pelagic) communities despite the increased supply of organic matter.
4. ZOOPLANKTON

One of the more important findings in the second special issue was the importance of microzooplankton to the ecosystem (Sherr et al., 2013). Microzooplankton biomass increases seasonally, and at least part of that increase is linked to the variability of mesozooplankton grazing control on microzooplankton during winter and spring. In contrast to experimental grazing observations, Morales et al. (2014), present stable isotope data that suggests mesozooplankton preferentially graze on diatoms and other primary producers, and that there is little to no evidence of grazing at more than one trophic level. This apparent lack of grazing control leads to increased microzooplankton biomass from spring to summer, consistent with the findings of Stoecker et al. (2014b) who observed that microzooplankton biomass was equal to or greater than phytoplankton biomass. Furthermore, Stoecker et al. (2014a), estimated that these high microzooplankton biomass stocks consume from ~60% to in excess of 100% of daily phytoplankton production along a cross-shelf transect. The impact of this near complete consumption of net primary production in summer on the growth of mesozooplankton through summer or fall is unknown. It is also unknown if this seasonal pattern of microzooplankton grazing and biomass accumulation is different in warm years, since these observations were all made in cold years. Clear changes in the relative abundance of small and large mesozooplankton in the fall have been observed between warm and cold years by Eisner et al. (2014), with large mesozooplankton increasing dramatically in abundance from warm to cold years. These changes did not occur abruptly at the end of the warm period, but built as the influence of sea ice and cold temperatures persisted. The change began one year earlier in the northern Bering Sea compared to the southeastern Bering Sea.

5. FISH

Walleye pollock (Gadus chalcogrammus) and Pacific cod (G. macrocephalus) are two of the largest and most valuable fisheries in the Bering Sea. Both species responded negatively to the warm period (2000–2005), with reduced recruitment resulting in a decrease of ~40% in annual walleye pollock commercial fishing quota in 2008–2010. It has been hypothesized that in cold years, euphausiid and copepod populations increased, resulting in a richer available prey resource that better prepared the pollock for winter (Heintz et al., 2013; Stabeno et al., 2012b). Strasburger et al. (2014) found that, while they have similar early life histories, in the cold years pollock and cod larvae begin to divide prey resources as they age rather than competing for the same prey. While their study focused on cold years, the authors suggest that during warm years with reduced prey abundance and prey of lower energetic quality, the two species may compete for the same limited resources, thus contributing to a decrease in recruitment of both species during these years. Other mechanisms, such as the successful transport of eggs and larvae to suitable nursery grounds, can also influence the recruitment of these fish species. Warm and cold years were associated with significantly different currents on the middle shelf (Stabeno et al., 2012b). In addition, Ladd (2014) observed that annual and interannual variability exists in the Bering Slope Current (BSC), with a stronger BSC in the winter months. Vestfals et al. (2014) found that the recruitment of groundfish was significantly correlated with both transport in the BSC and also onshelf flow. This was especially true for Pacific cod, but other species such as Pacific halibut (Hippoglossus stenolepis) also benefited from increased onshelf flow in the Bering Sea shelf canyons. Studying the spawning phenology of Pacific cod, Neidetcher et al. (2014) found interannual variations in the...
timing of spawning of up to 10 days between years (2005–2007). This is similar to Bering Sea Project results for pollock spawning between warm and cold periods reported by Smart et al. (2012). Such relatively small changes in timing could interact with the temporal changes in transport to impact the survival of eggs and larvae.

Arrowtooth flounder (Atheresthes stomias) and Kamchatka flounder (A. evermanni) have similar predation impacts and are prey to similar organisms in the Bering Sea. Directed fishing efforts on both species have increased in recent years and both species must be correctly separated and recorded in catch data, however juveniles cannot be easily distinguished. De Forest et al. (2014) developed a genetic technique to distinguish between the larvae and early juveniles of arrowtooth flounder and Kamchatka flounder using mtDNA. Larvae of arrowtooth and Kamchatka flounder were found to have similar distributions in the eastern Bering Sea, but juveniles have slightly different distributions with juvenile Kamchatka flounder closer to the shelf break and in deeper water. The larvae of the two flounder also showed a divergence in nutritional quality that suggested a separation in their diets and ecological niches, but there was no difference in lipid content as a measure of energy content between the species by the juvenile stages.

