Part 2—Synthesis of Research: A Contemporary Understanding of the Southeast Bering Sea Ecosystem

Results From the Synthesis Working Group on the Southeastern Bering Sea: Recent Advances in Knowledge From Bering Sea FOCI, Southeast Bering Sea Carrying Capacity and the Inner Front Program

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2.1 Introduction

2.1.1 Brief history and goals of recent research programs

The Bering Sea is a semi-enclosed sea that connects the North Pacific and Arctic Oceans. The 500-km-wide eastern continental shelf encompasses about one-half of its area and supports extraordinarily rich marine resources. These are of vital importance to the economic survival, subsistence, and cultural foundations of the many indigenous people of western Alaska (IARPC, 2001). Marine resources of the Bering Sea include fisheries equal to about one half of the United States' fishery production, about 80% of the seabirds found in the nation's waters, and substantial populations of marine mammals (NRC, 1996; IARPC, 2001). Its fishery landings include walleye pollock (*Theragra chalcogramma*, a nodal species in the shelf ecosystem), salmon, halibut and crab, and generate over $2 billion in revenue each year (IARPC, 2001). It is thus vital to the economic and social well being of the region that we understand the factors that determine the productivity of the Bering Sea. Such information will facilitate the wise exploitation and stewardship of this most important marine ecosystem.

Since the mid 1990s, two coordinated research programs, the Southeast Bering Sea Carrying Capacity (SEBSCC) project (1996–2002), supported by the Coastal Ocean Program of NOAA, and the Inner Front study (1997–2000), supported by the National Science Foundation (Prolonged Production and Trophic Transfer to Predators: Processes at the Inner Front of the S.E. Bering Sea), were active in the southeastern Bering Sea (Macklin *et al.*, 2002). These two studies were complementary, with one focused on the middle and outer shelf (SEBSCC) and the other (Inner Front) on the inner shelf. Collaboration between investigators in the two programs was strong. In addition, the Bering Sea FOCI (Fisheries-Oceanography Coordinated Investigations) program, funded by NOAA's Coastal Ocean Program,

was active from 1991 through 1997, and many of the FOCI investigators were also participants in the Inner Front and SEBSCC programs.

The goals of the Bering Sea FOCI program were to understand the factors that control the abundance of fish populations, and, in particular, the abundance and stock structure of walleye pollock in the Bering Sea (Macklin, 1999). A specific objective was to reduce uncertainty in managing these fish. The goals of the SEBSCC program were to increase understanding of the southeastern Bering Sea ecosystem, to document the ecological role of juvenile walleye pollock and factors that affect their survival, and to develop and test annual indices of pre-recruit (age-1) pollock abundance (Macklin *et al.*, 2002). SEBSCC focused on four central scientific issues: (1) How does climate variability influence the marine ecosystem of the Bering Sea? (2) What limits the growth of fish populations on the eastern Bering Sea shelf? (3) How do oceanographic conditions on the shelf influence distributions of fish and other species? (4) What determines the timing, amount, and fate of primary and secondary production? Underlying these broad goals was a narrower focus on walleye pollock. Of particular concern was the understanding of ecological factors that affect year-class strength and the ability to predict the potential of a year-class at the earliest possible time. The Inner Front program 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. Of particular interest was the potential for prolonged post-spring-bloom production at the front and its role in supporting upper trophic level organisms such as juvenile pollock and seabirds. Of concern to both programs was the role of interannual and longer-term variability in marine climates and their effects on the function of sub-arctic marine ecosystems and their ability to support upper trophic level organisms (see also Francis *et al.*, 1998).

2.1.2 Structure of synthesis report

In this section of the final report, we provide an overview of the contributions of the SEBSCC and Inner Front programs to our understanding of processes in the southeastern Bering Sea. We begin with a brief description of the physical environment and marine climate of the eastern Bering Sea. We follow with an examination of changes and mechanisms of change for the physical and biological components of the eastern Bering Sea ecosystem. We then discuss several conceptual hypotheses that provide possible avenues toward understanding changes in the amount and fate of production in the southeastern Bering Sea, and how climate change may affect the function of this ecosystem. Finally, we identify a series of questions that recent work suggests will be important to answer in our quest for a fuller understanding of the function of the eastern Bering Sea in a changing climate.

2.1.3 Brief description of the Southeastern Bering Sea

The Bering Sea consists of a deep central basin, a northwestern shelf in the Gulf of Anadyr that reaches south along the Kamchatka Peninsula, and a broad eastern shelf that stretches from the Alaska Peninsula to Russia and

