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Overview of the Inner Front and Southeast Bering Sea Carrying Capacity Programs

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1. Introduction

During the 1990s, there has been a significant increase in our understanding of the Bering Sea ecosystem. Two programs, NOAA's Coastal Ocean's Southeast Bering Sea Carrying Capacity (SEBSCC) and the National Science Foundation-supported Inner Front Program (IFP), led the way in new findings. SEBSCC, whose focus was on the middle and outer shelves, and the slope, and IFP, whose focus was on the inner shelf, complemented each other. Several scientists, including the authors of this paper, were investigators in both programs. This resulted in close collaboration between the programs, a sharing of ship time, data, and ideas, and culminated in the compilation of this volume.

Between 1995 and 2000, we had the good fortune to be studying the Bering Sea during a period of great variability. We were presented with the opportunity to study an extremely warm year (1997) and a cold year (1999). During the 1990s, there were other marked changes in the Bering Sea shelf ecosystem including extensive blooms of coccolithophores, increases in jellyfish, and the appearance of large baleen whales. We also observed a massive die off of shearwaters, the continued decline in northern fur seals (*Callorhinus ursinus*) and Steller sea lions (*Eumetopus jubatus*), and a sharp decrease in the number of salmon.

These changes in the ecosystem, together with advances in ocean technology, provided the opportunity to expand our understanding of this complex ecosystem. In this paper we summarize the major findings of the two programs, starting with the physical environment, progressing through primary production, and finally discussing upper trophic levels. We then discuss a new hypothesis (Hunt et al., 2002) that links ecosystem function to climate. In closing, we pose several questions that remain unanswered and suggest directions for future research.

2. Decadal variability

The Bering Sea is characterized by large year-to-year variability, but is also sensitive to climate changes on decadal and longer time scales (Overland et al., 1999; Stabeno et al., 2001). It has been only within the last 10 years that significant research has been done on decadal-scale variability of climate and how it impacts the eastern Bering Sea ecosystem. The Bering Sea responds to two dominant decadal oscillations, the Pacific Decadal Oscillation (PDO) and the Arctic Oscillation (AO) (Overland et al., 1999). The PDO is the first mode of decadal variability in the sea-surface temperature of the North Pacific and its major impact is in the North Pacific and the southern Bering Sea. Changes in fish populations and other ecosystem functions are correlated with oscillations in the PDO (Mantua et al., 1997; Hare and Mantua,

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2000). The AO is based on variability in atmospheric pressure over the Arctic and North America. When in its negative state, higher-than-average pressure occurs over the Arctic and weaker-than-average pressure over the mid-latitudes. When in its positive mode, there is an increase in the poleward transport of heat. The AO impacts not only the Arctic and the Bering Sea, but it is also a source of climate variability for the Northern Hemisphere. In 1976, there were shifts in both the PDO and the AO, while in 1989, only the AO changed sign (Overland et al., 1999). These changes and the associated ecosystem responses have come to be called regime shifts.

One of the more readily observed impacts of climate change on the Bering Sea ecosystem is the extent and duration of sea ice over the Bering Sea shelf. The Bering Sea is a marginal ice zone, which is typically ice-free from June through October. During November, cold winds from the Arctic cool the water and begin the formation of ice in the polynyas. As the prevailing winds advect the ice southward into warmer water, the ice melts, cooling the water column. During the last two decades, the timing of maximum ice extent over the southeastern Bering Sea, on average, occurred in March, but there was substantial interannual variability. Maximum ice extents have been as early as January (in 2000) and as late as the end of April (in 1976). During cold winters, ice can cover most of the eastern shelf and can persist until April or even late May (Stabeno et al., 2001). Alternately, during warmer winters, ice does not extend much farther south than St. Matthew Island. Analysis of ice charts (Fig. 1) revealed that while there is significant year-to-year variability, decadal patterns of variability are evident (Hunt et al., 2002). During the early and mid-1970s, ice arrived early over the southeastern shelf and persisted into spring. Following this cold period, there was a warmer period when sea ice was less common. Finally, in 1989 there appeared to be a shift to cooler conditions although not as cold as observed in 1972–1976 (Stabeno et al., 2001). An examination of the timing of the ice retreat and temperature at 500 hPa reveals that during the last decade there has been a marked change in the timing of spring transitions (Stabeno and Overland, 2001).

While sea-ice has extended farther south in the last decade, it has retreated more quickly, resulting in the northern Bering Sea being ice-free earlier than in previous decades. In addition, atmospheric temperature during May has increased by 3°C in the 1990s compared to the 1980s.

