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Collaborative research on the pelagic ecosystem of the southeastern Bering Sea shelf

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Abstract

Two Bering Sea marine research programs collaborated during the final years of the 1990s to forge advances in understanding the southeastern Bering Sea pelagic ecosystem. Southeast Bering Sea Carrying Capacity, sponsored by NOAA Coastal Ocean Program, investigated processes on the middle and outer shelf and the continental slope. The Inner Front Program, sponsored by NSF, investigated processes of the inner domain and the front between the inner and middle domains. The purposes of these programs were to (1) increase understanding of the southeastern Bering Sea ecosystem, including the roles of juvenile walleye pollock, (2) investigate the hypothesis that elevated primary production at the inner front provides a summer-long energy source for the food web, and (3) develop and test annual indices of pre-recruit pollock abundance. The observations occurred during a period of unusually large variability in the marine climate, including a possible regime shift. Sea-ice cover ranged from near zero to one of the heaviest ice years in recent decades. Sea-surface temperatures reached record highs during summer 1997, whereas 1999 was noted for its low Bering Sea temperatures. Moreover, the first recorded observations of coccolithophore blooms on the shelf were realized in 1997, and these blooms now appear to be persistent. The programs' results include an archive of physical and biological time series that emphasize large year-to-year regional variability, and an Oscillating Control Hypothesis that relates marine productivity to climate forcing. Further investigations are needed of the confluences of interannual and even intra-seasonal variability with low-frequency climate variability as potential producers of major, abrupt changes in the southeastern Bering Sea ecosystem.

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1. The Bering Sea

The Bering Sea (51°–66°N, 157°W–163°E) is a unique laboratory for many ocean processes. The sea surface is ice covered for a significant portion of the year. The region has large seasonal signals of light level, heat fluxes, and wind stresses. Large interannual variations in these parameters exist either as a result of, or contribute to, the Arctic

Oscillation, Pacific Decadal Oscillation and El Niño-Southern Oscillation (Overland et al., 2002). However, there are no significant trends in these Bering Sea signals (Royer and Grosch, 2002). In addition to the seasonal ice cover restricting vertical fluxes there, the accumulation of fresh-water in the North Pacific creates a vertical density gradient that serves as a lid that also inhibits vertical mixing. The deep global ocean circulation terminates in the North Pacific as it reverses direction, and this lid limits the formation of deep water in the North Pacific and Bering Sea. The

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Bering Sea also contributes to global ocean circulation patterns through the control of salt, volume, and heat fluxes into the Arctic Ocean (Schumacher and Stabeno, 1998).

The high latitude of the Bering Sea affects the atmosphere through the control of fluxes into the overlying air masses. Very cold and dry air masses from Siberia can move over the Bering Sea where massive amounts of heat and water can be extracted. Changes in these fluxes can have remote consequences on the atmosphere through global teleconnections. This is especially true for the conditions over North America, “downstream” of the Bering Sea. The presence of ice severely limits these fluxes so that year-to-year changes in ice cover there will affect interannual variations in atmospheric circulation. Though considered by many to be a remote sea, the influences of the Bering Sea are not isolated.

The Bering Sea contains abundant biological resources, including many species of fish, shellfish, seabirds, and marine mammals. Some of the world’s most extensive eelgrass beds, habitat for many marine species, are found here. Each summer brings additional migratory populations of seabirds and marine mammals. The biological productivity of the region has led to extensive harvest of resources. At present almost half of the US annual catch of fish and shellfish has its origin in Alaskan waters, and the large percentage of that comes from the eastern Bering Sea shelf. Dutch Harbor, Alaska, is one of the United States’ busiest fishing ports. The walleye pollock, salmon, halibut and crab fisheries generate over 2 billion dollars in revenue each year. Over the last few decades, some species of fish, shellfish, seabirds, and marine mammals have experienced significant fluctuations in abundance. Such changes have brought awareness of our relative ignorance in understanding the ecosystem and raised the need for research geared to promote better management of regional living resources.