6. SEABIRDS AND MARINE MAMMALS

The spatial distributions of seabirds and temporal changes in population size have been linked to a wide variety of marine phenomena at spatial scales from ocean basins to small-scale tidal fronts. A central theme of these studies has been the relationship between seabird foraging behavior and prey abundance, density and type, and consequent impacts on chick rearing and survivorship, changes in total populations and population centers of abundance. Renner et al. (2014), using a 36-year record of seabird abundance on the Pribilof Islands, found that breeding success was most closely related to the prior years success. This retrospective analysis found that chick survival was enhanced when chicks were fed fish rather than crustacean zooplankton, and was further enhanced when fed coastal fish species rather than oceanic species. However, long-term changes in population numbers were more closely related to the overall condition of the adults, highlighting a need to focus on non-breeding season foraging behavior to understand population dynamics. This is additionally highlighted by changes in the distributional patterns of albatrosses, which breed elsewhere but forage in the Bering Sea in their summer non-breeding season. Kuletz et al. (2014) examined the distribution of three albatross species within the Bering Sea, and found that centers of distribution of black-footed (Phoebastria nigripes) and short-tailed (P. albatrus) albatross have moved northward, while the Laysan albatross (P. immutabilis) has moved southward. This southward move was primarily due to increased abundance along the Aleutian Islands, although they were also found farther north in recent years. These changes are hypothesized to be related to the distribution and abundance of their primary prey (squid), rather than due to changes in climate.

There are two main feeding strategies in seabirds—surface foraging and pursuit diving. To better understand the distribution of seabirds that fit in each feeding category, Hunt et al. (2014) clustered seabird distributions by the depth range over which they fed to determine if they defined ecological domains. Indeed, birds aggregated into bathymetric bins (shallow, mid, deep) except in winter, when the ocean is less stratified and the shelf frontal structures weaker or non-existent. This analysis provided strong evidence for topographic anchoring of feeding regions (e.g., tied to fronts), which explained the seasonal movements of some seabird population distributions, and suggested that seabird populations were more attuned to movements of surface water masses than depth per se. This also connects to earlier Bering Sea Project work linking prey persistence to marine mammal and seabird foraging (Sigler et al. 2012) and relating cetacean distribution and abundance to oceanography (Friday et al. 2013). Jones et al. (2014), studying the δ15N signature of both seabirds and prey items (juvenile pollock and krill), found strong relationships between δ15N values in both predator and prey, implying that food source and feeding strategy could be inferred from δ15N values. The isotopic data suggested that thick-billed murres (Uria lomvia) foraged in specific locations where food quality and abundance were high, whereas black-legged kittiwakes (Rissa tridactyla) tended to be more opportunistic. Use of isotopic methods, which inherently integrate over a longer period of an organism's lifespan, may be useful in understanding behavior and condition of adults during the non-breeding season, a key period identified by Renner et al. (2014).

7. SUBSISTENCE HARVEST

In addition to providing ~40% of the US catch of fish and shellfish, the Bering Sea provides ~11 million kg of fish, marine mammals and birds to support Alaskan Natives and others living along the coastline and on the islands of the Bering Sea. Subsistence harvests provide a significant portion of the food consumed by Alaskan Native communities. Using a cluster analysis approach, Renner and Huntington (2014) found that the type of food harvested by different coastal communities split along geographic lines, reflecting food availability. For instance, in the villages in the northern Bering Sea and in the Chukchi and Beaufort Seas, harvest is dominated by marine mammals, while the harvest in villages in the southern Bering Sea is dominated by fish and other seafood. These harvest characteristics are similar to ecoregions defined on biological patterns Sigler et al. (2011). Changes in subsistence harvest could be used to monitor changes in individual species within regional ecosystems forced by climate change.

8. REFERENCES


The Bering Sea Project was powered by a tremendous group of people, including principal investigators, post-docs and graduate students, ship and fieldcamp crews, research technicians, program and fiscal managers, and many others. In the following few pages we introduce you to a sample of the characters who collectively built this project.
People of the Bering Sea Project

**Nick Bond**
*University of Washington*

**What was your role?**
I was in the lower-trophic level modeling group, representing the atmospheric/climate forcing element.

**What was the best/worst part of your job?**
It was very gratifying to be able to participate in a local traditional knowledge project lead by Henry Huntington on how sea ice concentrations and winds have impacted the success of walruses hunts from St. Lawrence Island. The vertically-integrated model that was developed for the Bering Sea project was by necessity very complicated, and hence required considerable computational resources and analysis time. This limited our ability to fully explore how past and future climate variations influence the ecosystem of the Bering Sea.

**What is one thing you take away from the experience?**
The Bering Sea project was the largest and most complex project in which I have participated. Efforts of this scope are necessary to be able to adequately tackle major problems related to how systems respond to variations in the physical environment.

**What’s next for you?**
My research will continue to focus on how present fluctuations and future trends in the climate are liable to play out in Alaskan waters. My attention is starting to be directed towards the Chukchi and Beaufort Seas, and the expertise I have gained as part of the Bering Sea Project is proving to be very useful.

**Ann Fienup-Riordan**
*Calista Elders Council*

**What was your role?**
I served as co-PI with Mark John on the Nelson Island Natural and Cultural History Project, one of two “land-based” components of the Bering Sea Project. We organized gatherings of elders from southwest Alaska on a range of topics—place names, weather, sea ice conditions, harvesting patterns, animal and plant communities—and traveled with youth and elders out on the land to better understand people’s experiences living on the Bering Sea coast.

**What was the best/worst part of your job?**
The best part of my job was working with Yup’ik elders—during gatherings and meetings in Nelson Island villages as well as during our summer circumnavigation of the island. They teach their youth, “Do not live without an elder,” and it’s good advice. The sad part is that many we worked with have since passed away, but their teachings live on.