During winter, strong storms prevail over the southeastern shelf, with a transition to calmer summer conditions occurring sometime in the spring. At a decadal scale, there has been a change in the timing of this transition. Since the regime shift of 1976, the timing of the transition from storminess of winter to calm conditions of summer has occurred earlier (Hunt et al., 2002). Similarly, calmer conditions have prevailed later into the fall. This change has a profound influence on the amount of mixing energy available to stir the upper mixed layer and to bring nutrients into the euphotic zone. Summer mixing events have been identified as important for the support of post-bloom new production (Sambrotto et al., 1986).

Thus, a major change in our thinking about processes in the Bering Sea is the realization that the dominant physical forcing mechanisms can operate not only at seasonal and annual time-scales, but also at the decadal scale. These decadal scale changes, or regime shifts, result in prolonged periods in which the extent, duration, and timing of ice cover, and the magnitude and direction of wind forcing can differ from regime to regime (Stabeno and Overland, 2001).

3. Frontal structure

It has been known since the 1970s that, during summer, the Bering Sea is divided into hydrographic domains by a series of fronts or transition zones. The inner front separates the well-mixed coastal shelf from the two-layer middle shelf domain, and the middle front, or more appropriately the middle transition zone, separates the middle shelf from the more oceanic outer shelf. It was hypothesized that the position of the inner front near the 50-m isobath resulted from a slight increase in the bottom slope at that location (Schumacher et al., 1979). Research completed as part of the IFP has shown that the position of the
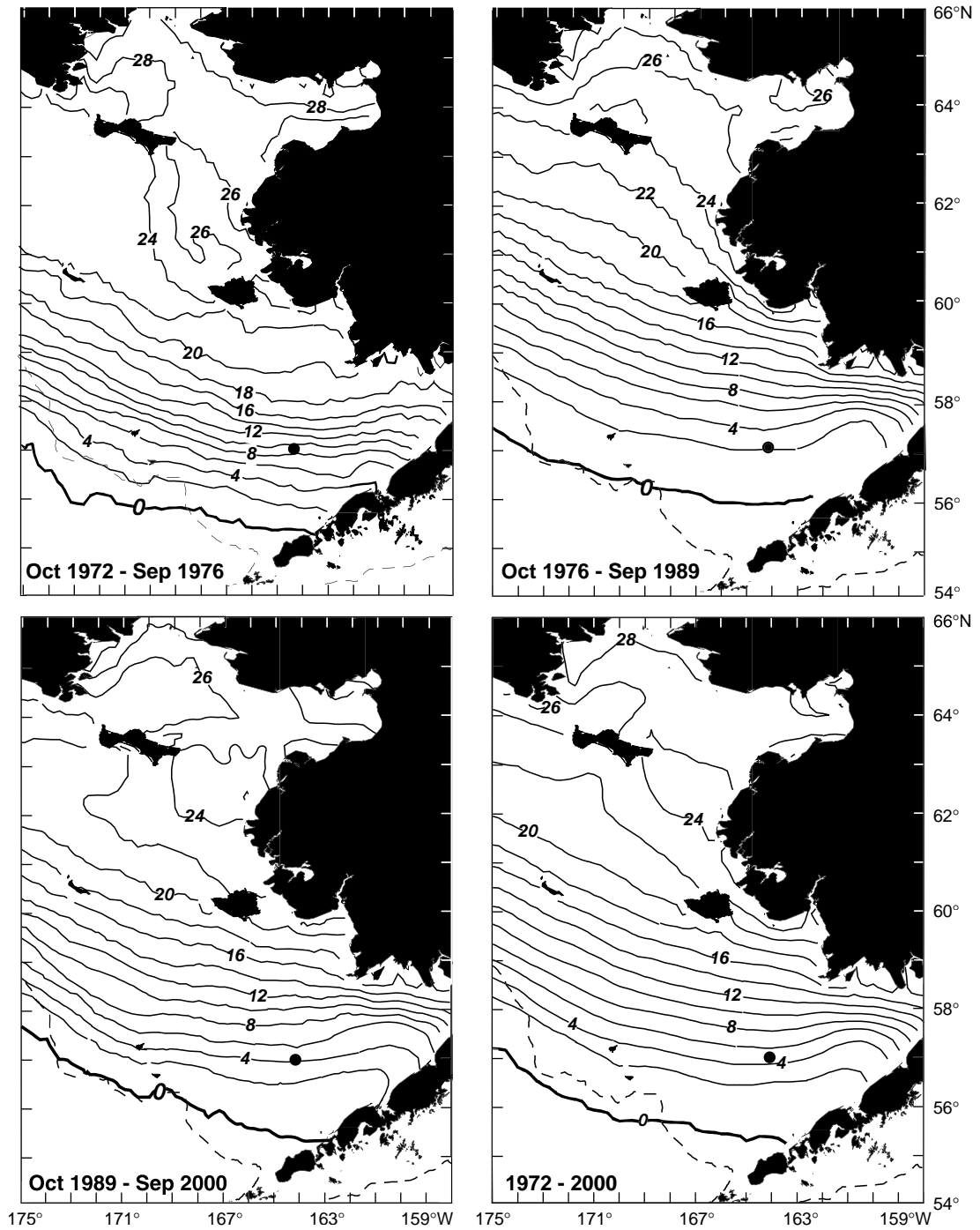
Fig. 1. Contours of the number of weeks per year that ice is present on the Bering Sea shelf. The data were divided into three time periods (a–c) that generally correspond to the regimes recognized over the Bering Sea. The overall mean (d) is also shown. This is an extension of data shown in Stabeno et al. (2001).