The process studies reported in this issue focus on the very broad (> 500 km) shelf of the southeastern Bering Sea (Fig. 1), which is one of the most productive regions of this sea and experiences a seasonal ice cover. There are several cross-shelf fronts that influence productivity, and these

fronts are the subject of some of these studies. Of particular interest are the mechanisms that inject nutrients into the euphotic zone. The studies were conducted during contrasting years with relatively warm and cold temperatures. There were also changes in regional biotic communities. For example, a recurrent coccolithophore bloom was first seen in 1997, the jellyfish biomass increased greatly, and populations of some species of birds and mammals declined or experienced unusually large mortality events. The significance and duration of these changes remain to be determined. Nevertheless, the results of the studies reported in this issue will provide a better understanding of processes on the shelf of the southeastern Bering Sea and can be applied to many similar marine processes elsewhere. A new hypothesis, the Oscillating Control Hypothesis (OCH), provides a conceptual model of the responses of the Bering Sea to alternating warm and cold periods and helps to outline the interactions of many trophic levels (Hunt et al., 2003). It may help in predicting how the trophic structure of the Bering Sea could respond to future climate changes.

The significance of results reported in this issue apply far beyond the geographic boundaries of the Bering Sea. These studies should provide insight into similar processes that occur in other high-latitude seas such as the Norwegian, Kara, Ross and Wedell seas. With a better understanding of climate variability that might accompany improved measurements and the possibility of low-frequency climate changes at high latitudes, the value of these studies should increase.

2. Two complementary research programs

During the last years of the 1990s, two research programs contributed jointly to the substantial marine research that has occurred over the last three decades on the southeastern Bering Sea. The two coordinated research programs are Inner Front (InFront; 1997–2000), which was supported by the National Science Foundation (Prolonged Production and Trophic Transfer to Predators: Processes at the Inner Front of the S.E. Bering Sea), and Southeast Bering Sea Carrying Capacity

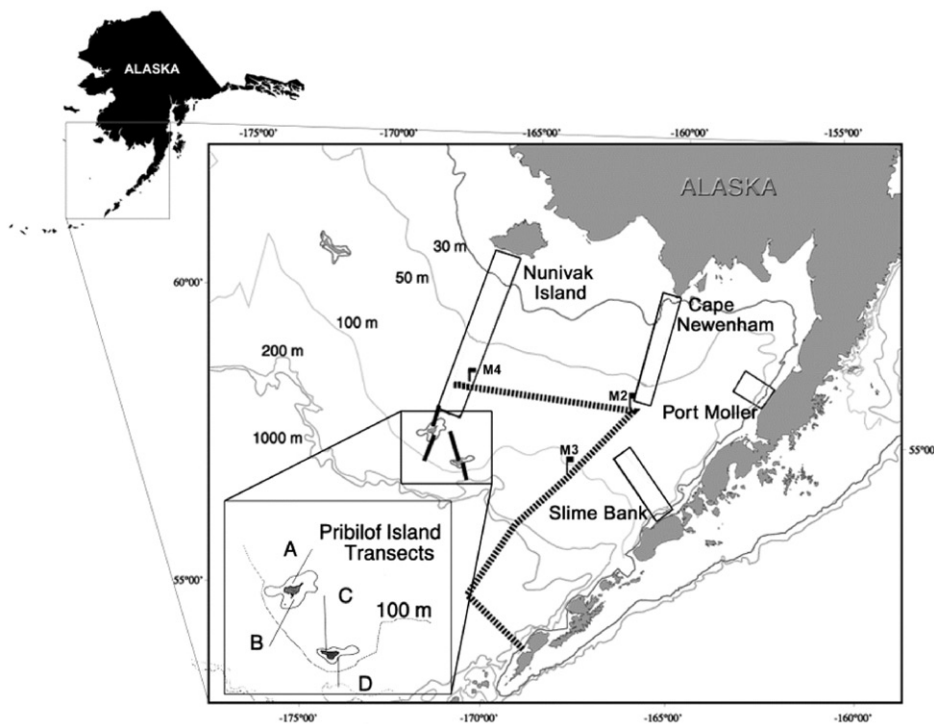


Fig. 1. A bathymetric map of the southeastern Bering Sea shelf shows the location of study areas investigated by the Inner Front (InFront) and the Southeastern Bering Sea Carrying Capacity (SEBSCC) programs. Dashed lines indicate transects covered by SEBSCC at least twice yearly when servicing the moorings at M2, M3, and M4. Transects A, B, C and D at the Pribilof islands were visited yearly in the fall and once in the summer by SEBSCC cruises. Rectangles at Nunivak Island, Cape Newenham, Port Moller and Slime Bank mark the locations of the principal study sites occupied during the InFront study. Collaborative summer cruises with Japanese researchers sampled juvenile pollock over an area similar to that shown by the Pribilof Island inset. (Illustration from Napp and Hunt, 2001).

