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The Eastern Bering Sea shelf: a highly productive seasonally ice-covered sea

Franz J. Mueter[1], George L. Hunt, Jr.[2], and Michael A. Litzow[3]

[1] 697 Fordham Drive, Fairbanks, Alaska, 99709, USA. E-mail: fmueter@alaska.net
[2] School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, WA 98195
[3] Alaska Fisheries Science Center, National Marine Fisheries Service, 301 Research Ct., Kodiak, AK 99615 USA

Abstract

The Eastern Bering Sea is characterized by its broad (> 500km), shallow (mean depth = 70m), and seasonally ice-covered shelf. The spatial extent of ice and the timing of ice retreat are driven by large-scale atmospheric forcing and vary considerably interannually. This variability affects the spatial distribution of fish and invertebrates, the timing of the spring bloom, and the flow of energy to upper trophic levels, including shifts between benthic and pelagic compartments. High productivity on the shelf (up to 200-250 gC m^{-2} y^{-1}) is fueled by nutrient-rich waters originating in the deep Aleutian Basin and supports a large community of demersal and pelagic fish and shellfish, as well as large populations of seabirds and marine mammals. Fish biomass and commercial catches (> 1.3 million tons annually) are dominated by gadids, in particular walleye pollock (*Theragra chalcogramma*), and flatfishes (*Pleuronectidae*). Although the composition of the fish community has remained relatively stable for several decades, a large-scale community reorganization affecting all trophic levels followed a 1976/77 climate regime shift. Walleye pollock currently play a key role in the food web of the Eastern Bering Sea, with much of the primary production transferred to higher trophic levels through predation on larval and juvenile pollock. The Eastern Bering Sea occupies the transition between the sub-arctic and the Arctic, which makes the region particularly sensitive to climatic change. With recent warming, the region may be undergoing a transition from Arctic to sub-arctic conditions, including a northward shift in the distribution of numerous demersal species and the emergence of newly dominant predators on commercially valuable species.

Keywords: Bering Sea, sea ice, productivity, fish community, warming

Dynamics of the eastern Bering Sea shelf

Among the subarctic seas, the Eastern Bering Sea stands out because of its broad (> 500km) and shallow (mostly < 100m) shelf (Fig. 1). The currents on the shelf and along the slope form part of the larger subarctic gyre of the North Pacific. Extensions of the Alaska Coastal Current and the Alaskan Stream enter the Bering Sea through several Aleutian passes and flow northward along the inner shelf (Alaska Coastal Current) or along the slope (Bering Slope Current, an extension of the Alaskan Stream). Most of the shelf is characterized by diffuse flows to the north, which exit through Bering Strait into the Arctic Ocean (1998). Unlike the subarctic seas in the Atlantic sector there is little advection of Arctic waters into the Bering Sea. The shelf is seasonally ice-covered and both the spatial extent of ice cover and the timing of ice retreat vary considerably from year to year (Niebauer 1998).

Figure 1: Bathymetry of the Eastern Bering Sea with minimum and maximum spatial extent of sea ice in March. Base map from NOAA Pacific Marine Environmental Laboratory. Ice extent based on Niebauer et al. (1999).

Variability in ice cover, wind mixing, and temperature conditions on the shelf are largely determined by the strength and position of the Aleutian Low pressure system, which determines the frequency and the path of storms over the shelf (Fig. 2, Overland et al. 1999). The Aleutian Low, in turn, varies in response to decadal climate variability over the North Pacific and in the Arctic, as well as to shorter term variability in the tropical Pacific. In the recent past, regime-like shifts in climate conditions have been observed around 1976/77 and around 1988/89. The 1976/77 shift was characterized by an intensification of the Aleutian Low with a shift to warmer conditions in the Eastern Bering Sea, whereas the main characteristic of the 1988/89 shift was a strengthening of the polar vortex as indicated by a change in the sign of the Arctic Oscillation index. These changes were associated with marked changes in numerous biological time series throughout the Northeast Pacific (Hare and Mantua 2000).