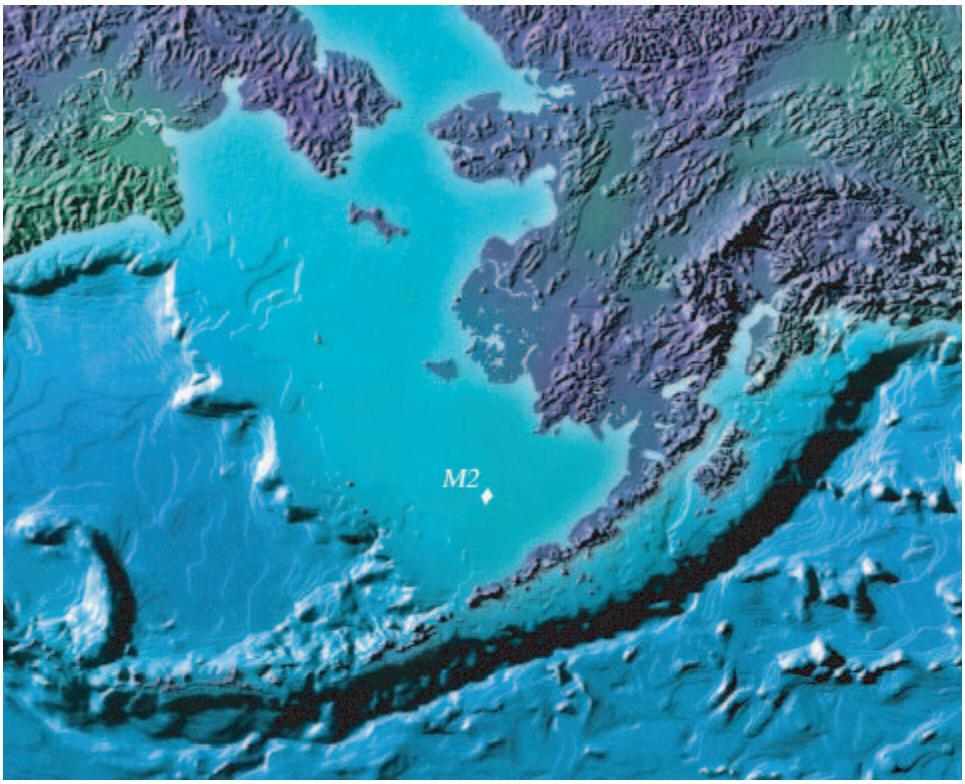

Figure 2.1: Three-dimensional view of the eastern Bering Sea, with location of the biophysical mooring M2 shown. Map courtesy of K. Birchfield.

the Bering Strait (Fig. 2.1). For the purposes of this report, the waters of the eastern Bering Sea can be divided into an Oceanic Regime that occupies the basin and a Shelf Regime that occupies the eastern shelf. The eastern shelf can be further sub-divided into the southeastern shelf and a northeastern shelf, with the dividing line running east-west just south of St. Matthew Island from the coast to the shelf edge.

The following overview of the Oceanic Regime is based on the description of Schumacher *et al.* (2003). The Oceanic Regime of the eastern basin is influenced by Alaska Stream water that enters the Bering Sea through Amchitka and Amukta passes in the Aleutian Islands, and turns right to form the Aleutian North Slope Current (ANSC; Reed and Stabeno, 1999) (Fig. 2.2). This current in turn provides the major source of water for the Bering Slope Current (BSC) that varies between following the depth contours of the eastern shelf northwestward with a regular flow, and becoming an ill-defined, variable flow characterized by numerous eddies and meanders (Stabeno *et al.*, 1999a). The eddies occur not only in water seaward of the eastern shelf (Schumacher and Reed, 1992), but also in waters as shallow as 100–122 m deep (Reed, 1998). These eddies are potentially important as habitat for larval and juvenile pollock, and can carry these fish, as well as nutrient salts, from the Oceanic Domain into the Outer Shelf Domain (Schumacher and Stabeno, 1994; Stabeno *et al.*, 1999a).

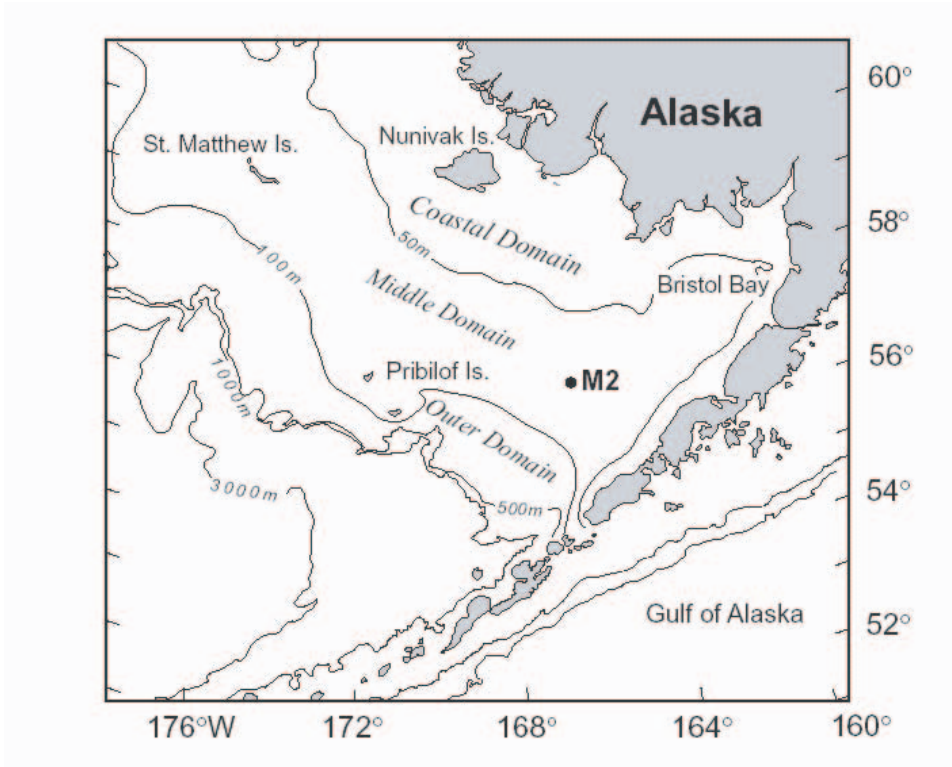

Figure 2.2: Southeastern Bering Sea showing isobaths and domains. Map courtesy of N. Kachel.