(SEBSCC; 1996–2002), which was supported by the Coastal Ocean Program of NOAA (Wenzel and Scavia, 1993).

InFront and SEBSCC emphasized collaborative, interdisciplinary, regional studies and the importance of long time series in understanding variability of the Bering Sea. The programs complemented each other, with InFront focused on the inner shelf and SEBSCC focused on the middle and outer shelf and the continental slope. Because several of the investigators in these two programs were involved with components of both studies, there was a strong incentive to collaborate and share data and ship time. As a result, both groups were able to leverage their resources and obtain a more integrated understanding of processes on the shelf than would have been possible

had the groups not collaborated in their field programs and analyses. The many multiple-authored papers acknowledging the support of both projects in this and other issues attest to the success of this integrated activity.

The goal of SEBSCC was to increase understanding of the southeastern Bering Sea ecosystem, to document the role of juvenile walleye pollock (*Theragra chalcogramma*) and factors that affect their survival, and to develop and test annual indices of pre-recruit (age-1) pollock abundance. SEBSCC was divided into monitoring, process, modeling, and retrospective and synthesis components. They focused on four central scientific issues: (1) How does climate variability influence the Bering Sea ecosystem? (2) What limits population growth on the Bering Sea shelf? (3) How do

oceanographic conditions on the shelf influence biological distributions? (4) What influences primary and secondary production regimes? These broad issues supported SEBSCC's narrower goal of understanding the ecosystem in terms of pollock and provided a basis for selection of research components. SEBSCC also was envisioned as a source of information to support the regional fishing industry and its management. For example, results from SEBSCC research related to short-term forecast of pollock recruitment may improve stock assessments used to recommend "allowable biological catch" estimates to the North Pacific Fishery Management Council. Similarly, research results pertaining to the availability of juvenile pollock to apex predators could assist Council decisions regarding restriction of fishing around marine mammal rookery areas. SEBSCC's focus on ecosystem response to changes in environmental conditions provides a context for resource management in a changing environment.

SEBSCC research spanned disciplines from atmospheric physics to marine ornithology and addressed questions on processes ranging from atmospheric teleconnections to intimate associations between juvenile pollock and tentacles of jellyfish. The centerpiece of SEBSCC research was a time series of physical and biological data from an oceanographic mooring located in 70 m water at site M2 (Fig. 1). First deployed in 1995, the site M2 mooring measured vertical profiles of temperature and salinity and time series of currents and fluorescence year around. SEBSCC shipboard studies were repeated several times annually along transects from the Bering Sea basin to the 70 m isobath, then northwestward along this isobath (M3–M4 in Fig. 1). One summer cruise and five fall cruises investigated the region around the Pribilof Islands that is believed to be an important nursery for young pollock. Annual, collaborative, summer cruises aboard the Japanese fishery training vessel *Oshoro Maru* enabled sampling and abundance estimates of juvenile pollock.

The InFront investigators hypothesized that elevated primary production at the inner front continues longer than production in the upper mixed layer of non-frontal waters, and that front-related production provides an energy source

throughout the summer for a food web that supports short-tailed shearwaters (*Puffinus tenuirostris*), juvenile fish, and their zooplankton prey. Research focused on the role of the structural front between the well-mixed waters of the coastal domain and the two-layer system of the middle domain (Fig. 1). Three spring and three summer/fall cruises addressed the temporal and spatial variability of this system at four principal sites, as well as at several areas that were visited opportunistically. Each year millions of short-tailed shearwaters migrate from Australia to the Bering Sea to forage over the inner shelf. The evolution of this annual trans-equatorial migration implies that extraordinary amounts of prey must be readily available to these birds in the Bering Sea. Because earlier workers had described shearwater foraging as concentrated near the inner front, it was hypothesized that this region should support processes conducive to an unusually great abundance or availability of prey (Schneider and Shuntov, 1993; Hunt et al., 1996). This is also a region where young fish and some species of crab larvae congregate to forage.