inner front is due to a balance of wind mixing and tidal mixing (Kachel et al., 2002). The position and width of the front are not static, but vary significantly depending upon the strength of the winds. This variability is now known to have a pronounced effect on the role of the front as a site for prolonged production, and as a barrier to exchange of fauna between the inner and middle domains.

The primary hypothesis of the IFP was that the inner front was a region of prolonged production during the summer. Usually, nutrients are exhausted from the surface mixed layer over the middle shelf by early summer, but there is still a reservoir in the bottom layer of the middle shelf. The introduction of these nutrients into the euphotic zone during summer supports new primary production in the vicinity of the inner front (Sambrotto et al., 1986). Observations during the IFP showed that there was great interannual variability in the role of the front in supporting primary production via the vertical transport of nutrients (Kachel et al., 2002). In 1997, a series of events depleted nutrients to a depth > 60 m, thus nutrients were not available for transport into the euphotic zone by frontal processes (Stabeno et al., 2001). Additionally, when the front was abnormally wide and weak (1997), there was little evidence of upward transport of salts (Kachel et al., 2002). In contrast, in 1999, the front was strong and narrow with a rich reservoir of nutrients available in the lower layer over the middle shelf. Upward transport of nutrients was observed in that year. It is now clear that this frontal system is more variable in time and space than previously thought, and that this variability has important ramifications for the role that the front plays in ecosystem structure and function.

4. Currents

Pioneering work on the Bering Sea shelf described a shelf system dominated by tidal diffusion and lacking in mechanisms for cross-shelf advection of salts and carbon (Coachman, 1986). In contrast to these earlier hypotheses, it is now clear that advection plays an important role on the Bering Sea shelf (Schumacher and Stabeno, 1998; Stabeno et al., 1999, 2001). Eddies, meanders of the slope flow, and topographic steering are all important mechanisms that introduce nutrient-rich slope water onto the shelf (Schumacher and Stabeno, 1994; Stabeno and van Meurs, 1999). While eddies and meanders are both episodic, the interaction of the slope flow with both Bering Canyon and Pribilof Canyon (Fig. 2) replenishes the shelf with nutrients in both winter and summer (Stabeno et al., 2002a).

Once on the shelf, nutrients can be advected across it. During winter, strong winds break down the frontal structure of the Bering Sea shelf and replenishment of nutrients and salt occurs (Stabeno et al., 2001). During summer, the existence of frontal structure and weaker winds reduces, but does not completely halt, cross-shelf fluxes (Fig. 3). While the existence of flow along the 50 m isobath paralleling the Alaska Peninsula and along the 100 m isobath were known earlier, the existence of an eastward flow north of the Pribilof Island was made using observations collected in the last decade (Reed and Stabeno, 1996). This current both supplies new nutrients to the middle shelf at the latitude of the Pribilof Islands during summer (Stabeno et al., 2002b), and separates the northern cold pool from the southern cold pool (Wyllie-Echeveria and Wooster, 1998). Although the middle shelf generally has weak flow during summer, on time scales of a few days to weeks, non-tidal currents can be significant (> 10 cm s^{-1}). Thus, contrary to earlier findings, the middle shelf of the Bering Sea is not static, and it is not necessary to postulate large tidal diffusivities for replenishment of the shelf with nutrients and salts (Coachman, 1986).