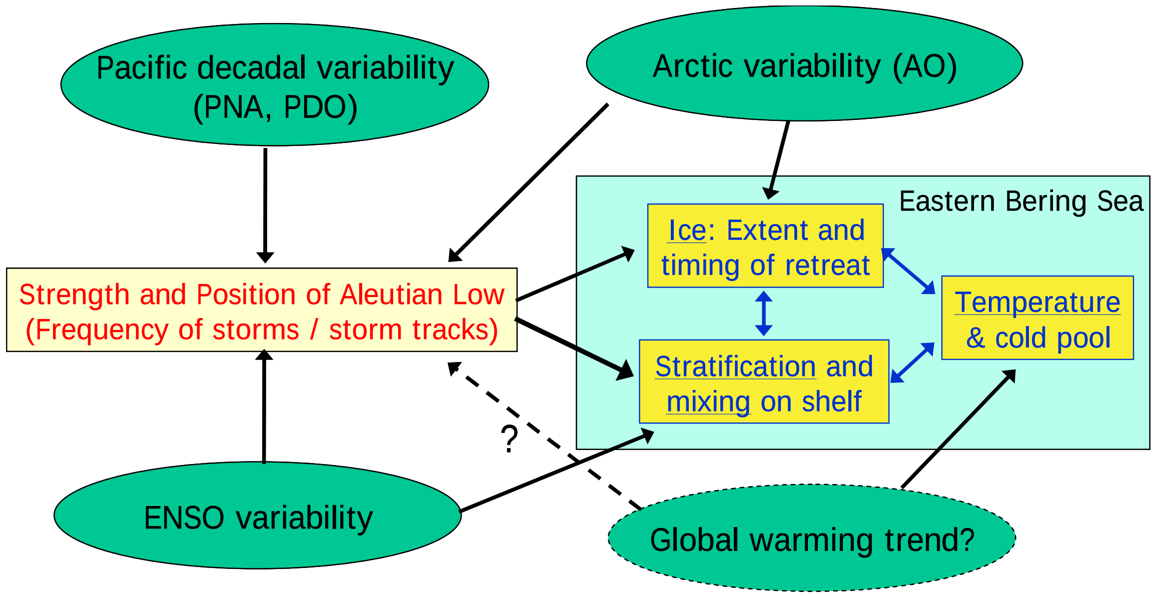

Figure 2: Major climate drivers affecting the Eastern Bering Sea ecosystem through changes in ice cover, temperature conditions, and stratification. Main sources of climate variability and corresponding indices are shown in green ovals (PNA = Pacific North American pattern, PDO = Pacific Decadal Oscillation, AO = Arctic Oscillation, ENSO = El Nino / Southern Oscillation). For details see text.

The Eastern Bering Sea shelf is an area of very high biological productivity, which is fueled by nutrient rich waters supplied to the Bering Sea basin via the global ocean "conveyor belt". Concentrations of nitrate, phosphate, and silicate in the deep waters of the Bering Sea basin are among the highest observed in the world's oceans and these nutrient-rich waters are the source for replenishing nutrients on the shelf (Whitledge and Luchin 1999). Cross-shelf fluxes are essential to supporting the high production observed on the shelf, but are poorly understood at present. The southern part of the shelf is divided into the well-mixed inner domain, which is separated by an inner front near the 50 m depth contour from the two-layer middle domain (Coachman 1986). The latter is separated by a middle front (near the 100 m depth contour) from the weakly stratified outer domain, which extends to the shelf break front. In the inner domain and in the surface mixed layer of the middle domain nutrients are rapidly depleted during the spring phytoplankton bloom. The bloom on the inner shelf domain occurs when sufficient sunlight becomes available, whereas the bloom in the middle domain also requires ice melt or insolation, combined with the cessation of winter storms, to stratify the water column and allow a phytoplankton bloom to develop (Sambrotto et al. 1986). Additional production may occur periodically or throughout the summer when additional nutrients are mixed into the surface layer or into the inner shelf domain through wind and/or tidal mixing.

The high primary productivity on the Southeast Bering Sea shelf (up to 200-250 gC m-2 y-1, Hunt and Drinkwater 2005) supports a large community of demersal and pelagic fish and shellfish, large populations of seabirds and marine mammals, and a number of important commercial fisheries. The fishery annually removes up to 2 million tons of demersal fishes from the Southeastern shelf and the Aleutian Islands (NPFMC 2005). Both the fish biomass and commercial catches are dominated by gadids, in particular walleye pollock (*Theragra* *chalcogramma*), and flatfishes (*Pleuronectidae*). Because of their large abundance and wide-spread distribution, walleye pollock currently play a key role in the food web of the Eastern Bering Sea (Springer 1992) and juvenile pollock are a major prey item for numerous predatory fishes (including adult pollock), seabirds, and marine mammals (Fig. 3, Aydin et al. 2002). Therefore, much of the primary productivity on the eastern Bering Sea shelf is transferred to higher trophic levels through the larvae and juveniles of walleye pollock.