To test this hypothesis, InFront investigators collected and interpreted observations on physical and biological features in the vicinity of the inner front. The project has shown that the inner front can facilitate the vertical flux of nutrients and, where this occurs, there is enhanced production at and near the front. Although data collection was restricted to the coastal regions of the southeastern Bering Sea, the results of InFront should be relevant to numerous continental shelf tidal fronts and ecosystems. Thus, the results have a general applicability to understanding and managing some of the world's most productive seas.

This special issue of *Deep-Sea Research II* presents results from the InFront and SEBSCC programs. The progress described here builds on research that has been summarized in earlier volumes. These include Hood and Kelly (1974), the Outer Continental Shelf Environmental Assessment Program (OCSEAP; Hood and Calder, 1981), Bering Sea Marginal Ice Zone Experiment (MIZEX; Muench, 1983), Processes and Resources of the Bering Sea Shelf (PROBES, Hood, 1986), Inner Shelf Transfer and Recycling

(ISHTAR, Coachman and Hansell, 1993) Mathisen and Coyle (1996), Bering Sea Fisheries-Oceanography Coordinated Investigations (BS FOCI; Macklin, 1999), and Loughlin and Ohtani (1999). The work of the PROBES program defined the specific hydrographic regimes for the region (the coastal or inner shelf domain, the middle shelf domain, the outer shelf domain, the continental slope, and the transitional areas or fronts between them) that were addressed separately and jointly by InFront and SEBSCC. Each of these domains is a different marine habitat. Research reported in this special issue spans these hydrographic domains.

3. Research setting and integrated results

InFront and SEBSCC were fortunate to conduct research during a period when there was unusually great variability in the marine climate and possibly a regime shift in the winter of 1998–1999. Sea-ice cover over the southeastern Bering Sea shelf varied from essentially zero in 1996 to one of the heaviest ice years in recent decades in 1999 (Stabeno et al., 2002). Sea surface temperatures were unusually high in late spring and summer of 1997, whereas 1999 was noted for its low temperatures (Stabeno et al., 2001). Coccolithophores bloomed for the first recorded time over the shelf in 1997 (Vance et al., 1998), and these blooms now appear to be a persistent feature of the southeastern shelf (Olson and Strom, 2002). In the late 1990s, there was also marked variation in the abundance of coastal copepod species, suggesting that the variability in marine climate was transferred through the shelf food webs to the zooplankton. Evidence that the variability was of consequence to upper trophic level organisms was reflected in a massive die-off of short-tailed shearwaters in 1997 (Baduini et al., 2001), and in considerable variability in the strength of pollock year classes.

The ability to study a system during a period of great interannual variability helped to focus attention on mechanisms by which climate can affect the amount and fate of annual production over the shelf. The result was the development of a

new hypothesis, the Oscillating Control Hypothesis (OCH; Hunt et al., 2003). OCH provides a rationale as to why the control of the recruitment of pollock and other large fish might shift from bottom up to top down with a change from a prolonged period of heavy ice years (cold regime) to a period of years with early ice retreat (warm regime). This variability also provided the opportunity to see how the southeastern shelf ecosystem might function if warmed by global change.

4. Case study of abrupt ecosystem change

From the work of InFront and SEBSCC, there is a growing appreciation that major, abrupt changes in the southeastern Bering Sea ecosystem may be precipitated by a confluence of events that pushes the system to a new state. These events that reshape the southeastern Bering Sea may be the result of the combining of large interannual and even intra-seasonal variability with low-frequency variability to produce extreme events. For example, consider the coccolithophores that first appeared during the summer of 1997 (Vance et al., 1998), and have persisted ever since, despite conditions that no longer appear to favor their prominence.