**What is one thing you take away from the experience?**
At the project’s beginning I had no idea how rich and rewarding our collaboration would be with oceanographers and other scientists. An apt revision of the old Yup’ik adage is “Do not live without a scientist.” They’re fun to work with, too.

**What’s next for you?**
Work on Nelson Island led both Mark and me directly into work on the lower Yukon and other Bering Sea communities. The Nelson Island Project was the first detailed regional study that the Calista Elders Council attempted. Different parts of southwest Alaska have hugely different histories, reflected in their present strengths and challenges. Focusing on one village group at a time was a strategy born directly out of the Bering Sea Project, and we’re learning how much these histories mean to local residents. I thought my work on the Yukon-Kuskokwim Delta was near done. Instead, it’s just beginning.

**Bob Campbell**
*University of Rhode Island*

**What was your role?**
I was part of the science team on the spring research cruises where I measured the feeding and reproductive rates of zooplankton to provide estimates of energy flow through this important component of the ecosystem.

**What was the best/worst part of your job?**
I have always loved going to sea and especially working in ice-covered waters on the US Coast Guard icebreaker Healy. The scenery is amazing, and the Healy is a really great platform from which to do science. As far as lowlights, the ever-increasing need to write more proposals to do research and the ever-decreasing funding success rates for those proposals are at the top of my list. In my opinion, it really isn’t the most productive way to do science.

**What is one thing you take away from the experience?**
I guess one thing that really surprised me was how highly productive the ice-associated spring bloom is in the Bering Sea and how quickly the zooplankton respond by ramping up reproduction. The life cycles of both lower and higher trophic level animals are inextricably linked to this event and therefore alterations to spring bloom timing due to climate change could have detrimental consequences for the productivity of the ecosystem, including important fisheries.

**What’s next for you?**
It became glaringly apparent to me in the course of this project that our lack of understanding of overwintering strategies and survival rates of key organisms is hampering our ability to fully understand the ecosystem and to predict the impacts a warmer ocean might have on the ecosystem as a whole and on economically important fisheries in particular. To this end, I am working with other US and European scientists to develop plans for future international ecosystem studies that will focus on winter in high latitude seas.

**Nate Jones**
*Moss Landing Marine Laboratories*

**What was your role?**
I spent three summers working on ships as a graduate student studying seabirds while they foraged on the open ocean.

**What was the best/worst part of your job?**
I was thrilled to spend time at sea with fine teams of fellow researchers and crew, and it was satisfying to find opportunities to share my results through presentations and papers. I was less excited about the many long hours spent behind computer screens filling out permits and applications, and teaching myself the computer programs necessary for data analyses.

**What is one thing you take away from the experience?**
I am privileged to have been a part of such a large and well-coordinated scientific effort. It’s amazing how teams of passionate researchers can be so creative and productive, and yet still understand so little; the marine environment is incredibly complex and difficult to study. There will always be more we can learn, and that is exciting!

**What’s next for you?**
The study of natural systems is the most inspiring challenge I have found. After working with the Bering Sea Project I understand how effective collaboration is when approaching this complex field. I will certainly employ a cooperative ethic as I continue to learn more about the world, from oceans to deserts, and back again.
Ron Heintz  
NOAA/Alaska Fisheries Science Center

**What was your role?**  
My role was to evaluate the general well being of the fish we caught on research surveys. My colleagues and I did this by measuring how fat the fish were. Fat is hard to come by for juvenile fish, and the fish that were fattest were doing the best. Ultimately we wanted to relate their fat content to measurements of environmental state so we could predict how fish will do in the future.

**What was the best/worst part of your job?**  
The best and worst part of the job was going to sea. Prior to the Bering Sea Project, I had never gone to sea on a large ship. I remember one day on the icebreaker Healy when I noticed that I could not see land in any direction from the deck. I realized that I had never been that far out to sea before. I am normally a lab guy and being that far out to sea was both exhilarating and scary. And on subsequent cruises the conditions were less hospitable and I found it difficult keeping my meals in my stomach.

**What is one thing you take away from the experience?**  
The one thing I took away from this project is that when a bunch of dedicated scientists put their collective minds together they can make incredible progress. I am honored to be considered part of this group.

**What’s next for you?**  
My next project is to better understand how environment influences the survival of juvenile fish, and the fish that were fattest were doing the best, ultimately we wanted to relate their fat content to measurements of environmental state so we could predict how fish will do in the future.

Katrin Iken  
University of Alaska Fairbanks

**What was your role?**  
I was one of the investigators investigating sea ice—we studied the organisms living within sea ice and their connection to the water column and seafloor organisms through food web linkages.

**What was the best/worst part of your job?**  
The best part was to go out on the field cruises and work with a group of amazing people and learn more about this unique environment. The worst part may have been not being able to go on all cruises during all seasons, especially during some of the exciting early spring times when there was the most sea ice.