The generally northward flow over the eastern shelf results in a net flux of carbon and nitrogen into the Arctic, although the magnitude of export is highly variable. Satellite images of the coccolithophore blooms (e.g., Fig. 3 in Stabeno, 1999) reveal the distinctive color of the coccolithophore bloom extending into the Arctic. The advection of warm water from the Bering Sea into the Arctic could play a role in the melting of the ice cap, which has occurred in recent years.
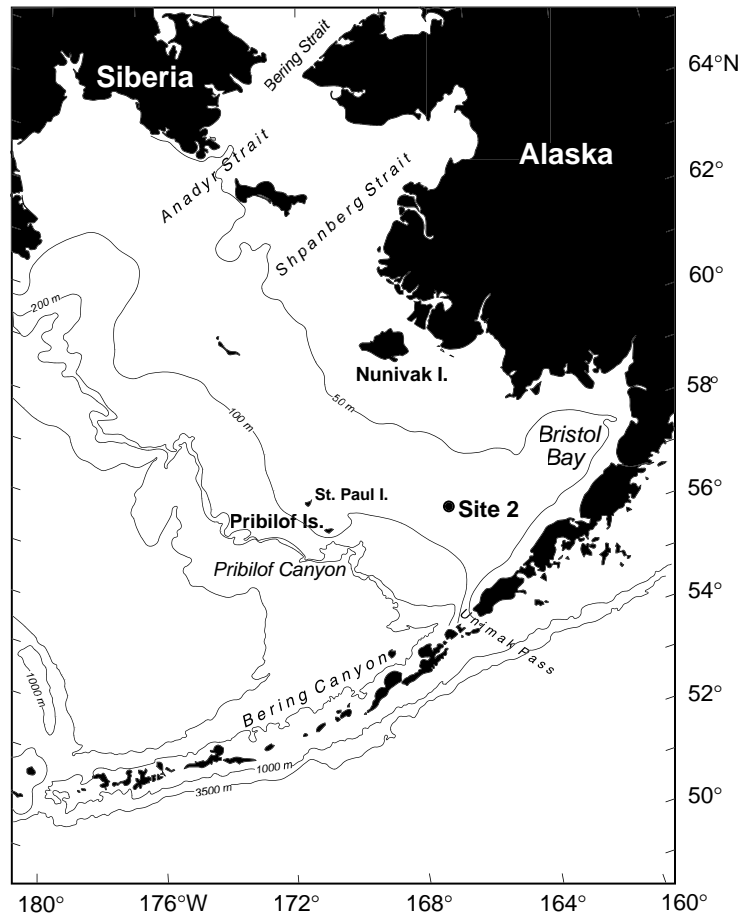
Fig. 2. Geography and place names in the eastern Bering Sea. The location of Site 2 is indicated. Depth contours are in meters.

5. Timing of the spring bloom

One of the important impacts of the seasonal Bering Sea ice is on the timing of the spring phytoplankton bloom. Research in the early 1970s emphasized the importance of ice for triggering an early bloom under the ice (Alexander and Chapman, 1981). During the late 1970s and early 1980s, research on the spring bloom focused on the importance of an open-water bloom in May that occurred subsequent to the stratification of the water column (Whitledge et al., 1986). These investigations came to differing conclusions because their respective field seasons were conducted during different climate regimes. The mid-1970s

were particularly cold with extensive ice, and the late 1970s and early 1980s were particularly warm with significantly less sea ice. Research in the last 7 years has revealed that during years when sea ice covered the southeastern shelf after mid-March, there was an early season, ice-associated phytoplankton bloom (Stabeno et al., 2001; Hunt et al., 2002). When ice was absent after mid-March, the spring bloom was delayed until the water column became stratified by surface heating, in May or even June.

The data needed to draw these conclusions came from a series of moorings that have been deployed over the southeastern Bering Sea since 1995 (Fig. 4). The moorings, particularly at Site 2
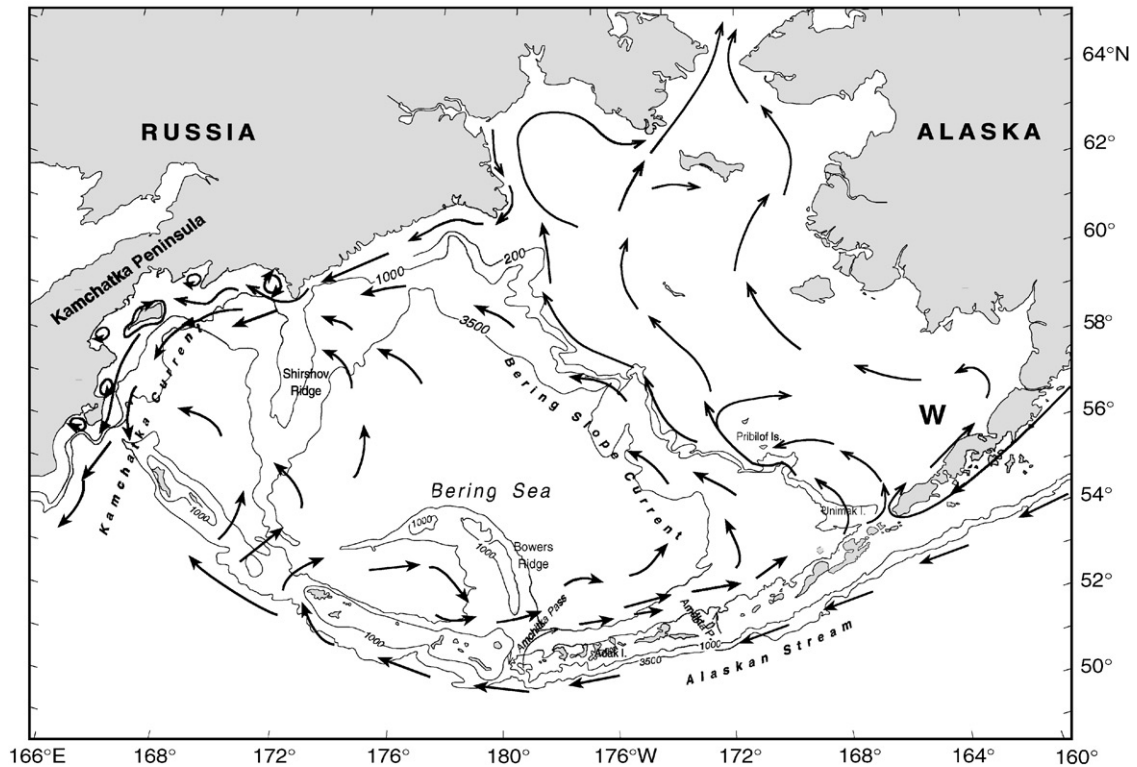
Fig. 3. A schematic of the upper ocean flow in the Bering Sea during the summer months. Depths are in meters (after Schumacher and Stabeno, 1998; Stabeno et al., 1999).