The broad continental shelf (up to 500 km wide) of the southeastern Bering Sea is differentiated into three bathymetrically fixed domains, which include the Coastal Domain that extends from the shore to about the 50-m isobath, the Middle Shelf Domain, between the 50-m and 100-m isobaths, and the Outer Shelf Domain that ranges from 100 m to 200 m in depth (Fig. 2.3) (Iverson *et al.*, 1979b; Coachman, 1986; Schumacher and Stabeno, 1998; Stabeno *et al.*, 2001). The domains are separated by fronts or transition zones, with the narrow (5 to 30 km) Inner Front or Structural Front between the Coastal Domain and the Middle Shelf Domain, the wide (>50 km) middle transition zone between the Middle Shelf Domain and the Outer Shelf Domain, and the Outer Front between the Outer Shelf Domain and the waters of the slope. In summer, the Coastal Domain is well mixed to weakly stratified, the Middle Shelf Domain is strongly stratified, and the Outer Shelf Domain has well mixed upper and lower layers with a zone of gradually increasing density between (Schumacher *et al.*, 2003). During summer in the Middle Shelf Domain, the temperature difference between the upper and lower layers can be greater than 8°C, and changes in density are dominated by temperature rather than salinity (Hunt *et al.*, 2002a). In the northeastern Bering Sea, changes in tidal energy and freshwater discharge from the Yukon River affect the location of the fronts, with the Inner Front occurring in water 30 m or less (Schumacher and Stabeno, 1998). During summer in

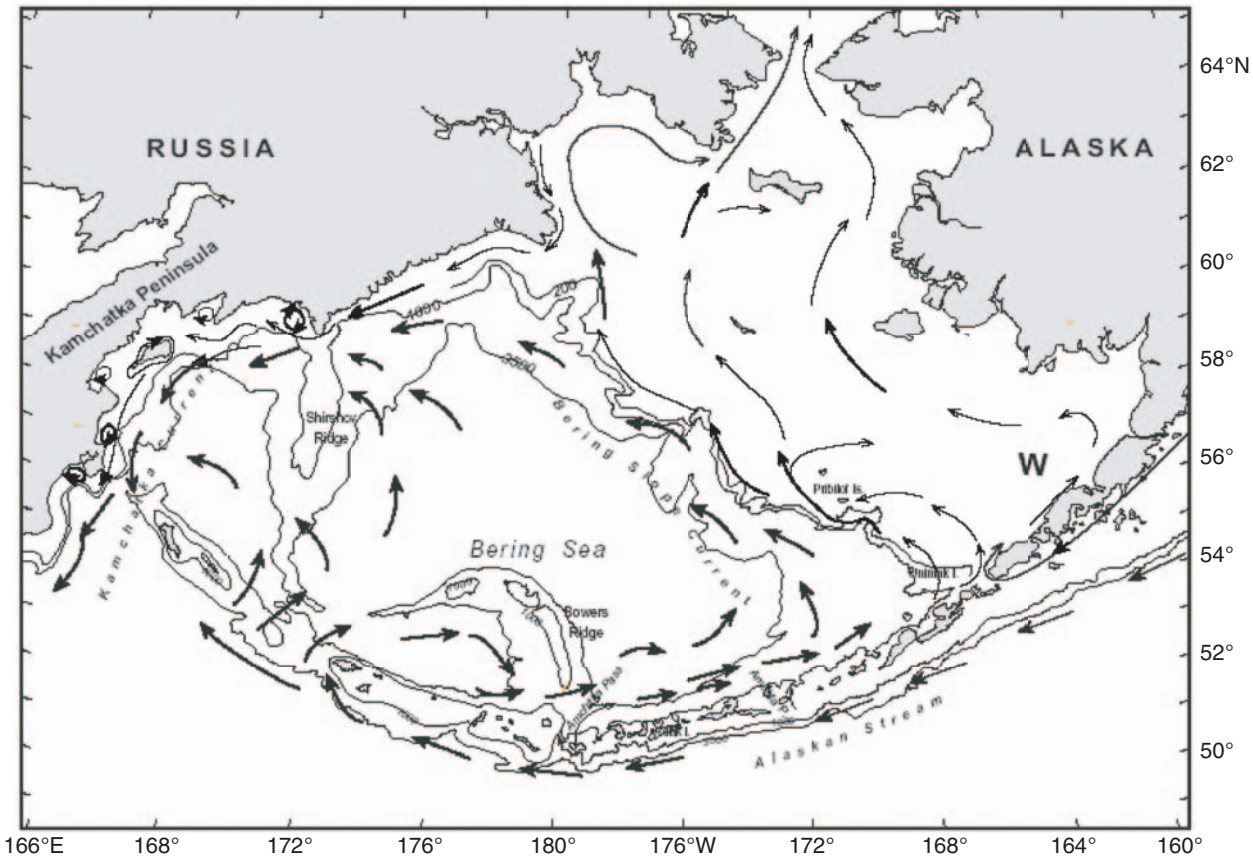

Figure 2.3: Schematic of major currents in the Bering Sea. From Stabeno *et al.* (1999a).

Norton Sound, a two-layered system can occur in water as shallow as 20 m. In winter, the water column there is well mixed.

2.2 Climate and the Bering Sea Marine Ecosystem

An important development in fisheries oceanography during the last decades of the twentieth century was the realization that climate variability, at the scale of decades, could have profound impacts on the function of marine ecosystems. Of particular importance was the realization that seemingly small shifts in the mean values of atmospheric variables, at least when compared to their interannual variability, could result in major changes in the productivity or standing stocks of fish populations. Recent work has suggested that climate variations may affect the mechanisms (e.g., bottom-up or top-down) that control populations, such that the impact on fish stocks of a given rate of harvest may be quite different in different climate patterns.