**What is one thing you take away from the experience?**  
It’s the network of people that I got to know and interact with during that time, and since then! The project ends but those connections last and spark new discussions and ideas. It also is very gratifying to see graduate students complete their work within a project and then move on to be young scientists in their own right.

**What’s next for you?**  
I am involved in a number of projects in the Arctic, and some of this work is based on the experiences I have gained during the time of the Bering Sea Project. In particular, we have made some important steps forward in the use of stable isotopes as a technique to investigate food webs, and we are applying and developing this new knowledge further now.

Lee Cooper and Jacqueline Grebmeier  
University of Maryland Center for Environmental Science

**What was your role?**  
Lee and I had leadership roles, including service as shipboard chief scientist during three icebreaker cruises in the northern Bering Sea that have led to a better understanding of the late winter ecosystem in the northern Bering Sea that provides a critical bivalve prey base for diving seaducks and walruses.

**What was the best/worst part of your job?**  
The highlight of our research was working in the field together during the cold, but beautiful, ice-covered late winter period south of St. Lawrence Island. This season is teeming with breeding spectacled eiders and transiting walruses, both that feed on the rich bottom animal life in the region. A low point was dealing with frozen seawater hoses and mud at below zero temperatures in the dark.

**What is one thing you take away from the experience?**  
The spectacled eiders “dance” when they court to attract a mate, while sharing a limited opening in the sea ice with thousands of other seaducks that socialize and dive to the ocean depths to feed on a rich base of clams living in the mud. At the same time, these seabirds must be ever alert to a sneaky walrus that might rise from the depth to eat them. This behavior by walruses and eider courtship had never been observed before our cruise when we hosted a BBC Frozen Planet camera crew.

**What’s next for you?**  
The northern Bering Sea ecosystem has regions of high benthic biomass or “hotspots” of biology that are susceptible to warming seawater temperatures and variable ice conditions. We are continuing to track these productive features through the international Distributed Biological Observatory, an observing network funded by NSF and other US and international agencies. We have also proposed to sample in late summer to track carbon transfer through the biological system and to develop a network model to evaluate status and trends as the ecosystem responds to environmental change.

Brie Drummond  
US Fish & Wildlife Service

**What was your role?**  
I participated in the fieldwork for the colony-based seabird studies at St. George Island and worked on data analysis and publication of results coming out of that work.

**What was the best/worst part of your job?**  
The first couple of years we had a hard time catching enough birds for the survival part of our study, so the third year we brought on additional personnel and really went at it hard and had great success catching and banding lots of birds — that was a big highlight. The downside was having to come back into the office every fall after grand adventures in the field!

**What is one thing you take away from the experience?**  
How diverse and complex the Bering Sea ecosystem is: Expanding from our small part in the project, I was amazed to find that seabirds from colonies on St. Paul and St. George islands foraged for food completely differently, despite the two islands being relatively close to each other.

**What’s next for you?**  
My current project is working on a large seabird diet database for the Alaska Maritime National Wildlife Refuge, which includes much of the seabird diet data collected during the Bering Sea Project. I enjoy seeing the data from that project built into the refuge’s long-term monitoring program.
Janet Duffy-Anderson  
NOAA/Alaska Fisheries Science Center

What was your role?
I was a lead investigator studying the influence of climate variability on the growth, survival, and recruitment of the early life stages of marine fish, particularly Pacific cod, arrowtooth flounder, and walleye pollock.

What was the best/worst part of your job?
By far the best part of my job was interacting with scientists, students, managers, and stakeholders who shared the same passion and concern for Bering Sea. This six-year process has re-shaped my thinking about ecosystem activators and constraints, and by that measure I count it as a high-water mark in my career. The worst part? Habitually waking up at sea with fish scales in my pajamas. Showers do nothing.

What is one thing you take away from the experience?
I had the great fortune to work with the bright and talented young researchers who will form the next generation of scientific excellence. The interns, undergraduate students, graduate students, and postdoctoral associates who were involved in this effort gave their all in terms of time, ideas, energy, and creativity; I count myself lucky to have been a part of their science!

What’s next for you?
I am continuing to follow the path that this integrated research effort opened. My next focus will be on overwintering ecology of young walleye pollock and Pacific cod, picking up my research where the Bering Sea Project left off. We think winters in Alaska are hard, but imagine spending three months living in water that’s just barely above freezing!

Kelly Benoit-Bird  
Oregon State University

What was your role?
The best part was working with a diverse team, bringing together the data and viewpoints from many different approaches – acoustics, biorenergetics, predator tagging, visual observations, and oceanography – to tell a story about how the Bering Sea works. My least favorite part was dealing with the unpredictable (and sometimes scary) weather the Bering Sea dealt us while we were sampling.

What was the best/worst part of your job?
I was reminded that when you’re in the middle of something, you don’t always have perspective on what’s really happening. During our project, my collaborator and I were working jointly on two vessels. While sampling one rough and foggy day, I looked over at his boat throwing violently and thought “I’m really glad I’m not on that boat”. I learned later that he was having the same thought looking back at us. It’s also been true for this project. It has taken a lot of time and perspective to understand how all of our data fits together to tell the Bering Sea’s story.