(Fig. 2), also provided data on the evolution of the temperature and salinity under the ice. As ice comes over the mooring, the water quickly cools to $<-1.7^{\circ}$C. Often the winds are strong enough that the water column mixes to the bottom (~ 70 m). Only in 1998 did the ice melt and leave behind a fresher surface lens of water, and even then strong winds after the retreat of the ice mixed the water column.

This observation suggests that in the southeastern Bering Sea it is not ice melt that sets up the stability required for the initiation of the bloom. This result is in contrast to earlier research where the melting ice was thought to set up a two-layer system with fresher water at the surface and more saline water nearer the bottom. Such a set-up may occur farther north, but it does not appear to occur over the southeastern shelf. Nevertheless, there is evidence of strong peaks in fluorescence in the water column. This fluorescence occurs under the ice and is accompanied by a depletion of nutrients in the surface waters. We do not know if this fluorescence results from the release of algae from the melting ice, or if it is a bloom of water-column algae. Sufficient wind energy is available to periodically mix the whole water column beneath the ice field. At present, we have no mechanism by which we can explain how the algae responsible for this fluorescence are able to remain in the euphotic zone, though the presence of more fluorescence in near-surface waters than deeper waters suggests that they are able to maintain a position high in the water column (Stabeno, unpublished data). New instrumentation on biophysical moorings that can take water samples to permit examination of the phytoplankton may help in understanding these under-ice blooms.
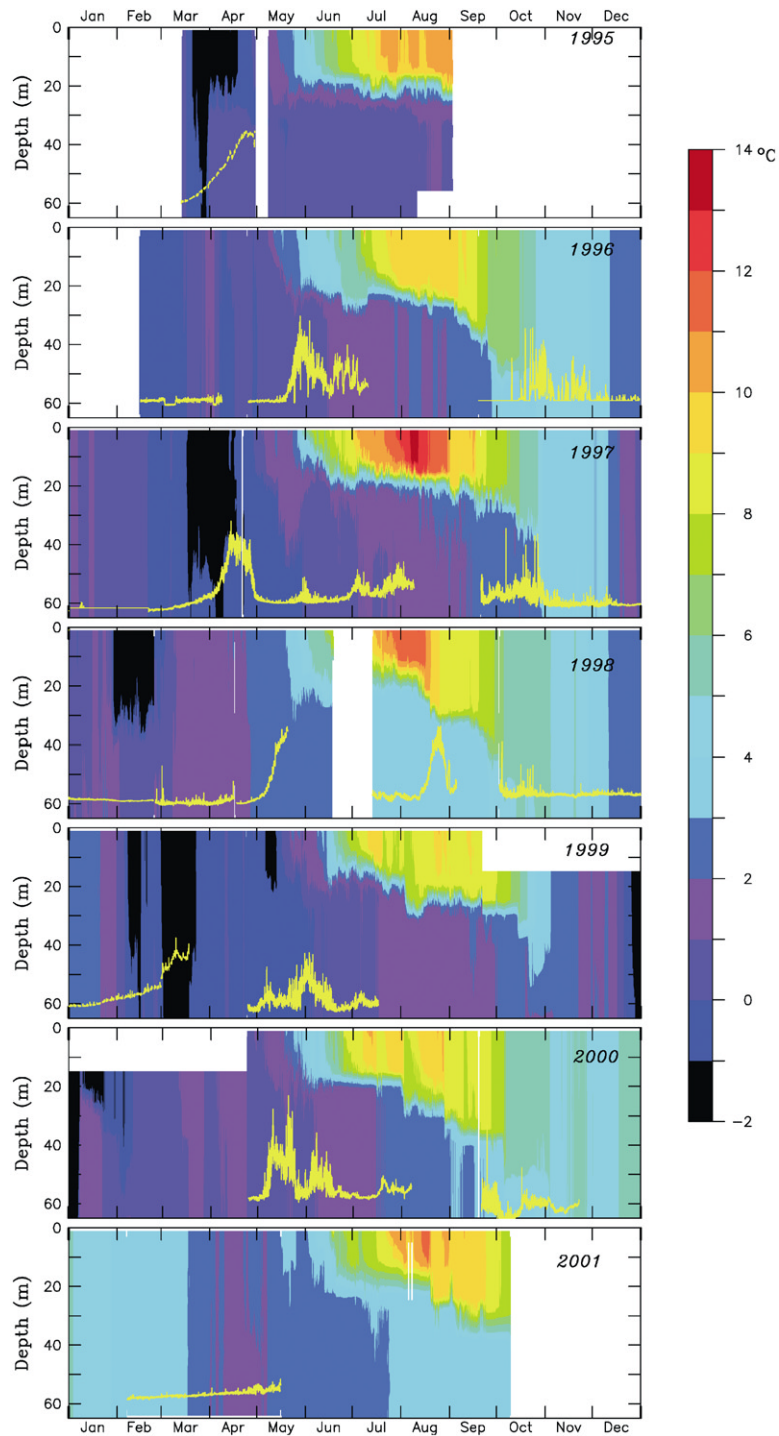
Fig. 4. Temperature and fluorescence at Site 2 (depth 70 m). The temperature was measured at ∼3 m intervals in the upper 30 m and 5–8 m intervals over the bottom portion of the water column. Moorings were typically recovered and deployed in February, May, and September. During summer, surface moorings were deployed providing ocean temperature at the surface. During winter, the upper instrument was ∼7 m and ocean temperature was extrapolated to the surface.