During spring and summer of 1997, atmospheric conditions over the eastern Bering Sea included uncharacteristically light winds, high temperatures and clear skies (Overland et al., 2001). These conditions resulted from forcing on multiple time scales: intra-seasonal, El Niño, Pacific Decadal Oscillation, and global warming (Overland et al., 2001). The atmosphere affected the ocean, causing a cascade through the ecosystem. Although, the exact mechanisms associated with the cascade are not well understood, Napp and Hunt (2001) and Stockwell et al. (2001) describe the following progression of events as a plausible scenario: An early April spring diatom bloom associated with sea ice depleted nutrients in the upper layer. One lone wind event occurred in mid-May that mixed the upper 45–50 m, introducing nutrients from the lower layer into the upper water column. A consequent phytoplankton bloom further reduced the reservoir of nutrients typically found

throughout the summer. Warm, nutrient-poor water set the stage for the switch from diatoms to a coccolithophore bloom unprecedented in recorded Bering Sea history. The coccolithophore bloom numerically dominated phytoplankton. A coincident inability of shearwaters to obtain their euphausiid prey, perhaps exacerbated by the clouding of the water by the coccolithophores, was indicated in the mass mortality of these seabirds. By contrast, 1998 was different in forcing, produced summer water conditions dissimilar to the year before, yet a similar coccolithophore bloom occurred. Each year since 1997, there has been a flourishing abundance of coccolithophores. They have occurred without a duplication of the meteorological and oceanographic events that first established the bloom. Thus, a physical event, sea ice in April coupled with calm winds and clear skies, produced a major ecosystem change, the coccolithophorid bloom, with repercussions up the food chain for several subsequent years.

5. Future studies

So-called regimes often have their largest ranges near the time of their major shifts. The ecosystem can be reorganized during such events, and the persistence of biological processes can prolong the reorganization after the physical system has shifted to more routine behavior. Such events may be occurring on decadal scales as well. For the previous two decades, the Southeast Bering Sea ecosystem has had a dominant pelagic species, the commercially fished walleye pollock. Pollock is a nodal species, constituting an integral part of the region's food chain as both prey and predator (Hunt et al., 2003). The strongest year classes were in 1978 and 1989. These were both periods of regime shifts where there was a dramatic change in wind forcing of the Bering Sea. Future research on the connections between climate and marine ecosystem function will need to examine the processes that link atmospheric forcing and the processes that control the amount and fate of production.

SEBSCC and InFront have extended the knowledge base of the southeastern Bering Sea at a critical moment. Increasing attention is being focused on the Bering Sea. Just a few years ago, while other fisheries of the United States were suffering serious declines, the eastern Bering Sea fishery was considered stable. In the past several years, there have been indications that this may no longer be the case. Commercial salmon failures, curtailment of fishing areas and times because of declining marine mammal populations, massive numbers of seabird deaths, and indications that a shift in springtime Bering Sea climate may be occurring all suggest that the Bering Sea ecosystem is changing in a significant way. It is clear that we must understand these changes to enable responsible management of regional resources. These two programs, InFront and SEBSCC, have contributed long-term measurements and results described in this special issue that are important to a more complete comprehension of the complex Bering Sea ecosystem.

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References

- Baduini, C.L., Hyrenbach, K.D., Coyle, K.O., Pinchuk, A., Mendenhall, V., Hunt Jr., G.L., 2001. Mass mortality of short-tailed shearwaters in the southeastern Bering Sea during summer 1997. *Fisheries Oceanography* 10, 117–130.
- Coachman, L.K., Hansell, D.A. (Eds.), 1993. ISHTAR: inner shelf transfer and recycling in the Bering and Chukchi Seas. *Continental Shelf Research* 13(5/6), 473–704.
- Hood, D.W. (Ed.), 1986. Processes and resources of the Bering Sea shelf (PROBES). *Continental Shelf Research* 5, 286.
- Hood, D.W., Calder, J.A. (Eds.), 1981. The Eastern Bering Sea Shelf. *Oceanography and Resources*, Vols. 1, 2. US Government Printing Office, Washington, DC, 1339pp (distributed by the University of Washington Press, Seattle).