What’s next for you?
In the Bering Sea, we were able to compare the strategies of three very different top predators when facing similar environmental challenges. This approach helped us to understand just how important the way food is distributed is for animal’s to successfully forage. I’m now working to expand this comparative approach across ecosystem types including consumers at various steps in the food web to try to understand the general rules animals follow to make a living in the ocean.

Alan Haynie  
NOAA/Alaska Fisheries Science Center

What was your role?
We combined a variety of data on commercial fishing locations and environmental conditions with different types of statistical models to examine and predict how management institutions, economics, and shifting fish populations jointly determine where, when, and how fishing occurs in the Bering Sea pollock and Pacific cod fisheries.

What was the best/worst part of your job?
The highlight of the project was being part of a wonderful group of interdisciplinary scientists and having the opportunity to see their work evolve over several years. The third annual principal investigators’ meeting was probably the peak of this experience, where interdisciplinary synergy took off as people began to really understand the issues of different parts of the project and provide deep and valuable input across disciplines. The low point was the awareness that true integration is challenging and time-consuming, although now more than ever I believe that it is worth the effort.

What is one thing you take away from the experience?
In the fisheries that we examined, we found that the benefits and costs of fishing in different places and the manner in which fish avoid very cold water both mean that fishing fleets will not merely shift to the north in the Bering Sea. While the manner in which climate impacts fisheries is very complex, we have management and monitoring choices that can help mitigate the negative impacts.

What’s next for you?
Our work in the Bering Sea Project has contributed directly to an ongoing NOAA Fisheries initiative, the Spatial Economics Toolbox for Fisheries (FishSET). FishSET combines data organization tools, best practices, and a large suite of models to allow us to better understand how climate, management, and economics impact different fisheries. As well as allowing us to study what’s important for sustainable and productive use of marine resources, this will allow managers to develop and modify policies to allow fisheries to better adjust to a changing environment.

Tadayasu Uchiyama  
University of Alaska Fairbanks

What was your role?
As a PhD student supervised by Gordon Kruse and Franz Mueter, I developed multispecies biomass dynamics models of the eastern Bering Sea groundfish community— including walleye pollock, Pacific cod, arrowtooth flounder, yellowfin sole, rock sole, flathead sole, Alaska plaice— and predator-prey interactions among them. Using the models I developed, I also assessed possible effects of the changing climate on how these fishes interact with each other.

What was the best/worst part of your job?
The best part of my job was learning and exploring various types of population models and tools to build and implement such models in the context of natural resource management. For the worst, many would point to a lack of fieldwork in my project, but it didn’t bother me too much. Instead, I suffered more from a constant dilemma between improving my models and still keeping them relatively simple, as the type of model I worked on was fairly simple by design (for good reasons!) compared to cohort-based or individual-based population models.

What is one thing you take away from the experience?
Through working on this project, I have learned that Alaska’s fisheries are not only one of the most productive, but also one of the best managed for sustainability, based on extensive scientific research and data. It feels good to think that my work has been a part of an ongoing effort to further our understanding of the Bering Sea system, and that it may contribute to protection and wise use of our marine resources.

What’s next for you?
This research was part of my dissertation work at University of Alaska Fairbanks, School of Fisheries and Ocean Sciences. I wish to continue working in the field of fisheries resource management.
What was your role?
I led the research in the community of Emmonak, focusing on changes in how residents experience and interact with their landscape and the animals they rely on for subsistence.

What was the best/worst part of your job?
I love working on the ground in communities, so my time conducting fieldwork in Emmonak was a definite highlight. Beyond what I learn in the research, part of what makes fieldwork so much fun for me is working side-by-side with people fishing or picking berries or just chatting at their kitchen tables over tea and dry fish. These human connections really help me understand what’s important about our research. On the flip side, we collect a lot of survey data that all needs to be coded. Hunching over pages and pages of survey data with a red pen is definitely not the most glamorous part of my job.

What is one thing you take away from the experience?
One of our findings from Emmonak involved dramatic changes in the seasonality and species-focus of seal harvests. As a researcher who usually works in interior Alaska communities, I’m less familiar with marine mammal harvest patterns. It was really interesting for me to work with local residents and other research colleagues to better understand the role and importance of marine mammal harvests in subsistence economies.

What’s next for you?
This research occurred right at the cusp of serious declines in the Yukon River Chinook salmon run, the backbone of Emmonak’s subsistence economy. While salmon were not a focal species of the BSERP project, our research in Emmonak launched a series of research projects to address this decline. We are currently working on projects looking at historical and between seasons and years. This is also very challenging to do.

What was the best/worst part of your job?
The best part was being on a ship in the Bering Sea in summer—looking at the plankton and birds and whales at the end of the day. The hardest part was organizing and condensing data from many different stations, regions, and years so that it could be used by other scientists.