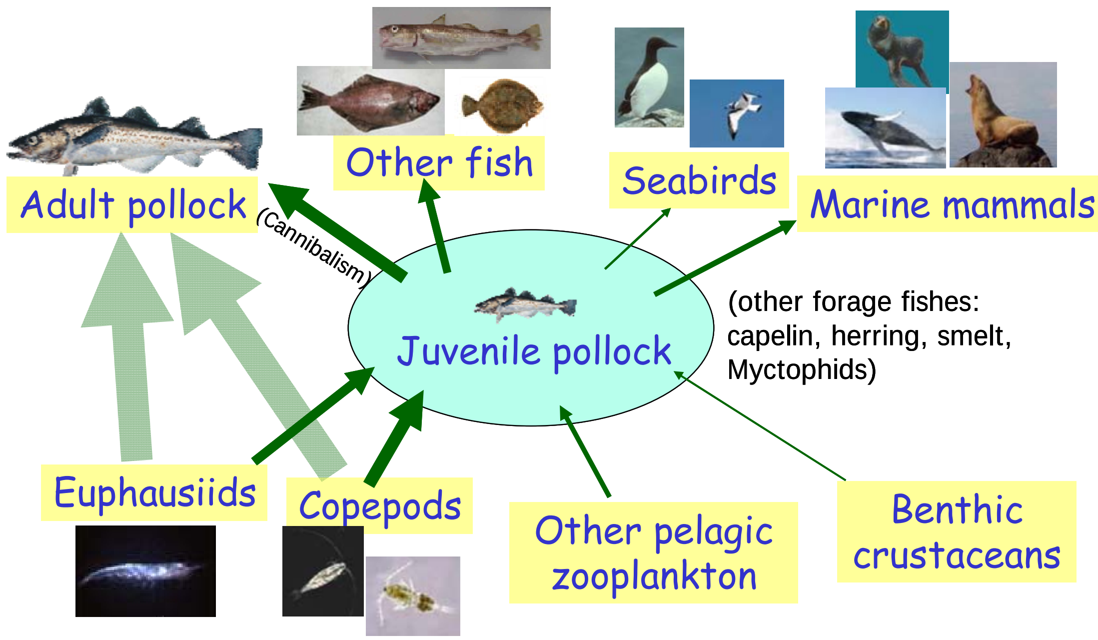

Figure 3: Simplified food web depicting the central role of walleye pollock (Theragra chalcogramma) in the Eastern Bering Sea. Arrows depict biomass flows from lower trophic level prey items to juvenile pollock and from juvenile pollock to major predators. Widths of arrows are proportional to estimated consumption based on Ecopath model (Kerim Aydin, AFSC, NOAA, pers. comm.)

Although the composition of the fish community has remained relatively stable for several decades, a large-scale community reorganization that affected all trophic levels was observed following the 1976/77 climate regime shift (Francis et al. 1998). The recruitment and abundance of walleye pollock and of other demersal and pelagic fishes, such as Pacific cod (*Gadus macrocephalus*), flatfishes, and sockeye salmon (*Oncorhynchyus nerka*) increased substantially after the 1976/77 climate regime shift (Adkison et al. 1996, Conners et al. 2002). These species support some of the largest commercial fisheries in the United States. In contrast, several crab stocks declined to very low levels in the early 1980s and some, in particular red king crab (*Paralithodes camtschaticus*), have not recovered to date (Zheng and Kruse 2006). Other notable changes include large declines in Steller sea lions (*Eumetopias jubatus*) and northern fur seals (*Callorhinus ursinus*), as well as several seabird populations on the Pribilof Islands. Pinniped populations were overharvested in the latter part of the 19th and in the first part of the 20th century, underwent a period of recovery, and have experienced severe declines in abundance in recent decades. The causes of these declines are still not understood and may include both anthropogenic (e.g. competition for prey) and natural factors (e.g. changes in relative prey composition associated with the 1976/77 regime shift). Unlike pinniped populations, whale populations on the Eastern Bering Sea shelf appear to be increasing (Moore et al. 2000) after being nearly driven to extinction by the 1960s (NRC 1996).