While the details of the phytoplankton bloom are still in question, the control of its timing is not. Quite simply, over the middle shelf of the southeastern Bering Sea, if there is sea ice after mid March, there is a bloom associated with the ice. If there is no ice, then the bloom does not occur until May or June when the water column becomes stratified.

The timing of the bloom has important repercussions on the zooplankton. The metabolic rates of all living ocean organisms are related to temperature. Ice-related blooms occur in cold water ($< -1^{\circ}C$), and zooplankton consumption of the bloom under these circumstances is limited by slowed physiological processes. Thus, in the case of ice-edge blooms, zooplankton production is reduced and much of the phytoplankton will fall to the bottom to feed a benthic community (Walsh and McRoy, 1986). These early blooms consume most of the available nutrients, thus limiting the possibility of open-water blooms later in the season when water temperatures are warmer. Early departure of the ice (before late March) results in an open-water bloom that occurs in May or even June, when water temperatures are warmer. Under these circumstances, the zooplankton are able to crop a larger portion of the bloom and zooplankton production is greater.

6. Coccolithophore bloom

Probably the most spectacular visual event in the Bering Sea in the last decade is the sudden and unexpected appearance of extensive blooms of coccolithophores, which are small calcareous phytoplankton (Fig. 5). During the calm conditions that prevailed during the summer of 1997, an extensive bloom of coccolithophores was observed both from ships and by the SeaWiFs satellite (Vance et al., 1998). The calcium carbonate plates that surround the small cells turned the water aquamarine. Surprisingly, the bloom has reappeared each succeeding year through 2001. Conditions in each of these subsequent years were colder than occurred in 1997. While the area covered by the blooms each year was similar (except 2001 when it appeared to be less extensive),

its location varied from year to year. For instance in 1998 the bloom of coccolithophores extended northward along the Alaskan coast through Bering Strait, while in 1999 the bloom was limited to the region south of St. Lawrence Island (Fig. 5). What caused the change in the summer assemblages of phytoplankton, how long it will continue, and what determines where on the shelf it occurs are all unknown. The coccolithophore bloom did, however, awaken the need to look at microzooplankton in the cycling of energy (Olson and Strom, 2002). It is likely that, compared to a diatom-based food web, one or two additional trophic steps will be required to get energy from this small phytoplankton to the top predators. The ultimate impact of the coccolithophores on the ecosystem, however, remains to be determined.