What is one thing you take away from the experience?
Two things: 1. Dilution grazing experiments may underestimate microzooplankton grazing during certain stages of blooms due to production and release of something called “allelochemicals.” 2. Mixotrophic ciliates (organisms that produce their own food, like plants, and also eat, like animals) are unusually abundant during summer stratification on the eastern Bering Sea continental shelf, and this may affect both primary production and secondary production by microzooplankton.

What’s next for you?
The Bering Sea project rekindled my interest in the chemical ecology of phytoplankton and in the role of mixotrophic ciliates in marine ecosystems. I’ve been part of a Norwegian Research Council project investigating Phaeocystis blooms and grazing by microzooplankton and copepods in the Barents Sea, and I am a co-investigator on an NSF project investigating polyunsaturated fatty acid production by diatoms, and its effects on microzooplankton and trophic transfer to copepods. Mixotrophic ciliates are ubiquitous in Arctic seas during stratification, and I am working with colleagues to synthesize data on their occurrence and potential significance.

What was your role?
I investigated the distribution, abundance and grazing by microzooplankton in summer and provided data for inclusion of microzooplankton (small planktonic grazers, < 200 microns in size) in models of the Bering Sea ecosystem.

What was the best/worst part of your job?
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People of the Bering Sea Project

Peggy Sullivan
University of Washington

What was your role?
I performed time-series and ice-data analysis looking at ice-influenced seasonal changes in the water column over the eastern Bering Sea shelf. Additionally, management of incoming data, metadata and distribution was on my plate, and I participated in research-cruise collection of hydrographic data.

What was the best/worst part of your job?
Being immersed in our data was the highlight of my work. In analyzing these years of data along with satellite data and earlier sets from the same key biophysical mooring sites (named M2, M4, M5, MB), interesting longer-term trends and repeated patterns emerged. The data showed the influence of ice formation and ice melt on temperature and salinity signatures, and spoke to fresh-water movement over the shelf. Metadata woes presented a lowlight to the project. Though a vital element for data use and further research, this descriptive mechanism is tedious to compile and is confusing, as standards and practices only slowly seep into research projects. Fortunately the metadata angst has steered the project onto a better-defined track towards metadata expertise.

What is one thing you take away from the experience?
Amid many data deadlines and evolving data and metadata specifications, I acquired a huge appreciation for the NCAR/EOL software and data experts who created and implemented the data archive. They presented professional and highly informative guidance toward compiling appropriate metadata and working with useable data formats and specifications. They frequently went the extra mile to support our success on the data and metadata side of the project, and I look forward to working with them in the future.

What’s next for you?
I am working on ice draft data sets from the Chukchi Sea that are fairly new to our data-collection activities, and that are very dense and require some wrangling. The seasonality of ice cover in this Arctic region will be an interesting comparison to seasonal ice in the Bering Sea.

Carol Ladd
NOAA/Pacific Marine Environmental Laboratories

What was your role?
As a research scientist, my role was to study the physical oceanography of the Bering Sea. I went to sea to gather data, analyzed field and satellite data, and wrote and published papers describing my results.

What was the best/worst part of your job?
Going to sea is always the best part of my job and the worst. I participated on four cruises over the duration of the project, including two on the US Coast Guard icebreaker Healy. I love the feel of the ocean, the camaraderie of life on a ship, and the physical aspect of the work. The worst part is that going to sea is very disruptive to the rest of my life and by the end of a three-week cruise, I can’t wait to get home to see my family.

What is one thing you take away from the experience?
It was very satisfying to be involved in such a large, successful program that really enhanced our understanding of the Bering Sea ecosystem. The experiences that will stay with me for the rest of my life revolve around the field work. Working on the sea ice is probably one of the most spectacular experiences of my life. The scenery is stunning and standing on a thin sheet of ice in the middle of the Bering Sea is something that very few people get to experience.

What’s next for you?
The ocean circulation of the Bering Sea flows through Bering Strait into the Arctic Ocean. Following that circulation pathway, my latest research is focused on the physical oceanography of the Arctic and how the physics of the ocean influences Arctic ecosystems.

George Noongwook
Savoonga Whaling Captains Association, Savoonga, Alaska

What was your role?
I was the researcher in charge of the LITK study in Savoonga, my home town.

What was the best/worst part of your job?
The best part was interacting with people and meeting people with whom I shared common interests, for example ice and weather and how things are changing. That part I liked, because we could learn so much from all the scientists and others looking at the whole Bering Sea. And I got to learn a lot about my own culture, interacting with people from other regions, too, which made me appreciate what I have. The only thing I didn’t like was having to travel so much, since the meetings were a long way from Savoonga, but it was still worth it to meet people.

What is one thing you take away from the experience?
The ability to replicate something that we already know and apply that to science to make our knowledge work both ways. The cooperative sharing of information is wonderful, and we learned how to do it in a productive way.

What’s next for you?
I want to continue, to put together the whole package of my own views, beliefs, and opinions, about what we know here. I want to put it in one place, about our environment, our dancing, our culture, to see what I come up with, to show what a Yupik person is. I just need the time!