2.2.1 Climate indices

For the North Pacific Ocean, among many potential indices of climate variability, there are three well-studied indices of climate patterns that de-

pend on variability in winter, the Pacific Decadal Oscillation (PDO), the El Niño/Southern Oscillation (ENSO), and the Arctic Oscillation (AO). The PDO is defined as the leading mode of sea surface temperature variability in the North Pacific (north of 20°N), and has time scales of 20–30 years (Ladd *et al.*, unpublished manuscript; Mantua and Hare, 2002) (Fig. 2.4). The PDO is a major mode of variability (Wallace *et al.*, 1992), yet it explains only 21% of the variance of the monthly SST and is primarily centered on the central North Pacific rather than the Gulf of Alaska and Bering Sea. The ENSO has widespread influence on global climate variability at time scales of 2–7 years, and has its greatest influence in the tropics. Recently, ENSO has been shown to have a small but significant influence on the marine climate of the Bering Sea via atmospheric teleconnections (Niebauer, 1998; Hollowed *et al.*, 2001; Martin *et al.*, 2001; Overland *et al.*, 2001). The AO is defined as the leading mode of sea level pressure variability north of 20°N, and consists of a pattern of zonally symmetric variability in the strength of the polar vortex (Thompson and Wallace, 1998; Ladd *et al.*, unpublished manuscript). The AO has its largest variance in winter (January–March). The strongest mode of variability in the AO is interannual, but it also varies at decadal scales, having changed sign in 1976 and again in 1989 (Thompson and Wallace, 1998; Overland *et al.*, 1999) (Fig. 2.4). The AO has an influence on the Bering Sea through its affect on the Aleutian Low, which is the monthly or seasonal mean location of the center of low sea level pressure over the North Pacific (Overland *et al.*, 1999). The value and position of the Aleutian Low reflects the strength and distribution of storm tracks in the southern Bering Sea and sub-arctic Pacific Ocean. These storms have great influence on the marine climate of the Bering Sea in winter.

A fourth index of atmospheric pressure, the North Pacific (NP) pattern, represents the leading mode in spring of the 700 hPa height and is most prominent from March through July (Barnston and Livezey, 1987; Ladd *et al.*, unpublished manuscript). The NP consists of a north-south pressure dipole, and its strong variance in spring relates to storminess in the Bering Sea (Overland *et al.*, 2002).

In the North Pacific region, the wintertime indices, in conjunction with indices of biological responses in marine ecosystems, have been used to identify abrupt shifts in climatic forcing and ecosystem response at decadal time scales (e.g., Trenberth and Hurrell, 1995; Mantua *et al.*, 1997; Francis *et al.*, 1998; Hare and Mantua, 2000; McFarlane *et al.*, 2000; Hollowed *et al.*, 2001). Two of these regime shifts have been identified in the past thirty years. One followed the winter of 1976–1977, in which the PDO and the AO both shifted (Fig. 2.4). A second shift, of just the AO, occurred after the winter of 1988–1989 (Ebbesmeyer *et al.*, 1991; Hare and Francis, 1995; Sugimoto and Tadokoro, 1998; Beamish *et al.*, 1999b; Brodeur *et al.*, 1999a; Hare and Mantua, 2000). There is some evidence of a third shift in the winter of 1998–1999 (Schwing and Moore, 2000; Peterson *et al.*, 2002). Although the ENSO appears to alternate between two states that are repeatedly visited, that does not appear to be the case for regime shifts in the southeastern Bering Sea, where the few regimes documented so far have each had unique characteristics.

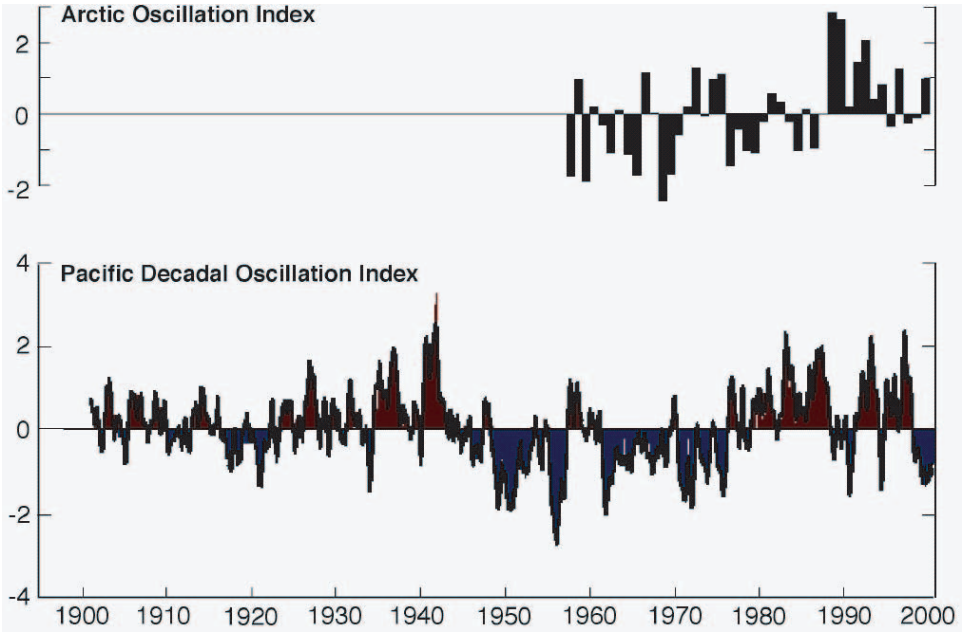

Figure 2.4: Time series of the Arctic Oscillation (AO) and the Pacific Decadal Oscillation (PDO). Note the change from negative to positive in the PDO as of 1977 and from positive to negative in 1998. The AO showed a shift from negative to positive about 1989. Updated from Overland *et al.* (1999).

The main climate feature influencing the southeastern Bering Sea is the Aleutian Low (Fig. 2.5). The Bering Sea lies between the cold Arctic air mass to the north and warmer maritime air mass of the North Pacific. Over the Bering Sea, there is a region of strong gradients in sea-level pressure (SLP) between the Aleutian Low and the high pressure over the Arctic. Considerable interest has developed around low frequency (multi-decadal) variability in the North Pacific in both the physical and biological portions of the North Pacific ecosystem (Minobe, 1999). Hare and Mantua (2000) found evidence in 100 time series for regime-like jumps in these records near 1977 and 1989. The evidence was clearer in the biological data than in the physical data. Their second mode showed strong covariability between physical and biological variations in the Bering Sea over the past 40 years.

