Climate Change in the Southeastern Bering Sea and Some Consequences for Biota

by

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INTRODUCTION

Dramatic changes are occurring throughout the Arctic (Weller *et al.*, 1997). The systematic modification in wintertime climate of Alaska and the Bering Sea that occurred in 1976–1977 illustrates the magnitude and nature of these changes. Among the effects documented are a step-like increase of nearly 2°C in air temperature (Bowling, 1995), an ~5% decrease in sea-ice extent (Niebauer, 1998), and decreases in sea-ice thickness (Wadhams, 1995). Many local residents around the Bering Sea have also noted changes in ice thickness and strength (Gibson and Schullinger, 1998). Over longer time scales, the extent of glaciers has decreased markedly. Permafrost temperatures measured in bore-holes in northern Alaska are 2–4°C warmer than they were 50–100 years ago (Lachenbruch and Marshall, 1986). Discontinuous permafrost has warmed considerably and is thawing in some locations (Osterkamp, 1994). For the Bering Sea region (Figure 1) the warming may reflect a natural multi-decadal cycle (regime shift) superimposed on a warming trend due to the greenhouse effect. Given our present understanding of the Earth climate system, the latter mechanism provides compelling reasons for legitimate public and management concern over future changes resulting from the increased concentrations of green house gases (AGU Report, 1999).

Substantial natural and human induced variability occurs in the ecosystem of the eastern Bering Sea which includes some of the most productive fisheries on Earth (NRC Report, 1996). Besides lucrative crab, halibut and salmon fisheries, most of the world catch of walleye pollock (*Theragra chalcogramma*) occurs here and these resources represent 2–5% of the world's fishery production and ~50% of the U.S. fishery production (NRC Report, 1996). The Bering Sea is home to at least 450 species of fish, crustaceans, and mollusks; 50 species of seabirds; and 25 species of marine mammals. Walleye pollock is a nodal species in the food web (NRC Report, 1996) with juveniles providing the dominant prey of fishes, seabirds, and marine mammals (Springer and Byrd, 1989; Livingston, 1993; Brodeur *et al.*, 1996).. In the past, climate variations altered species composition and at present may be reducing carrying capacity (Kruse,

1998; Napp and Hunt, in press). Such changes impact sustained ecosystem health and should dictate management of human activities and utilization of this rich ecosystem.

Changes forecast for the Bering Sea due to warming (US GLOBEC Report, 1996; Weller *et al.*, 1997; Schumacher and Alexander, 1999) include decreases in storms (mixing energy), the supply of nutrients and sea ice extent/thickness and an increase in sea surface temperature. Physical conditions observed during 1997 fit these predictions well. During 1998, some conditions continued to be abnormal. It is too early to tell whether these conditions will persist, or transition back to those characteristic of the historical record. Nevertheless, it is clear that the recent changes in the physical environment had immediate and profound consequences on biota. The complex mechanisms that link physical and biological elements preclude precise prediction of ecosystem changes, but it is likely major evolutions will occur. Below, we provide an update of previous work on biophysical processes (Incze and Schumacher, 1986) and use recent conditions to suggest mechanisms and biotic responses. We conclude with a scenario for potential future ecosystem change and a brief discussion of management of concerns.

THE BIOPHYSICAL ENVIRONMENT

Recent results germane to biophysical mechanisms in the southeastern Bering Sea include: refinement of our understanding of the Bering Slope and Aleutian North Slope Current (Stabeno *et al.*, 1999; Reed and Stabeno, 1999) and the potential importance of these to fish stocks (Reed, 1995), discovery of eddies over the outer shelf (Reed, 1998) and slope (Schumacher and Stabeno, 1994) and suggestions of their biological importance, discovery of a mean flow across the shelf (Reed and Stabeno, 1996; Reed, 1998), observations from moored instruments of the ice associated phytoplankton bloom without water column stratification and the role advection has on stratification (Stabeno *et al.*, 1998), determination of the critical nature of timing of sea ice melt and wind mixing to bloom dynamics (Stabeno *et al.*, in press), clarification of the relationship between inner front dynamics and prolonged production (Hunt *et al.*, in press), the potential influence that wind drift currents and cannibalism have on recruitment

of pollock (Wespestad *et al.*, in press), and the importance of warm season climate (Overland *et al.*, in press).

The southeastern Bering Sea consists of Oceanic and Shelf Regimes. Within the latter regime, three distinct Domains exist characterized by contrasts in water column structure, currents and biota (Iverson *et al.*, 1979a; Coachman, 1986; Schumacher and Stabeno, 1998). These are the Coastal (<50 m deep, weak stratification), Middle Shelf (50–100 m deep, strong stratification), and Outer Shelf (100–200 m deep, mixed upper and lower layers separated by slowly increasing density). The Domains provide unique habitats for biota. The zooplankton community in the two shallower Domains is comprised primarily of the small copepods and euphausiids, whereas in the Outer Shelf Domain and in the Oceanic Regime large copepods dominate (Cooney and Coyle, 1982; Vidal and Smith, 1986).