In contrast to the Southeast Bering Sea, the northern Bering Sea shelf does not support any commercially important fish populations. Primary production on the northern Bering Sea shelf are estimated to be substantially higher (>500 gC m^{-2} y^{-1}, Springer et al. 1996) than on the southeastern shelf. High primary productivity is supported by the direct advection of nutrient-rich waters onto the shelf via the Anadyr Current and northward flows along the outer shelf. Large abundances of zooplankton are supported by local production as well as by the advection of oceanic species onto the shelf (Springer et al. 1996). Much of the high production in this region settles to the benthos, supporting very high benthic productivity (Highsmith and Coyle 1990). The resulting biomass of lower trophic level benthos on the northern Bering Sea shelf (primarily bivalves and amphipods) is an order of magnitude higher than on the southeast shelf (Alton 1974). The abundance of large demersal fish and crustaceans on the northern shelf is limited by cold bottom temperatures and much of the benthic production is consumed by benthic-feeding seabirds and marine mammals such as sea ducks, gray whales (*Eschrichtius robustus*), and walrus (*Odobenus rosmarus*) (Grebmeier et al. 1989). However, the flow of carbon to the benthos, as well as benthic productivity, has declined in recent years and the northern Bering Sea may be changing from Arctic to subarctic conditions (Grebmeier et al. 2006). It is unclear whether this is the result of a reduced nutrient supply and decreased primary productivity or increased consumption within the water column.

Effects of sea-ice dynamics on fish and fisheries

One of the defining characteristics of most subarctic seas is the seasonal presence of sea ice. Nowhere is this seasonal variability more extreme than in the Bering Sea, where the annual advance and retreat of sea ice averages approximately 1,700 km (Walsh and Johnson 1979). The northern and northeastern portion of the broad continental shelf is generally covered by sea ice in winter, whereas the spatial extent of ice cover in the western and southeastern Bering Sea and the timing of ice advance and retreat are highly variable from year to year. Recent warming trends in the Arctic and Sub-arctic have resulted in reduced ice cover and early ice retreat in the Bering Sea. Here we explore some of the consequences of ice and temperature variability in general, and of the recent warming trend in particular, on the ecology and biogeography of the southeastern Bering Sea.

Sea ice can affect the abundance and species composition of the fish community through effects on productivity, recruitment, survival, and spatial distribution. Interannual variability in primary and secondary productivity on the eastern Bering Sea shelf and effects of ice on productivity are poorly understood. Clearly, the spatial extent of ice cover may restrict mixing and advection on the shelf, and hence the replenishment of nutrients in the shelf waters during winter. This is supported by the observation that late winter nutrient concentrations on the inner shelf were lower during 1980, a year with average ice concentration, than in 1979, a year with very little ice in the region (Fig. 8 in Whitledge and Luchin 1999). The timing of ice retreat may also affect the length of the production season, and therefore total summer production. This is supported by low primary production (PP) in years with a late ice retreat (e.g. 1999 and 2006, Fig. 4) and is consistent with a positive relationship between net PP and sea-surface temperature (Mueter, unpubl. data). Annual net PP on the southeastern Bering Sea shelf[1] was significantly and negatively correlated with an index of ice retreat over the middle shelf[2] ($R^2 = 0.77$, $P = 0.0019$).These observations suggest that productivity at all trophic levels may be higher in warm years that have little ice and an early ice retreat.

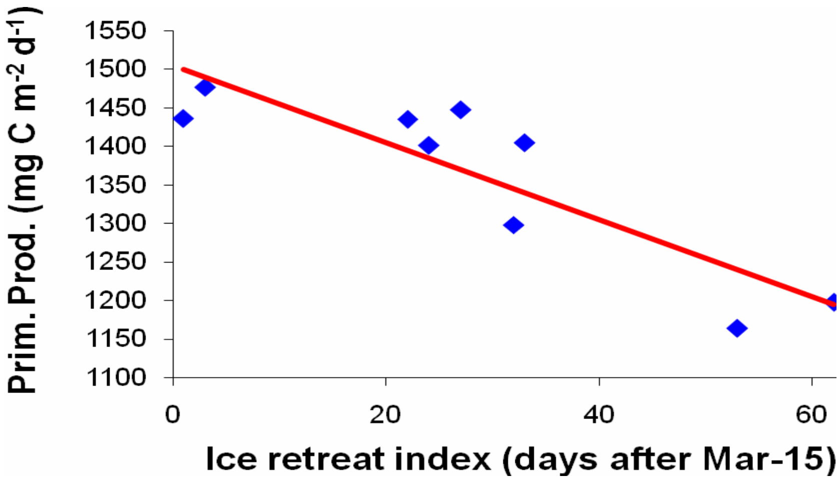

Figure 4: Satellite-derived estimates of April=September primary production averaged over the southeastern Bering Sea as a function of the timing of ice retreat from the shelf.