- Hood, D.W., Kelly, E.J. (Eds.), 1974. Oceanography of the Bering Sea with Emphasis on Renewable Resources. Institute of Marine Sciences, Occasional Publication Vol. 2. University of Alaska, Fairbanks, 623pp.
- Hunt Jr., G.L., Coyle, K.O., Hoffman, S., Decker, M.B., Flint, E.N., 1996. Foraging ecology of short-tailed shearwaters near the Pribilof Islands, Bering Sea. *Marine Ecology Progress Series* 141, 1–11.
- Hunt, Jr. G.L., Stabeno, P.J., Walters, G.E., Sinclair, E.H., Brodeur, R.D., Napp, J.M., Bond, N.A., 2003. Climate change and control of the southeastern Bering Sea pelagic ecosystem.
- Loughlin, T.R., Ohtani, K. (Eds.), 1999. Dynamics of the Bering Sea. University of Alaska Sea Grant, AK-SG-99-03, Fairbanks, 838pp.
- Macklin, S.A. (Ed.), 1999. Bering Sea FOCI 1991–1997, Final Report. ERL Special Report, NTIS: PB99-147308, 167pp.
- Mathisen, O.A., Coyle, K.O. (Eds.), 1996. Ecology of the Bering Sea: A review of Russian literature. University of Alaska Sea, Grant, AK-SG-96-01, Fairbanks, 306pp.
- Muench, R.D. (Ed.), 1983. Marginal ice zones. *Journal of Geophysical Research* 88, 2713–2966.
- Napp, J.M., Hunt, G.L., 2001. Anomalous conditions in the southeastern Bering Sea, 1997: linkages among climate, weather, ocean and biology. *Fisheries Oceanography* 10, 61–68.
- Olson, M.B., Strom, S.L., 2002. Phytoplankton growth, microzooplankton herbivory and community structure in the southeast Bering Sea: insight into the formation and temporal persistence of an *Emiliana huxleyi* bloom. *Deep-Sea Research II*, this issue (PII: S0967-0645(02)00329-6).
- Overland, J.E., Bond, N.A., Adams, J.M., 2001. North Pacific atmospheric and SST anomalies in 1997: links to ENSO? *Fisheries Oceanography* 10, 69–80.
- Overland, J.E., Bond, N.A., Adams, J.M., 2002. The relation of surface forcing of the Bering Sea to large-scale climate patterns. *Deep-Sea Research II*, this issue (PII: S0967-0645(02)00322-3).
- Royer, T.C., Grosch, C.E., 2002. Ocean Climate Variability as a Potential Influence on Steller Sea Lion Populations. Presented at the Steller Sea Lion Principal Investigator's Meeting, 19–21 March 2002, Anchorage.
- Schneider, D.C., Shuntov, V.P., 1993. The trophic organization of the marine bird community in the Bering Sea. *Review of Fisheries Science* 1, 311–335.
- Schumacher, J.D., Stabeno, P.J., 1998. Continental shelf of the Bering Sea. In: Robinson, A.R., Brink, K.H. (Eds.), *The Sea. The Global Coastal Ocean*, Vol. 11. Wiley, New York, pp. 789–822.
- Stabeno, P.J., Bond, N.A., Kachel, N.B., Salo, S.A., Schumacher, J.D., 2001. On the temporal variability of the physical environment over the southeastern Bering Sea. *Fisheries Oceanography* 10, 81–98.
- Stabeno, P.J., Kachel, N.B., Sullivan, M., Whitley, T.E., 2002. Variability along the 70-m isobath of the Southeast Bering Sea. *Deep-Sea Research II*, this issue (PII: S0967-0645(02)00327-2).
- Stockwell, D.A., Whitley, T.E., Zeeman, S.I., Coyle, K.O., Napp, J.M., Brodeur, R.D., Pinchuk, A.I., Hunt Jr., G.L., 2001. Anomalous conditions in the southeastern Bering Sea, 1997: nutrients, phytoplankton and zooplankton. *Fisheries Oceanography* 10, 99–116.
- Vance, T.C., Baier, C., Brodeur, R.D., Coyle, K., Decker, M.B., Wyllie-Echeverria, T., Hunt, G., Napp, J.M., Schumacher, J.D., Stabeno, P.J., Stockwell, D., Tynan, C., Whitley, T.E., Zeeman, S., 1998. Ecosystem anomalies in the eastern Bering Sea: Including blooms, birds and other biota. *EOS, Transactions of the American Geophysical Union* 79 (10), 121–126.
- Wenzel, L., Scavia, D., 1993. NOAA's Coastal Ocean Program. *Oceanus* 36, 85–92.