The Oceanic Regime is influenced by the Alaskan Stream flowing through Amchitka and Amukta Pass, producing the Aleutian North Slope Current (ANSC: Reed and Stabeno, 1999). The ANSC provides the main source of the Bering Slope Current (BSC) which exists either as an ill-defined, variable flow interspersed with eddies and meanders, or as a more regular northwestward flowing current (Stabeno *et al.*, 1999). Shelf/slope exchange likely differs depending upon which mode is dominant. The importance of these currents to dissolved or planktonic material is twofold: they can provide transport from the Oceanic Regime (including an important spawning region for pollock) to the Outer Shelf Domain and their inherent eddies may temporarily provide habitat that favors survival (Schumacher and Stabeno, 1994). Eddies are also common in waters just seaward of the shelf break (Schumacher and Reed, 1992) and exist even in the region between 100 and 122 m (Reed, 1998). Transport of high concentrations of pollock larvae onto the shelf by eddies occurs (Schumacher and Stabeno, 1994).

The amount of sea ice cover depends on storm tracks (Schumacher and Stabeno, 1998) and varies by »40% about the mean (Niebauer, 1998). Ice advection and melting play a critical role in fluxes of heat and salt and generation of both baroclinic flow and the cold pool located over the Middle Shelf Domain (Schumacher and Stabeno, 1998; Wyllie-Echeverria and Wooster,

1998). The positive buoyancy from melting ice initiates both baroclinic transport along the marginal ice zone and stratification. Cooling and mixing associated with ice advance help to condition the entire water column over the Middle Shelf Domain (Stabeno *et al.*, 1998). With seasonal heating, the lower layer becomes insulated and temperatures often remain below 2.0°C (Reed, 1995). The area of this cold pool varies by $\sim 2.0 \times 10^5$ km² between maximum and minimum extent. A bloom of phytoplankton is associated with the sea ice and accounts for 10–65% of the total annual primary production (Niebauer *et al.*, 1995). Ice and the cold pool both influence distributions of higher trophic level biota (Ohtani and Azumaya, 1995; Wyllie-Echeverria and Wooster, 1998; Brodeur *et al.*, 1999a).

RECENT ANOMALIES

Recently, the Bering Sea exhibited a host of noteworthy physical and biological conditions (Kruse, 1998; Vance *et al.*, 1998; Tynan, 1998; Baduini *et al.*, in press; Napp and Hunt, in press; Hunt *et al.*, in press; Stabeno *et al.*, in press): major coccolithophorid blooms (1997, 1998, and 1999), large die-off of shearwaters (1997), salmon returns far below predictions (1997 and 1998), the unusual presence of whales in over the middle shelf (1997 and 1998), unusually warm sea surface temperatures (1997 and 1998), and a decrease in the onshore transport of slope water (1997). It is instructive to consider these events in the context of the historical records.

Changes in the regional environment are related to the state of the entire North Pacific/Arctic climate system. Much of the variance herein is accounted for by a few modes. Particularly systematic effects appear to be linked to the El Niño-Southern Oscillation (ENSO) on 2–7 year time scales and associated with the Pacific Decadal Oscillation (PDO: Mantua *et al.*, 1997) on decadal to multi-decadal time scales. In brief, both ENSO and the PDO impact the Bering Sea during winter through their positive correlation with the strength of the Aleutian Low (Figure 2). The Aleutian Low is important to the Bering Sea through its impact on surface winds (advection and mixing of the upper ocean and production/advection of ice) and heat flux

(mixing and ice formation). The time series of both the ENSO and PDO indices show a marked change between 1976 and 1977; the well known "regime shift" (e.g., Trenberth and Hurrell, 1995). While the anomalies were less extreme than during the 1970s, the Aleutian Low has undergone significant recent variations between being weaker than normal in 1995, stronger than normal from 1996 through 1998 and then weaker than normal in 1999. As noted below, this contributed to substantial differences in timing and persistence of ice cover.

Sea ice characteristics represent an integrated measure of winter atmospheric forcing. An index of sea ice developed for Site #2 (Figure 3) shows that the most extensive ice years coincided with a strong negative PDO (Figure 2). Sea ice arrived as early as January and remained as late as mid May. Between 1979–1981, ice was largely absent. Beginning in the early 1990's, ice again became more common, although not to the extent observed in the early 1970's. Even though ENSO and the PDO are the best understood (and potentially predictable) components of the climate variability for the Bering Sea in winter, they do not actually account for much of the interannual fluctuation in sea ice cover: ENSO accounts for only ~7% of the variance (Niebauer, 1998). To illustrate the variability in sea ice extent over the Bering Sea shelf, we divided the ice observations into three subsets according to generally agreed upon short-term climate regimes (Stabeno et al., in press: Figure 4): 1972–1976 (cold period), 1977–1988 (warm period), and 1989–1998 (weaker cold period) to characterize the temporal variability in the spatial pattern of sea ice. During the first period, ice covered the shelf out to and over the slope and remained around St. Paul Island for more than a month. During the later years of this period, ice did not extend as far seaward and its residence time was typically 2 to 4 weeks less than during the cold period. The differences between the two latter regimes is more subtle, but still evident. Along 59°N, there were 2–4 weeks more ice during 1989–98, than during 1977–1988.