The timing of ice retreat also plays an important role in the timing, amount, and fate of primary production over the shelf (Hunt and Stabeno 2002). In general, much of the production from ice-associated blooms in cold water sinks to the benthos. An earlier ice retreat or the absence of sea-ice from the eastern Bering Sea shelf, as observed in some recent years, is expected to redirect energy flows from the benthic to the pelagic system. This is consistent with enhanced survival of pelagic-feeding fishes such as walleye pollock during warm years with an early ice retreat and enhanced survival of benthic-feeding fishes such as yellowfin sole during years with a late ice retreat and an ice-associated bloom (Mueter et al. 2006).

Finally, sea ice plays an important role in the distribution of Arctic and subarctic biota. The ice-water interface provides important structural habitat for sea-ice algae, zooplankton, and Arctic fish species, while ice-associated seals, walrus, and polar bears depend on ice for reproduction and feeding. In the spring, the retreating ice edge is a zone of heightened biological activity because it provides access to the water column and to the underlying benthos for ice-associated mammals and because melting ice may trigger an ice-associated spring bloom by stabilizing the water column. While providing important habitat for many Arctic species, sea ice excludes many seabirds and whales that depend on open water and it limits the distribution of temperate fish species that are intolerant of the low temperatures of the underlying water column.

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[1] Monthly estimates based on satellite-based chlorophyll concentrations and the Vertically Generalized Production Model of Behrenfeld and Falkowski (1997). are available at http://web.science.oregonstate.edu/ocean.productivity, and were compiled by Kevin Friedland, NMFS, NOAA

[2] Timing of ice retreat was indexed by the number of days with ice cover after March 15 near a mooring location on the middle shelf (see http://www.beringclimate.noaa.gov).

The summer distribution of demersal fish and invertebrates is closely linked to winter surface conditions, especially the extent of sea ice, on the eastern Bering Sea shelf. The formation of sea ice during winter generates cold, salty water over the central shelf region, resulting in the formation of a pool of cold (<2°C) bottom water which extends into the southeastern Middle Domain in summer (Fig. 5). This cold pool, which is protected from summer mixing by the seasonal thermocline, determines the boundary between Arctic and subarctic demersal communities. The cold pool has retreated ~230 km northwards since the early 1980s, and bottom trawl surveys of fish and invertebrates (1982-2006) show a coincident reorganization in demersal biogeography. There were community-wide northward distribution shifts (Fig. 6) and total demersal biomass, species richness and average trophic level increased in the former cold pool area as subarctic fauna colonized newly favorable habitats (Mueter and Litzow, in review). In contrast, Arctic fauna decreased in abundance and / or retreated northward. Shifts in distribution and other community metrics were linearly related to bottom temperature, suggesting that climate changes are the primary cause of the changing biogeography. However, residual variability in distribution that were not explained by temperature or other climate variables showed a strong non-linear trend over time (Fig. 6), suggesting that internal community dynamics also contributed to the changing biogeography (Mueter and Litzow, in review).