Franz Mueter
University of Alaska Fairbanks

What was your role?
I was co-investigator on three project components: The first analyzed historical data sets to provide a long-term context for the four field seasons, as well as forecasting the response of walleye pollock in the Bering Sea to climate change. The second component developed multi-species models to examine the role of species interactions in determining the ups and downs of commercial fish species in response to fishing and climate variability. The third component examined how the early life history stages of commercially important fish species respond to climate variability.

What was the best/worst part of your job?
A highlight of my job was collaborating with other researchers, in particular students, and contributing to several groundbreaking papers and stories that really helped us understand the processes that determine the survival of young walleye pollock and how they may respond to climate change in the future. The worst part has to be the endless string of semi-annual reports for three project components.

What is one thing you take away from the experience?
It has been both frustrating and rewarding to work with a large number of co-investigators on a project that included such a wide range of studies. Integrating and synthesizing across these many studies is nearly impossible, but there were moments when fruitful ideas and conclusions emerged from the ‘collective mind’ that might otherwise not have seen the light of day or would have emerged much later.

What’s next for you?
While data analyses and interpreting the results remain my favorite aspects of any research project, I definitely learned a thing or two about working in a multi-investigator, multi-disciplinary project. This has given me the courage to apply for and take on other large projects in the Gulf of Alaska and the Arctic. My experiences during the Bering Sea Project have also broadened my perspective considerably, and I see my future research expanding to tackle both the ecological and socio-economic dimensions of marine ecosystems.
People of the Bering Sea Project

**Jessica Cross**
NOAA/Pacific Marine Environmental Laboratory

**What was your role?**
I was a doctoral student collecting inorganic and organic carbon chemistry data in order to better understand Ocean Acidification and carbon transformation processes in the Bering Sea.

**What was the best/worst part of your job?**
While I was in school and even now that I’ve graduated, I always tell other students that the best way to learn oceanography is by going to sea during an interdisciplinary project. The opportunity to experience different types of research in one context made the science of oceanography very real for me, and kept every day in the field interesting. However, there are challenges to fieldwork, and my least favorite was jellyfish! While the species in the Bering Sea don’t sting, their tentacles can stain your skin and clothes, and worst of all they often clog instruments.

**What is one thing you take away from the experience?**
This project was an excellent opportunity to immerse myself in collaborative, interdisciplinary research. The interconnected focus of the project conducted helped me to think of the entire project as a whole and put my research project in a much larger, ecosystem-level context from the very beginning. It also allowed me to form important connections with a very broad cross-section of the scientific community. Especially as a student, this never permitted me to form the bad habit of thinking of too narrowly around just my subject, group, or department. I learned the value of synthesis very early, and continue to prioritize big-picture thinking in my current work.

**What’s next for you?**
After earning my Ph.D. through the Bering Sea Project, I took a postdoctoral position at the Ocean Acidification Research Center at the University of Alaska, Fairbanks. We focus on an even bigger picture: Our work uses cutting edge technology and new data to better understand acidification, carbon transport and transformation processes for all the shelf seas along the Alaskan coast, and the implications of these processes for the Arctic Ocean.

**André Punt**
University of Washington

**What was your role?**
I led the management strategy evaluation component of the Bering Sea Project, and was involved in linking that component to the FEAST and FAMINE models, which were developed by other project participants. I was also the University of Washington Principal Investigator for the project.

**What was the best/worst part of your job?**
Seeing that it is possible to develop a vertically-integrated model that is spatially resolved and that links processes from climate through to management. My involvement was limited to that of a supervisor – it is much more fun to get into the coding of the model – when the model works!

**What is one thing you take away from the experience?**
Constructing a spatially-resolved vertically-integrated model is much more complicated in practice than in theory. A key outcome from the MSE project was a paper co-authored with project partners on lessons learnt from implementing the model; those lessons don’t only relate to science and modelling but also to people and time.

**What’s next for you?**
I am involved in many projects at present, some of which are scientific! I am continuing to implement Management Strategy Approaches with an ecosystem focus, most recently in the fishery for small pelagic fishes off southern Australia. I am also providing strategic advice for the modelling group that is part of the Gulf of Alaska Integrated Ecosystem Research Program, based on my experiences with the Bering Sea Project.

**Nancy Kachel**
NOAA/Pacific Marine Environmental Laboratories

**What was your role?**
I took a big role in planning and logistics for most the cruises, was the lead hydrographer organizing water sampling and collecting data on four of the cruises, and a chief scientist on fall Eco-FOCI cruises.

**What was the best/worst part of your job?**
The best part of this project was working together with a whole range of scientists focused on understanding the Bering Sea ecosystem, who support and collaborated with one another in unforeseen ways over a long enough period of time so that the knowledge gained is truly remarkable.

**What is one thing you take away from the experience?**
It was a magnificent privilege to walk out on the sea ice to collect samples from the ice and seawater below, although challenging when a foot of snow covered the uneven ice. After donning dry suits, hauling about 200 pounds of gear forward to the bow, and climbing down the steep ramp to the ice, we resembled circus clowns falling down so often while hauling our sleds that the Coasties watching us were in stitches from laughing so hard.