Until recently, studies of the causes and implications of climate variations for the North Pacific and Bering Sea have focused almost exclusively on the winter season. Interest and awareness is growing, however, in warm season climate variations. While these may not be as

large as those during winter, they can stand out above background atmospheric conditions (Trenberth *et al.*, 1998) and can have an impact on the upper ocean and its biota. For example, the unusually warm SST's in the eastern Bering Sea (summer 1997) were ascribed mainly to atmospheric anomalies associated with the concurrent strong El Niño (Overland *et al.*, in press). This type of research is in its infancy, but we now have new tools, in particular ~40-year long data sets (e.g., the NCEP/NCAR reanalysis) for estimating aspects of the atmospheric forcing (e.g., radiative effects) that were formerly unavailable. Preliminary results using this data indicate that the eastern shelf is experiencing a trend toward sunnier summers. The consequence is that about 20 w/m² of additional heating has occurred during recent years as compared with 30–40 years ago. This is a substantial change and may be attributable to a positive feed back between sea surface temperature and cloud cover. We expect rapid progress in identifying and understanding the variability in the warm season climate of the Bering Sea.

Temperature records from 1995 into 1999 (Figure 5) illustrate the seasonal cycle typical for the southeastern middle shelf. In January, the water column is well mixed. The coldest temperatures typically occur in February or early March with the arrival of sea ice. This condition persists until buoyancy is introduced to the water column either through ice melt or solar heating. Generally, this stratification develops during April. The water column exhibits a well defined two-layer structure throughout the summer consisting of a 15–25 m wind mixed layer and a 35–40 m tidally mixed bottom layer. Deepening of the mixed layer by strong winds and heat loss begins as early as mid August, and by early November the water column is again unstratified.

During 1997 through 1999, variations in winds resulted in dramatic changes in the structure and function of the ecosystem. The timing and duration of the transition from winter to spring and summer conditions dictated whether there was an ice associated bloom (1997) or prolonged primary production by diatoms (1998). In 1997, moderate winds resulted in average ice cover that persisted into April; in 1998 weak winds with a more southwesterly component resulted in minimal ice cover of brief duration; whereas in 1999, northerly winds resulted in less

extensive ice cover than occurred in 1997, but it remained over the southeastern shelf into May. In 1997, ice was present when adequate light existed to support an ice-related bloom. In 1998, however, ice departed prior to the existence of sufficient light levels and as a consequence a bloom occurred in May/June when stratification of the water column occurred. The strength and stability of the inner front was also modified by the prevailing wind conditions. Weak winds in spring and summer 1997 resulted in a broad, diffuse front with undetectable nitrate to 60 m depth and few nutrients entering the upper mixed layer. In contrast, the strong storms of spring and the lack of an ice-edge bloom in 1998 resulted in a slow draw down of nutrients. During 1999, the stability of the front permitted events of vertical mixing/upwelling to supply nutrients to the upper mixed layer throughout summer, supporting prolonged production. Interannual variation in the shelf production regimes was reflected in the body condition of migrant short-tailed shearwaters (*Puffinus tenuirostris*), which starved in fall 1997, were emaciated but survived in fall 1998, and were of healthy body mass in 1999 (Hunt *et al.*, in press).

BIOTIC RESPONSES

Identifying and understanding mechanisms that transfer climate change via the ocean to biota (Figure 6) is essential if we are to understand ecosystem dynamics (Francis *et al.*, 1998). Fluctuations in the physical environment can impact the ecosystem through both changes in the nutrient-phytoplankton-zooplankton sequence (i.e., bottom-up control), and/or by altering habitat resulting in changes in abundance and/or composition of higher trophic level animals (i.e., topdown control). For the eastern Bering Sea, top-down control may be responsible for year to year fluctuation of zoo-and phytoplankton biomass, while bottom-up control has been suggested as the mechanism for longer period (decadal) variations (Sugimoto and Tadokoro, 1997). A feature not present in more temperate ecosystems, sea ice and its interannual variation, has marked ramifications for both the physical and biological environment. Distributions of marine mammals (Tynan and DeMaster, 1997) and fish (Wyllie-Echeverria and Wooster, 1998; Brodeur *et al.*, 1999b) as well as survival of age-1 pollock (Ohtani and Azumaya, 1995) respond to the

extent of sea ice itself and to its associated cold pool. The substantial increase in jellyfish biomass over the eastern shelf of the Bering Sea may be linked to climate change through ice cover (Brodeur *et al.*, 1999a). The extent, timing, and persistence of ice cover can dramatically alter time/space characteristics of primary production (Niebauer *et al.*, 1995; Stabeno *et al.*, 1998), and secondary production as food for larval fishes (Napp *et al.*, in press).