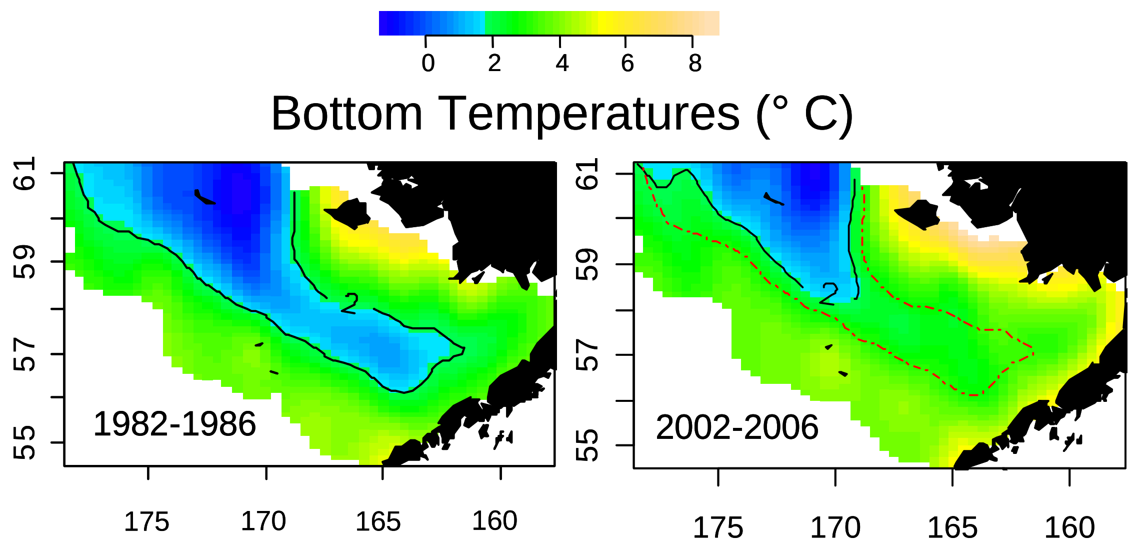

Figure 5: Mean position and extent of the cold pool (summer bottom temperature < 2° C) in 1982-1986 and 2002-2006. Dashed line indicates average cold-pool position in 1982-1986. Spatial extent of temperature data corresponds to area of bottom trawl survey.

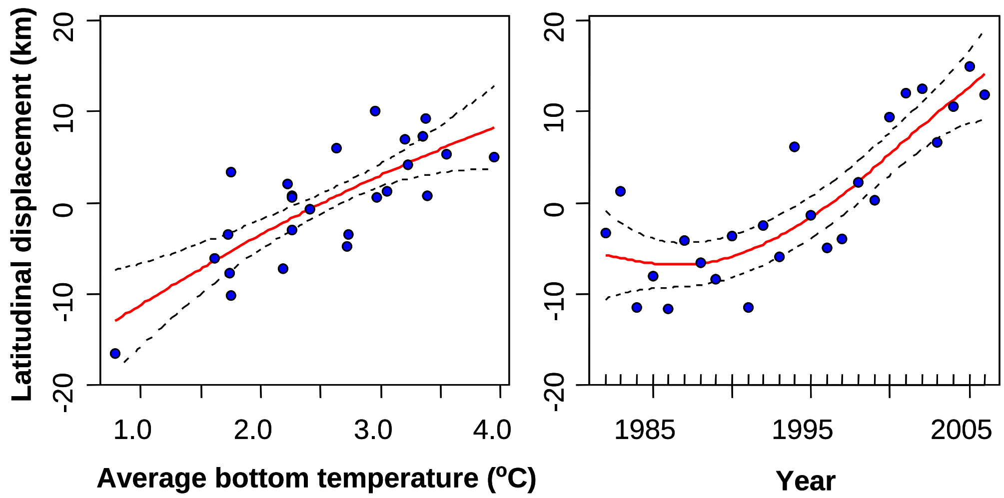

Figure 6: Average latitudinal shift in center of distribution (deviation from long-term mean in km) from 1982-2006 across 51 demersal taxa in the southeastern Bering Sea as a function of average bottom temperature and residual shift in center of distribution (after adjusting for temperature effect) from 1982-2006.

In summary, the Eastern Bering Sea shelf supports an extraordinary diversity and abundance of marine life that forms the basis of important commercial fisheries, as well as important subsistence harvests by Alaska Natives. Marine fish, seabird, and mammal populations have undergone large changes in the past in response to both harvesting and changes in climate. The location of the Eastern Bering Sea at the transition point between the subarctic and the Arctic makes the region particularly sensitive to climatic changes. In particular, changes in the extent and timing of ice retreat may have profound effects on the flow of energy through the system and on the relative importance of benthic vs. pelagic pathways. There are indications that the region is currently undergoing a transition from Arctic to subarctic conditions related to recent warming trends (Grebmeier et al. 2006, Mueter and Litzow in review, Overland and Stabeno 2004). Clearly, sea ice dynamics play a dominant role in the biogeography of the southeastern Bering Sea. Changes in sea ice cover associated with regional and global climate variability affect the productivity, abundance, and distribution of biota at all trophic levels. Recent warming trends resulted in wide-spread northward distribution shifts of demersal fish and invertebrates, including commercial and non-commercial species, and in a shift from Arctic to subarctic conditions over a large portion of the middle shelf. The potential for further shifts in community state and the emergence of non-linear effects in response to changing climate conditions provide serious challenges to the management of fisheries resources in the eastern Bering Sea and require an ecosystem-level approach to research and management. If warming trends continue as predicted (IPCC 2001), profound changes in the structure and functioning of the Eastern Bering Sea ecosystem are likely to occur. However, the cascading effects of a warming climate on the ecology of the Eastern Bering Sea cannot be predicted with any certainty based on our current understanding of system dynamics.

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