7. Zooplankton

Some species of zooplankton have responded at annual and decadal-scales to changes in the southeastern shelf ecosystem, whereas others have not. The abundance of several species of small copepods increased between the early 1980s and the mid-1990s (Stockwell et al., 2001; Napp et al., 2002). In contrast, no significant change in the abundance of euphausiids was found (Stockwell et al., 2001; Coyle and Pinchuk, 2002a). Likewise, reanalysis of the Oshoro Maru summer zooplankton time series showed no evidence of decadal-scale trends in zooplankton biomass (Hunt et al., 2002; Napp et al., 2002). Within the late 1990s, there was a 90% reduction in copepods between 1997–1998, and 1999 over the inner shelf that was associated with the decline in ocean temperature between these years (Coyle and Pinchuk, 2002b). In both 1997 and 1998, the depth-integrated temperature was well above average; in contrast, in 1999 temperatures were cooler than average. These results emphasize the possible importance of the temperature of the water column in influencing the pathways of energy flux. They explicitly tie shifts in the pattern of energy flux through the food web to the timing of ice retreat over the southeastern shelf.
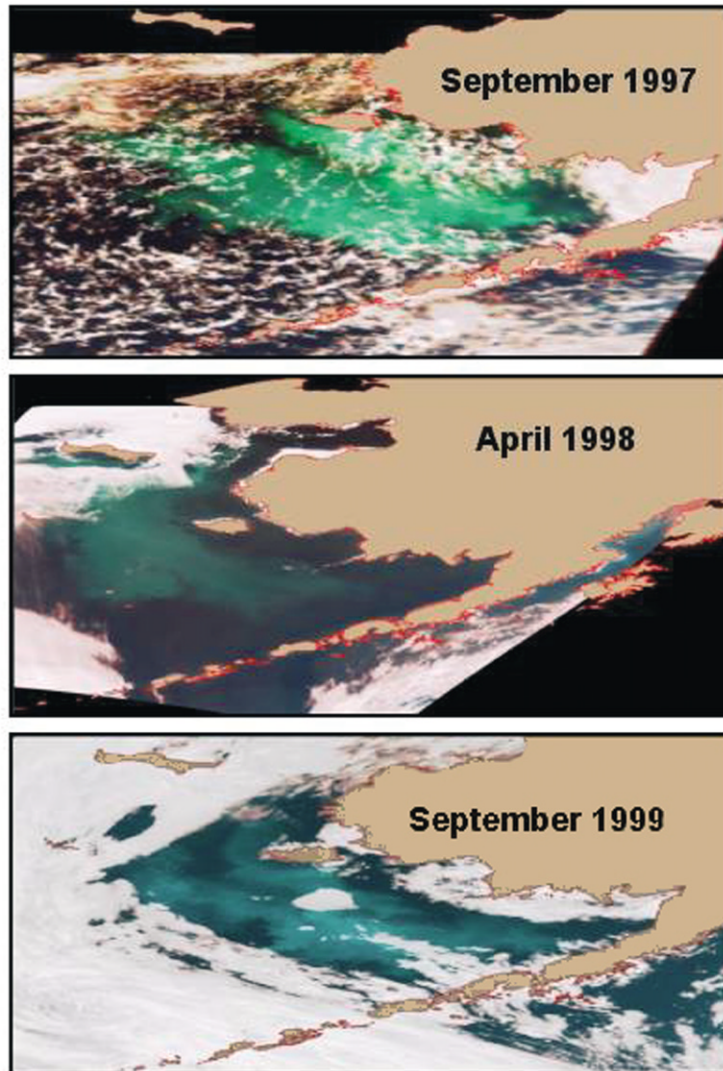
Fig. 5. SeaWiFs composite chlorophyll images for the three years—1997, 1998, and 1999. Data for the images were provided by the SeaWiFs Project, and the Distributed Active Archive Center at the Goddard Space Flight Center, Greenbelt, MD. NASA's "Mission to Planet Earth Program" sponsors these activities.

8. Gelatinous macrozooplankton

Over the last decade a sharp increase in the population of jellyfish has been observed over the eastern Bering Sea shelf (Brodeur et al., 1999). The cause of this rise is not known, but several hypotheses have been presented (Hunt et al., 2002; Brodeur et al., 1999). While it has generally been thought that the large scyphozoan medusae do not

over-winter, it is possible that the changing conditions on the shelf have permitted them to live longer. Alternately, the increase in jellyfish may reflect a release from competition with forage fishes, in particular, age-0 and age-1 walleye pollock (*Theragra chalcogramma*). The increase in large jellyfish coincided with a decrease in the numbers of forage fish, and jellyfish may have benefited from a decrease in the consumption of

zooplankton by these small fish (Brodeur et al., 2003). Regardless of the cause of their increase, the transfer of substantial amounts of energy to jellyfish on the eastern Bering Sea shelf is an apparently new phenomenon, with unknown ecological consequences. Since the jellyfish are largely predator-free, much of the energy transferred to them is unavailable to upper trophic level organisms, including commercially valuable species. In contrast, energy flow to forage fish is available to support a wide array of piscivorous fishes, seabirds, and marine mammals.