As the climate over the Bering Sea warmed, changes occurred in sea ice, the ocean itself and biota. Recent results support the belief that interannual and decadal changes in the environment (using ocean temperature as an index) play a significant role in salmon production in Alaskan waters (Downton and Miller, 1998; Kruse, 1998; Welch *et al.*, 1998). In the southeastern Bering Sea, the mechanism of advection of the planktonic stages of pollock (Wespestad *et al.*, in press) and Tanner crabs (Rosenkranz *et al.*, 1998) accounts for some of the observed fluctuations in year-class strength. In these studies the mechanism which links advection to year-class strength is predation. The advection models use wind-drift of the planktonic stages either to or away from regions where strong predation pressure exists. In the case of marine mammals and seabirds, climate effects appear to be mediated through the food web, although in some cases the links may be direct (Springer, 1998). These studies show that we are making progress towards linking climate changes and biological processes to form a more realistic and complete understanding of the ecosystem.

Coccolithophorid blooms have existed since 1997 under different environmental conditions (Hunt *et al.*, in press). Why this happened and what the implications are for the future is not known. Perhaps coccolithophores will replace the small flagellates that normally dominate in summer. It is likely that favoring another trophic level between primary producer and consumer (i.e., microzooplankton; Nejstgarrd *et al.*, 1997) will affect ecosystem dynamics (Napp and Hunt, in press). Attenuation and scattering of light by whole cells and detached liths alters submarine light fields (Voss *et al.*, 1998), influencing competition among phytoplankton species and affecting the quality and quantity of light for subsurface visual predators (e.g., diving seabirds). Dense concentrations of coccolithophores also alter regional biogeochemical cycles

making large positive contributions to calcite and dimethylsulfide production (Matrai and Keller, 1993; Brown and Podesta, 1997).

Changes in the ecosystem occurred which emphasize the importance of biological interactions. During the regime shift of the mid-1970's, the physical system experienced significant changes. Atmospheric conditions which had favored strong winds from the north, extreme ice cover and an extensive cold pool became those which generated minimal ice cover and magnitude/extent of the cold pool. During winter and spring of 1977/78, a set of environmental conditions occurred that promoted development of the extremely large 1978 year class of pollock. The role of cannibalism in influencing population dynamics resulting from the strong year class has been examined (Livingston and Methot, 1998). Age-1 pollock mortality due to cannibalism increased in the mid-1980's due to the influence of the large 1978 year class attaining the adult, more cannibalistic size (Figure 7). Predation model results show that several year classes subsequent to the 1978 year class may have initially been more abundant than the 1978 year class but adult cannibalism played a large role in reducing the number of juvenile pollock that eventually recruited to the fishery (Livingston and Methot, 1998). The model results indicated the possibility of two different spawner-recruit relationships, one for average to cold years and one for warmer years. The main mechanism influencing differential survival of pollock in cold versus warm years may initially be due to differences in physical transport of surface waters that moves pollock larvae to areas where feeding success is higher or where they are more separated from cannibalistic adults (Wespestad et al., in press). These results highlight the importance of studying the biotic interactions in order to pinpoint which life history stage of a given population is most influence by abiotic and biotic factors. Because of the interplay between predation and climate factors, it is possible that a year class as large as the 1978 year class will not be observed again until there is a combination of a relatively low adult population and winter/spring conditions favoring larval survival.

The relative importance of bottom-up and top-down processes in controlling production in marine ecosystems continues to be debated (Micheli, 1999). In addition to losses to natural

predators, human harvests of living marine resources in the eastern Bering Sea have averaged over 1.6 million metric tons in the period from 1979 to 1998 (Figure 8), with the majority of the catch consisting of pollock. Harvest rates of pollock and other resources have been relatively conservative over the last 25 years, with exploitation rates (catch/mature biomass) of 20 percent or less (Livingston *et al.*, 1999). Despite these conservative exploitation rates, a variety of species in diverse trophic groups have shown either long-term increases or decreases in abundance while others have shown cyclic fluctuations in abundance over the last two decades (Figure 9).

Total biomass in the inshore benthic infauna consumer trophic guild is higher than two decades ago. Within this group, rock sole and predatory starfish biomass have increased, yellowfin sole and Alaska plaice have decreased, and crabs have shown two periods of fluctuations in abundance, with recent trends indicating several crab species are now at very low abundance and three stocks have been placed in the overfished category. Offshore pelagic fish consumers are dominated in biomass by walleye pollock, which have undergone at least two periods of fluctuation, and are now at a lower abundance level than in the 1980's. The long-term pattern of increasing arrowtooth flounder abundance and decreasing Greenland turbot abundance is continuing, although arrowtooth flounder abundance may now be leveling off. Northern fur seal and piscivorous bird populations declined in the late 1970's and early 1980's but have also leveled off. Crab/fish consumer's biomass is generally declining although skate and halibut biomass within that group is higher in the 1990's than in the 1980's.