**What’s next for you?**
I officially retired at the end of 2014, but am continuing to work finishing up manuscripts for the Bering Sea Project’s fourth special issue, and for the Gulf of Alaska Integrated Ecosystem Research Program, synthesizing almost 20 years of work in the Bering and 30 years in the Gulf of Alaska.

**Thomas Van Pelt**
North Pacific Research Board

**What was your role?**
My job was mainly desk work, but early in the project I spent several weeks on board the icebreaker Healy, helping with the fieldwork. That time at sea in the frozen ocean with a great bunch of scientists and crew was a major highlight. In terms of lowlights, it’s hard to compete with having to triple-check a two-foot high stack of funding paperwork!

**What was the best/worst part of your job?**
It has been gratifying to see papers published that feature new collaborations and integrated perspectives. With nearly 100 principal investigators involved, integration and cooperation among quite different groups of scientists was challenging. But there was a transition midway through the Bering Sea Project when the idea that the whole of the project was more than the sum of the individual research seemed to get more traction.

**What is one thing you take away from the experience?**
I started my career as a biologist working with puffins and their prey—a pretty niche field of study. In contrast, management of the Bering Sea Project has been an immersion in mega-scale research. I’ll be aiming for a middle ground in my next project!
What was your role?
I oversaw measurements of nutrients and oxygen from many thousands of water samples, ice melt samples, and from the science water-supply systems aboard the ships. I also helped manage synthesis of the multi-disciplinary data sets.

What was the best/worst part of your job?
Sailing through the ice on the icebreaker Healy and working on the ice was the highlight of the program for me. At the same time, being away from home during a family crisis can make these expeditions especially difficult.

What is one thing you take away from the experience?
Success of the Bering Sea Project was due in large part from the multi-disciplinary, multi-agency approach to study the ecosystem. It is my hope that the Bering Sea program serves as a model for future ecosystem studies.

What’s next for you?
I continue to work with NOAA in collecting data from the Bering Sea. These data will be especially important if a stanza of warm years once again disrupts the ecosystem.

What was your role?
I was a PhD student during the Bering Sea Project and worked with both the Ichthyoplankton Dynamics and Seasonal Bioenergetics groups; my dissertation focused on the ecology and energetics of early life stages of walleye pollock in the eastern Bering Sea. I participated in three field seasons, sorted and processed samples in the lab, and learned a lot about the statistical software called “R”.

What was the best/worst part of your job?
After the 2008 Bering Sea survey, I got off the USCG icebreaker Healy at St. Paul Island in the Pribilof Islands. We were scheduled to fly home later that same day, but got weathered in for a few extra days due to fog and high winds. That time spent on St. Paul was definitely a highlight – wildflowers, birds, fur seals, and arctic foxes! Back in the office, a common lowlight was requesting, querying, obtaining, QA/QC’ing, and pre-processing data from multiple sources necessary for my analyses.

What is one thing you take away from the experience?
Before working on the Bering Sea Project, my research had focused on subtidal ecology. I spent nearly a decade doing scientific diving research, mostly from small boats, just a dive buddy and myself. When I was looking at PhD programs, I wanted a more collaborative project. With ~100 principal investigators in the Bering Sea Project, I certainly got my wish and learned the benefits of collaboration! I was fortunate to work with, and continue to work with, great people who are also great scientists.

What’s next for you?
I am currently an NRC Postdoctoral Research Associate at NOAA Fisheries in Juneau, Alaska. My research looks at predator-prey dynamics for several focal species, including walleye pollock, in the North Pacific under variable climate conditions. I am also involved in a project focused on seasonal and interannual changes in ichthyoplankton and fish community composition in the eastern Bering Sea. My work builds on collaborations formed during the Bering Sea Project.

What was your role?
I was responsible for data management support to the Bering Sea Project, archiving of data and research products from the project, and development of a web site for easy access for anyone to browse and download data from the archive.

What was the best/worst part of your job?
The part of the job I liked least? Well, I’m uncomfortable being the only one talking in a group of people, so I would have to say that it was getting up in front of a room full of scientists and program managers and presenting the yearly report on data management. Always thought it was much more interesting when I finished and took questions.

What is one thing you take away from the experience?
The Calista Elders Council guided a Local and Traditional Knowledge project led by Ann Fienup-Riordan. We developed a place-based website that maps more than 400 historic names on Nelson Island, Alaska. This web site was originally intended to be password protected, but when it was completed the reception was so positive that community members embraced the idea of using the Internet to provide public access. It was explained to me that not only would this help the young people learn the Yup’ik way of living, but precise place names could actually be life-saving knowledge to find someone caught in a storm. That’s when I realized the immeasurable value of these data.

What’s next for you?
The Earth Observing Laboratory has developed a web site and begun archiving datasets from the long term Distributed Biological Observatory (DBO), a multi-national project to investigate biological responses to a rapidly changing Arctic marine ecosystem. The DBO includes the northern Bering Sea.
Pictured here are many of the faces of Bering Sea Project people, including PIs, students, and others.