To investigate this variability, the strength of the Aleutian Low is plotted in Fig. 2.6 for 1900 through 2000. Visually, there are some indications of a lowering of SLP after 1927, higher pressures from 1947–1977, and an event near 1990. However, the main feature of this plot is the large change from year to year. In fact, almost two-thirds of the variance in this record is at time scales shorter than 5 years (Overland *et al.*, 1999). When one looks at the time series after 1977, almost half the years have SLP values near or slightly above the mean (horizontal line) that occur between years of record low SLP. Using a 5-year running mean is not particularly representative of individual years, either for periods when the values were near average or for

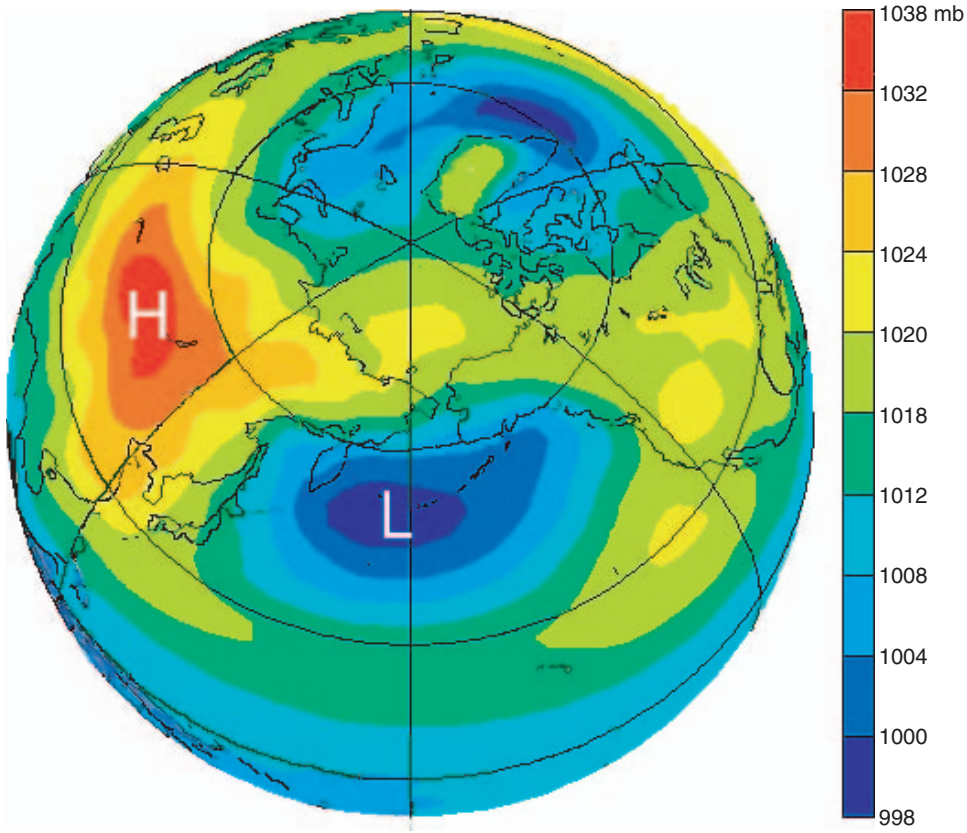

Figure 2.5: The location of the Aleutian Low, the statistical mean location of winter low pressure cells in the northern North Pacific. Figure courtesy of J.E. Overland.

those periods with large negative anomalies, as the averaged data remove the signal from the extreme years that may force the system.

One approach to modeling the variability of the Aleutian low time series is to fit its auto-correlation function, the correlation of the time series with itself as a function of lag between the series. Fig. 2.7 shows the auto-correlation function (the vertical stick plots) repeated in all three plots as a function of lag in years. The values are all small, generally less than 0.3; however, the values are mostly positive, suggesting a broad contribution of frequencies to the original time series, rather than a Gaussian distribution of random errors. The solid heavy lines represent three models of the time series (Percival *et al.*, 2001). The left plot is an Auto-Regressive (AR) red noise model that rapidly decays to zero. The middle plot is a long memory (LM) model that rapidly decays in the first years but then has a broad contribution from longer lags. The third model (right) is a 50-year oscillation plus white noise. All three models are fit with two free parameters and all are candidates to represent the Aleutian Low, because a 100-year record is too short an interval to say one model is superior based on classical statistical grounds.

We have additional information that favors the long memory model. The

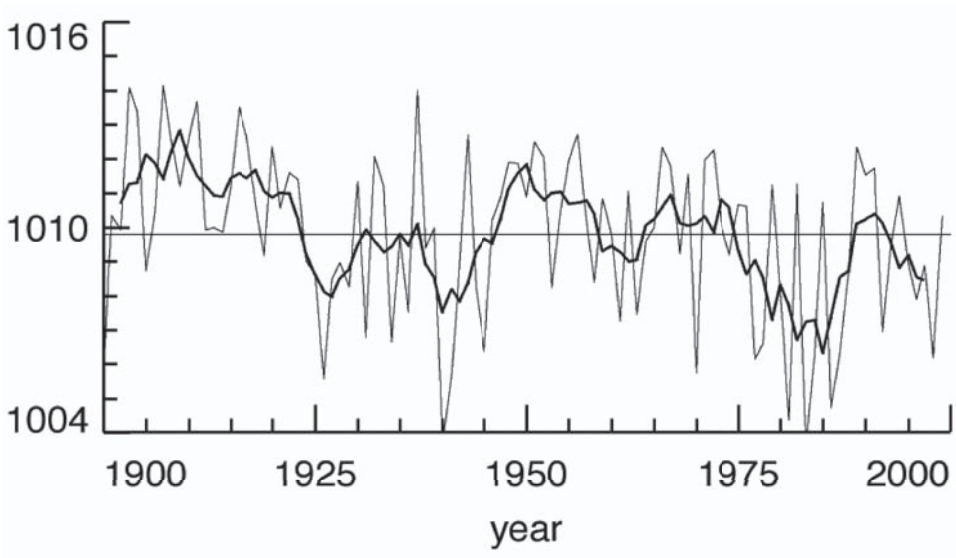

Figure 2.6: The strength of the Aleutian Low with respect to the long-term mean, annual signal, and 5-year running mean. Note that the signal is dominated by extremely strong interannual variability. From Percival *et al.* (2001).