Several lines of evidence suggest that the overall production or allocation of resources has changed over the last few decades. Smaller than average adult salmon returning to western Alaska has been linked to changes in ocean conditions that influence growth and survival (Kruse, 1998). Decreases in the numbers of seabirds breeding on the Pribilof Islands since the mid 1970s point to a recent change in the carrying capacity of the middle shelf region (Hunt and Byrd, 1999). Zooplankton biomass in this region appears to have declined in the 1990s (Figure 10). Food may be becoming a limiting resource for populations such as walleye pollock

due to the increased abundance of some planktivorous marine mammals which are rebounding from decades of whaling (Tynan, 1998). Further pressure on food resources results from the marked increase in biomass of jellyfish (Figure 10), which may feed on some of the same zooplankton resources as larval and juvenile fishes (Brodeur *et al.*, 1999a). As noted by Napp and Hunt (in press), if food becomes limiting, then climate induced perturbations that affect production and availability of zooplankton may have an even greater effect on the structure of trophic webs than was observed in 1997.

There are indications that the population changes of fish, marine mammals and marine birds in the last 20 years are driven, at least partly, by environmentally driven recruitment changes (Hollowed *et al.*, 1998; Kruse, 1998; Rosenkranz *et al.*, 1998; Springer, 1998; Zheng and Kruse, 1998). Different species may respond to environmental changes that occur at either interannual or decadal scales. The increasing, decreasing or periodic fluctuation patterns seen in eastern Bering Sea species in the last two decades may be due to whether their recruitment or the recruitment of a major prey source is driven by decadal or interannual scale forcing. Understanding the responses of species to climate forcing is progressing rapidly in the North Pacific. Predicting future climate states and developing fishery management strategies that take changing climate into account must now make similar advancements.

MANAGEMENT CONCERNS

Many issues surround management of human use of shell fish and other fish stocks in the Bering Sea. Activities associated with these industries can impact the ecosystem through many pathways, including: overfishing, waste from bycatch, habitat destruction, benthic disturbance and marine debris. These threats to maintaining a healthy ecosystem are compounded by variations in climate that can cascade through the ecosystem. In this region where indigenous peoples abound, issues such as subsistence harvest and the lack of involvement of local communities in resource management decisions add crucial concerns. These human factors play out on the Earth's natural variability which itself has already been impacted by green house

gasses. Part of the solution to this complex challenge is to attain an understanding of the mechanisms which dictate ecosystem vitality and health.

We have provided only a few examples of changes in ecosystem dynamics of the eastern Bering Sea and have suggested that these are mainly due to climate change. We must continue discovering how mechanisms causing natural fluctuations function in order to have a reliable basis for managing human impact on various populations (Livingston *et al.*, 1999). To make further advances in our understanding of how this ecosystem functions requires a greater monitoring effort of both physical and biological parameters. This will allow identification of the important fluctuations and elucidation of the mechanisms by which changes in physical phenomenon are transferred to biota. In addition, this would permit the development of more complete knowledge of the life histories of the central species in the ecosystem and elucidate the role of biological mechanisms such as predation. Long-term monitoring programs appear to be the most direct way to establish causal mechanisms responsible for inducing ecosystem change.

THE NEXT DECADE

Prediction through mechanistic understanding is the goal of many applied sciences (e.g., Schumacher and Kendall, 1995). Using our increasing knowledge of processes important to the functioning of the Bering Sea ecosystem, we speculate below what might happen if the majority of years within the next decade resemble environmental conditions observed during spring and summer of 1997. We note that as atmospheric CO_2 and temperature over the arctic have increased, decreases in primary (1965–1990) and secondary production (1965–1993) have been inferred from time series of carbon isotope ratios in whale baleens (Schell, 1998) and summertime zooplankton biomass over the southeastern shelf (Sugimoto and Tadokoro, 1997).

From a mechanistic view, the reduction of onshelf transport during 1997 stands out as a fundamental process regulating production on the shelf. This transport is important for supplying inorganic nutrients, heat and salt (thereby affecting stratification) to the shelf. Assuming that the next decade has decreased on shelf flux of nutrients, weaker stratification,

reduced influence of sea ice, and warmer water temperatures, we envision the following changes. Annual primary production will decline and the spring phytoplankton bloom (in the absence of ice) will also be of lower magnitude but longer duration. This will favor planktonic rather than benthic production. In addition, those zooplankton species that are temperature, rather than food limited, may initially have higher rates of secondary production under a warming scenario. Predation by invertebrates, mammals, and seabirds also has an important role in structuring marine ecosystems. In recent decades, marine mammal populations have been protected from harvest. As their population size increases, we expect to see increased inter- and intraspecific competition for food. In 1999 sightings of dead beachcast of Pacific gray whales increased (Rugh et al., 1999) with scientists hypothesizing that inadequate food resources in their traditional feeding grounds (northern Bering and Chukchi seas) as the cause. Under limiting resources, prey switching (increasing diet breadth) can be expected. Recent examples include hypothesized use of sea otters by Killer whales (Orcinus orca, Estes et al., 1998) and diet breadth expansion in planktivorous short-tailed shearwaters (Puffinus tenuirostris) when adult euphausiids were not available in 1997 (Baduini et al., in press). Increased competition for planktonic prey such as euphausiids may also explain the recent decrease in size at maturity of Bristol Bay Pacific sockeye salmon (Kruse, 1998). A decrease in the presence of sea ice in the southeastern Bering Sea and under ice phytoplankton blooms may reverse the recent dramatic increase in schyphomedusae (jellyfish) which prey on zooplankton.