9. Responses of marine birds and mammals

During the 1990s, populations of marine birds and mammals in the southeastern Bering Sea showed considerable, and sometimes alarming, change. Pinnipeds, including harbor seals along the coast of Bristol Bay, northern fur seals at the Pribilof Islands, and Steller sea lions at the Pribilof Islands continued to decline as did some seabird populations at the Pribilof Islands (Hunt et al., 2002). During 1997, up to 11% of short-tailed shearwaters (*Puffinus tenuirostris*), a trans-equatorial migrant that spends the austral summer in the Bering Sea, died of starvation (Baduini et al., 2001a). In 1998, shearwaters were again emaciated, but no die-off occurred (Baduini et al., 2001b). It is not clear whether their primary prey, euphausiids, were less abundant or if the birds had greater than normal difficulty in obtaining prey, because of a change in the vertical distribution of prey or difficulty in locating prey in the cocco-lithophore-clouded waters. Calm winds in 1997 may have exacerbated the difficulties that the shearwaters encountered, as flapping flight in calm weather is more energetically expensive than flap-gliding in moderate winds.

From 1997 to 2000, high numbers of large baleen whales were observed over the middle domain. It is thought that increased numbers of these large baleen whales may consume sufficient food to significantly impact this ecosystem. Due to intensive whaling, the population of whales was significantly reduced prior to the mid-1970s, and it has been hypothesized that their removal possibly opened the way for a single species, walleye pollock, to dominate the pelagic biomass over the eastern Bering Sea shelf (Merrick, 1995; Merrick, 1997).

10. Oscillating control hypothesis (OCH)

To provide a conceptual framework for understanding recent patterns of change in the southeastern Bering Sea, a new hypothesis, the oscillating control hypothesis (OCH), was developed to relate alternation between bottom-up and top-down control of pollock recruitment in the eastern Bering Sea to decadal-scale changes in climate (Hunt and Stabeno, 2002; Hunt et al., 2002). This hypothesis predicts that when there is a prolonged series of years with delayed ice retreat and blooms in cold water, the production of large, piscivorous fish, such as pollock should be limited from the bottom-up by a lack of sufficient zooplankton, in particular calanoid copepods, to support the prey requirements of larval and juvenile fish. In contrast, in periods of late blooms in warm water, there will be greater supplies of copepods that will initially result in higher rates of pollock recruitment. However, as these large year-classes mature and become cannibalistic, limitation of recruitment will become top-down. Although a number of data are in congruence with the predictions and assumptions of the OCH (Hunt et al., 2002), we lack necessary time series during a period of successive late-ice years to demonstrate a switch to bottom-up control.

11. Unanswered questions

Coincidence of research and ecosystem variability during the decade of the 1990s provided insight into how the Bering Sea functions; however, many questions remain unanswered. While climate change impacts the ecosystem, the mechanisms are not well understood. Why do species of fish, mammals, and birds do better when the PDO or AO is negative (or positive)? What will be the impact of long-term warming on this ecosystem? The synthesis of data collected during the

warm years of 1997 and 1998 may begin to provide some answers.

Similarly, considerable research has been done on the spring bloom, but many questions remain. For instance, what is the coupling between phytoplankton and zooplankton during summer and fall? Is a certain level of productivity necessary to prepare species for winter? An early spring bloom is thought to export most of its production to the benthos. Does this result in a smaller population of zooplankton that in turn limits fish production?

Cross-shelf fluxes of nutrients are critical for production on the Bering Sea shelf, and measurements during winter are critical to understand the mechanisms that resupply nutrients to the shelf. The availability of new technology, particularly the moored nutrient sensors, will permit scientists to examine the temporal variability of nutrients. How will changes in climate impact the dynamics at the slope and the mechanisms that supply nutrients to the shelf? The Pribilof Islands are unique on the Bering Sea shelf in their proximity to the shelf break. Nutrients are advected onto the shelf in the vicinity of the islands through Pribilof Canyon. How variable is this supply of nutrients, and how critical is it to the birds and mammals that raise their young on the islands?

These are just a few of the outstanding questions that remain to be addressed on the Being Sea. This sea provides approximately half the US commercial catch of fish and shellfish and the extensive estuaries and offshore waters provide breeding, feeding and migrating habitat for approximately 36 million seabirds, 26 species of marine mammals, including sea lions, walrus, sea otters, whales, dolphins, and porpoises. Improving our understanding of how the Bering Sea functions will permit management of human activities to minimize our impact on this rich ecosystem.

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