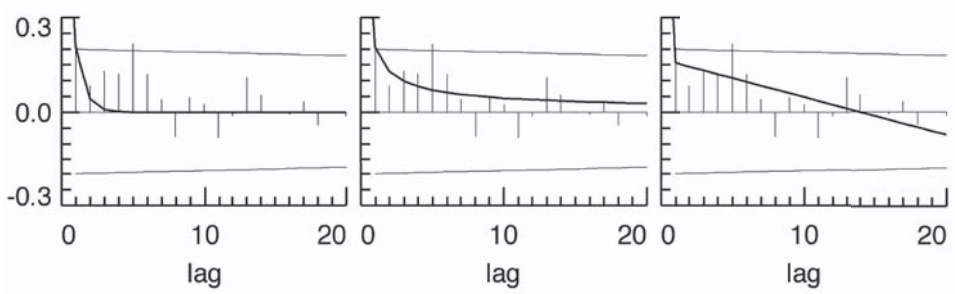

Figure 2.7: Auto-correlation functions (stick plots) of the Aleutian Low time series, with three models of the time series: **Left:** Auto-Regressive, **Middle:** Long memory, and **Right:** 50-year oscillation plus white noise. (From Percival *et al.*, 2001.)

LM model assumes contributions from many processes with different time lags, while the AR model represents a single time scale. It is more reasonable to expect that many processes, such as North Pacific SST, Arctic air masses, ENSO, and Siberian storm systems, influence atmospheric variability over the Bering Sea. We also know from the work of Hare and Mantua (2000) that regime-like behavior favors the LM and oscillator models, as the LM model is about 5 times more likely to have a 20-year run of all positive or negative values than the AR model.

What does this mean for the biology of the Bering Sea? Instead of a pure regime shift model of the physical system with changes spread over 20+ years, we have a physical system that has a strong response in 1 or 2

years. The low frequencies contribute to the timing of these strong events. In this conceptual model, the impact of the change in the physical system is large enough to promote the reorganization of the ecosystem. The massive increase in pollock after 1978 and 1989 (Wespestad *et al.*, 2000) and the 1997 coccolithophore event (Sukhanova and Flint, 1998; Vance *et al.*, 1998; Overland *et al.*, 2001) follow these patterns. Thus, the regimes seen in the biological data of Hare and Mantua (2000) may be the result of a continuing decadal ecosystem reorganization following a major meteorological extreme.

2.2.2 Meteorological forcing

Variability in SST warming is expected to be a dominant factor on the Bering Sea shelf during the warm season. Figure 2.8 summarizes the 40-year record of the rate of warming in early summer and 1 August SST (top panel); two crucial components of the surface heating, the downward shortwave (solar) radiation and latent heat fluxes (middle panel); and two aspects of the wind, the rate of wind mixing (u_x^3) (Fig. 2.8, bottom panel), and along-shelfbreak wind stress (Fig. 2.9, bottom panel). These time series reveal that recent August SSTs are roughly 1°C warmer than those typifying the 1960s. Much of the trend in this heating can be attributed to a long-term tendency toward more solar heating and decreasing surface latent heat fluxes, or evaporative cooling, over the 40-year record. Interannual variability in the summertime warming appears to be due to a combination of variations in solar heating and wind mixing.

The physical state of the ocean over the shelf during spring and summer has been well documented only since 1995, which compromises interpretation of decadal-scale changes in the marine ecosystem. Recent work has indicated that there exists a viable approach for addressing this lack of direct oceanographic observations for retrospective analyses. Specifically, it appears that reasonably accurate hindcasts of the evolution of thermal profiles over the shelf can be made using a 1-D ocean model (the Price-Weller-Pinkel or PWP model) forced by surface winds and heat fluxes generated from reanalysis of historical records (Ladd *et al.*, unpublished manuscript). These hindcasts can be used to estimate not just temperatures (an important factor for zooplankton growth rates) but also the supply of nutrients to the euphotic zone, with implications for summertime primary production.

Progress has been made in understanding the impact of climate variations on the Bering Sea shelf, but there remain a host of important but unanswered questions. For example, while the mean flow on the shelf is sluggish, it is likely at times to be significant. It remains unclear which aspects of atmospheric forcing are important to cross-shelf flow, and what time scales are of primary importance to these events. In general, the sources and potential predictability of climate variations for the Bering Sea in spring through fall are poorly understood. In particular, little attention has been devoted to air-sea interactions during fall and the possible ramifications of their variability for the ecosystem. Thus, while there is a growing appreciation that relatively short-lived but intense events can account for a disproportionate share of the seasonally integrated forcing, it remains unknown how the fre-