We emphasize that these speculations form, in part, a test of our knowledge of structuring mechanisms of the Bering Sea ecosystem. They are based on observations of previous states of the ecosystem. It is possible that multiple stable points exist for this resourcerich ecosystem. Formulation of hypotheses and collection of observations designed to test them is an essential part of increasing and refining our knowledge.

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Figures

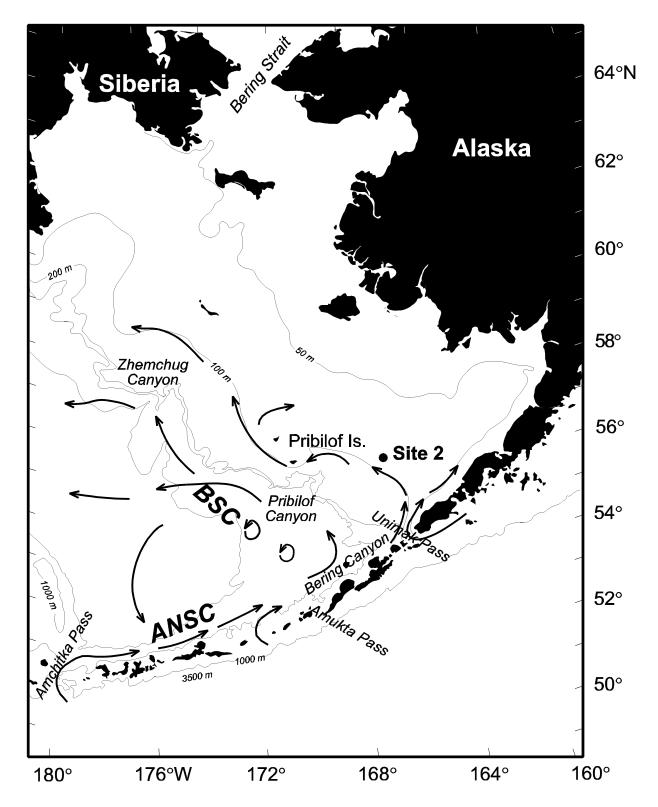


Figure 1. Eastern Bering Sea showing geographic names and the location of the FOCI moored biophysical platform (Site #2). Also shown is a schematic of the mean circulation.

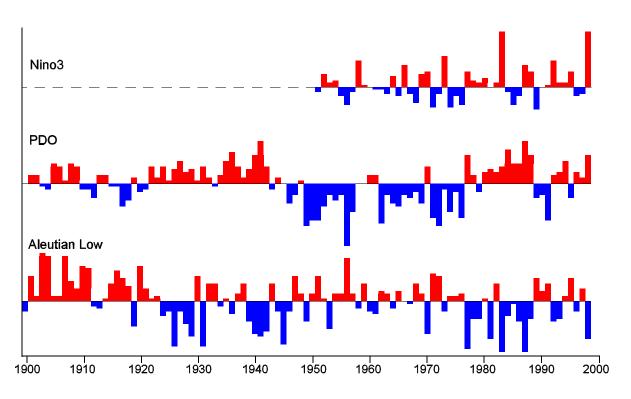


Figure 2. Atmospheric indices for the North Pacific and Bering Sea: an index of ENSO (the NINO3 index), the PDO (after Mantua *et al.*, 1997) and the Aleutian Low (from Stabeno *et al.*, in press).

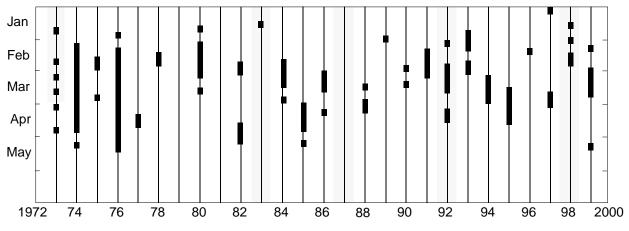


Figure 3. The persistence of ice cover at the position of Site #2 is indicated by the dark bars. The shaded areas indicate periods when an El Niño was occurring on the equator.