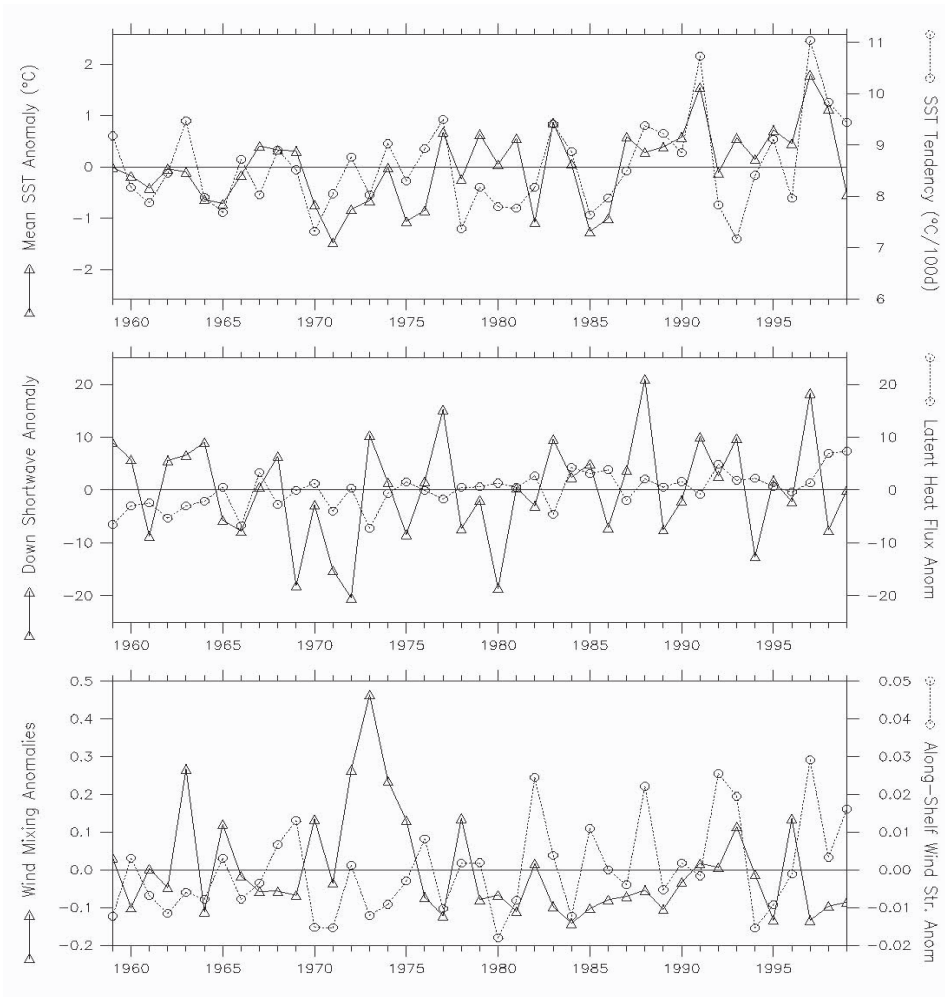

Figure 2.8: Summer season averages for 1959–1999. **Top:** SST tendency (solid line, °C 100 d^{-1}) and SST anomaly on 1 August (dotted line, °C), both at 57°N, 164°W. The zero anomaly line for SST also represents the value of the mean SST tendency. **Middle:** Downward shortwave radiative heat flux anomaly (solid line, W m^{-2}) and surface latent heat flux (dotted line, W m^{-2}), both at 57°N, 167°W. **Bottom:** Wind mixing anomaly at 57°N, 164°W (solid line, m^3 s^{-3} × 100) and along-shelf wind stress anomaly at 56°N, 169°W (dotted line, N m^{-2}). From Bond and Adams (2002).

quency and timing of these events relate to the longer-term variations in climate.

2.3 Physical Components of the Eastern Bering Sea Ecosystem

2.3.1 Sea Ice in the Eastern Bering Sea

Sea ice extent is a crucial aspect of the physical environment of the eastern Bering Sea shelf. The Bering Sea is a marginal ice zone, which is typically ice free from June through October. Beginning in November, cold winds from the Arctic cool the water and begin the formation of ice in the polynyas