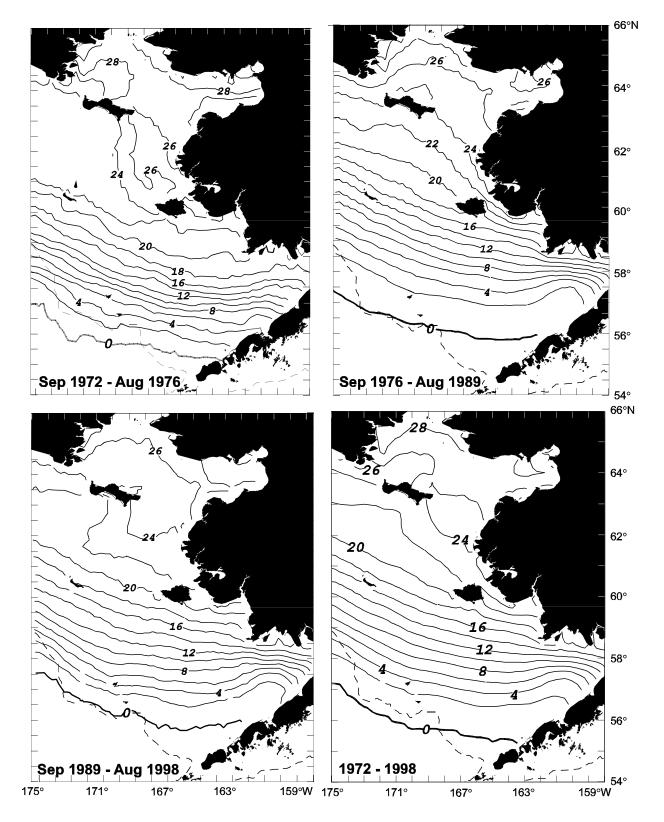


Figure 4. Contours of the number of weeks that sea ice was present over the Bering Sea shelf shown as the average ice coverage during: a) 1972–1976, b) 1977–1988, c) 1989–1998, and d) 1972–1998.

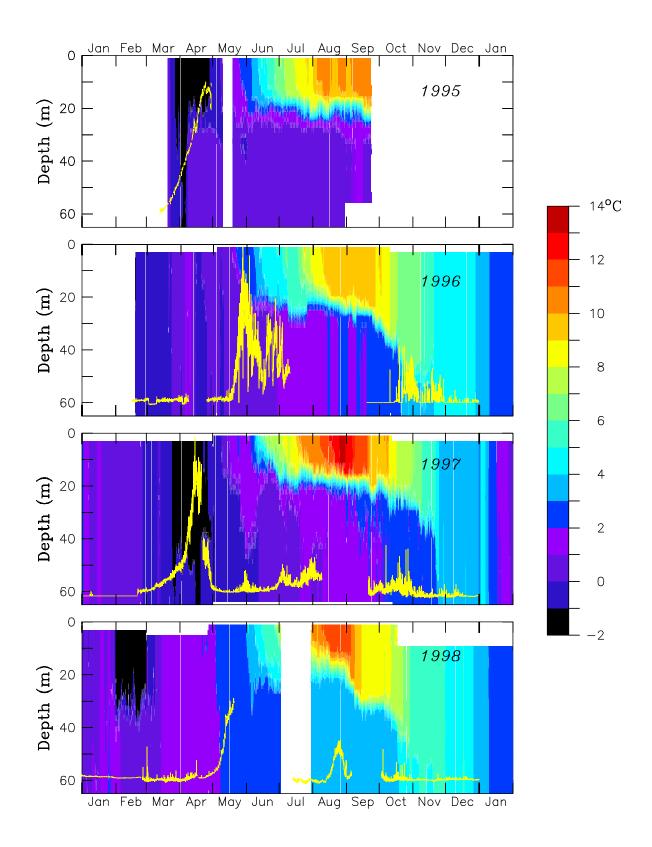


Figure 5. Time-series of water temperature and chlorophyll/fluorescence collected at Site #2. The coldest temperatures indicate the presence of ice (from Stabeno *et al.*, in press).

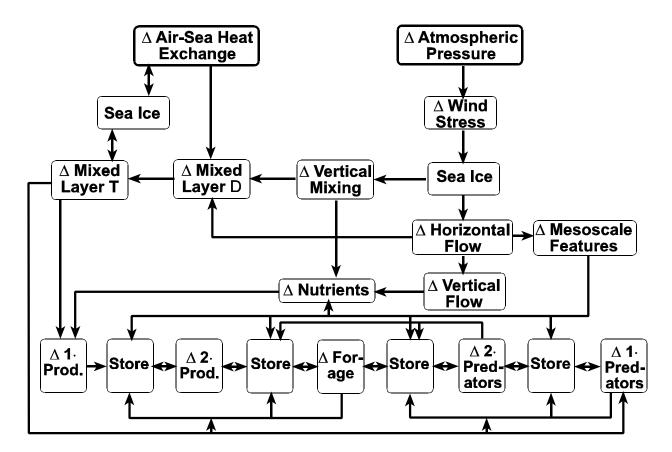


Figure 6. Pathways that changes in climatic influence the biological environment (after Francis *et al.*, 1998). We have added ice which couples atmospheric phenomenon to the ocean thereby effecting biota in a bottom-up mode. The presence of ice also directly influences distributions of marine mammals exerting an aspect of top-down control. Note that the presence of a coccolithophorid bloom also has direct influence on light penetration (primary production) and success of visual feeders.

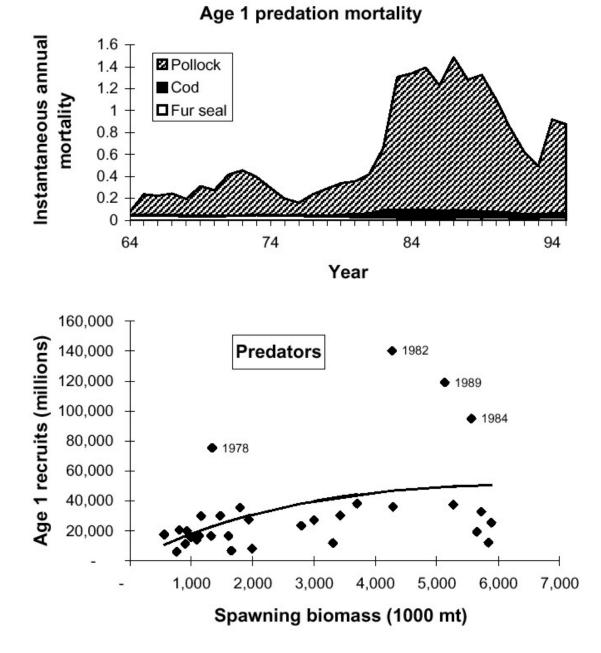


Figure 7. Predation mortality of age-1 walleye pollock from 1963 to 1995 estimated by the eastern Bering Sea pollock population model with predation by adult pollock, Pacific cod and northern fur seals (top). Estimates of age-1 recruitment of pollock recruits versus pollock spawning biomass from the pollock population model with predators and the fitted Ricker stock recruitment curves (bottom). (from Livingston and Methot, 1998).

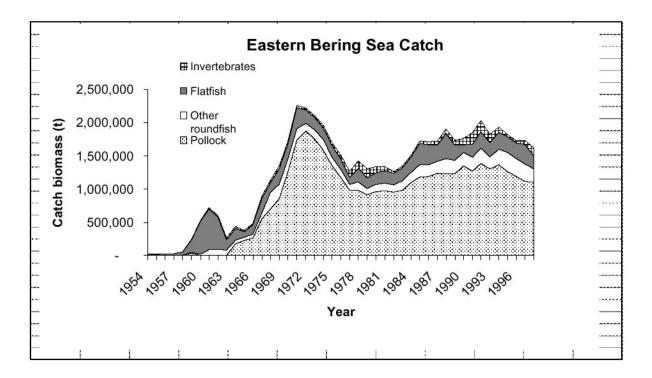


Figure 8. Catch biomass of pollock, other roundfish, flatfish, and invertebrates in the eastern Bering Sea from 1954 to 1998.

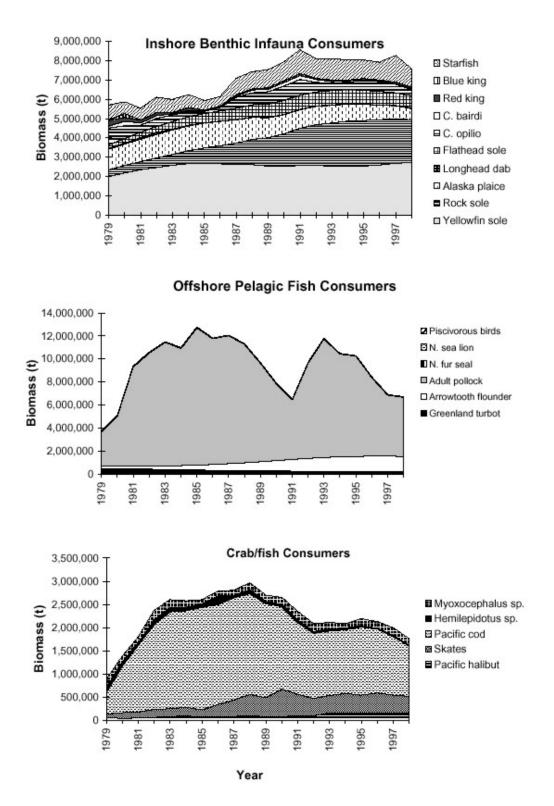


Figure 9. Biomass trends of three major trophic guilds in the eastern Bering Sea from 1979 to 1998.

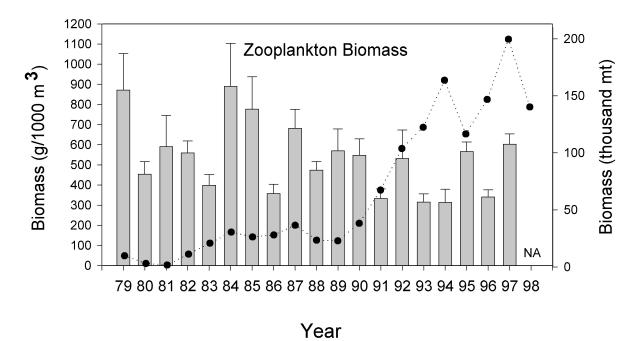


Figure 10. Biomass of zooplankton in the Eastern Bering Sea. The bars represent mesozooplankton collected by Norpac nets (see Sugimoto and Tadokoro, 1997) and the circles and dash lines represent the biomass of large medusae (in thousand MT) collected in standardized trawl surveys (modified from Brodeur *et al.*, 1999a). All error bars are standard errors of the mean.