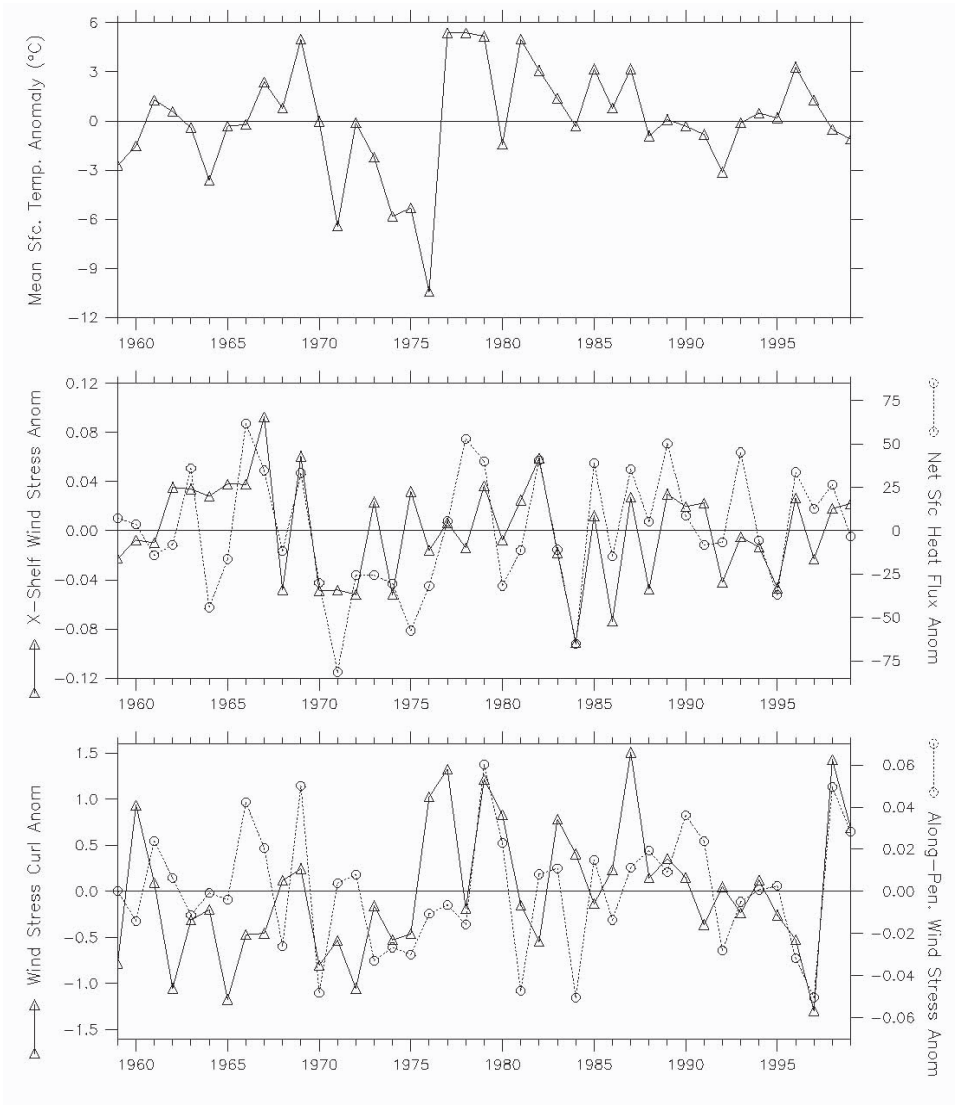

Figure 2.9: Winter season average anomalies for 1959–1999. **Top:** Surface temperature at 57°N, 164°W (solid line, °C). **Middle:** Cross-shelf wind stress at 57°N, 164°W (solid line, N m^{-2}), and net surface-heat flux at 56°N, 172°W (dotted line, W m^{-2}). **Bottom:** Wind stress curl at 55°N, 173°W (solid line, N $m^{-3} \times 10^7$) and along-peninsula wind stress at 53°N, 173°W (dotted line, N m^{-2}). From Bond and Adams (2002).

that form on the lee sides of islands and coasts. Throughout winter, the prevailing winds advect the ice southward into warmer water where the ice melts at its southern edge, cooling and freshening the seawater (Pease, 1980; Niebauer *et al.*, 1999). Recently, Niebauer (1998) has found that the position and depth (strength) of the Aleutian Low has a significant effect on the sea ice cover of the Bering Sea, and that the effect of the Aleutian Low is linked to ENSO events. The maximum southerly extent of the ice and the amount of ice melt affect fluxes of heat and salt, thereby influencing both baroclinic flow and the temperature at the bottom (the cold pool)

in the Middle Shelf Domain (Ohtani and Azumaya, 1995; Schumacher and Stabeno, 1998; Wyllie-Echeverria and Wooster, 1998).

One of the more readily observed impacts of climate change on the eastern Bering Sea ecosystem is the extent and duration of sea ice over the Bering Sea shelf (Niebauer, 1998; Stabeno *et al.*, 2001; Hunt *et al.*, 2002a). The seasonal variation in the position of the ice edge is about 1700 km, the most extensive of any Arctic or sub-arctic region (Niebauer, 1998). In an average winter, about 75% of the eastern shelf is ice covered, but the amount and duration of ice cover can vary interannually by up to 25% of the seasonal range, depending on the wind field (Niebauer, 1983, 1998; Schumacher and Stabeno, 1998). During the last two decades, the maximum ice extent over the eastern shelf occurred, on average, in March, but maximum ice extents have been as early as January (in 2000), and as late as the end of April (in 1976) (Stabeno and Hunt, 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 those observed in 1972–1976 (Stabeno *et al.*, 2001).

During cold winters, ice can cover most of the eastern shelf (Stabeno *et al.*, 2001). Alternately, during warmer winters, ice does not extend much farther south than St. Matthew Island. Analysis of ice charts (Fig. 2.10) shows that decadal patterns of variability are evident (Niebauer, 1998; Hunt *et al.*, 2002a). In the period from 1977 to 1996, there was a 5% reduction of ice cover as compared to 1947–1977 (Niebauer, 1998). Interannual and decadal-scale variability in sea-ice coverage was greater at the southernmost edge of the ice field than farther north (Fig. 2.10). Between 57 and 58°N, there was an apparent decrease in days with ice after 1 January between 1972–1976 (mean number of days with ice 130 ± 18 SD) as compared with 1977–1989 (67 ± 26 SD, $t = 1.767$, $p = 0.096$) and 1990–2000 (76 ± 23.3 SD, $t = 2.036$, $p = 0.061$). The average pattern of ice coverage has also changed since the early 1970s (Fig. 2.11), when the maximum extent of the zone in which ≥10% ice cover was present annually for >2 weeks extended farther south and west than it did in the 1980s or the 1990s (Stabeno *et al.*, 2001). Additionally, in the 1980s and 1990s, the zone where ice lasted for at least 2 weeks withdrew northeastward along the Alaska Peninsula. Most of the north side of the Peninsula has been ice free since 1990. The 1989 regime shift did not result in a return to the extensive ice conditions present before 1977.

In the eastern Bering Sea, a proxy for sea ice extent is the mean winter (Jan–Apr) surface temperature (Bond and Adams, 2002). The 40-year record for the site of Mooring 2 (top panel of Fig. 2.9) shows a notably cold period in the early to middle 1970s, and a warm period in the late 1970s into early 1980s, but conditions during the 1990s are similar to those in the 1960s. The time series of atmospheric parameters directly related to sea ice (middle panel of Fig. 2.9) indicate that the presence of sea ice is a function of not just the cross-shelf component of the wind, but is also strongly related to the net surface heat fluxes, which are determined by air and water temperatures and wind speed. Niebauer (1998) found that before the regime

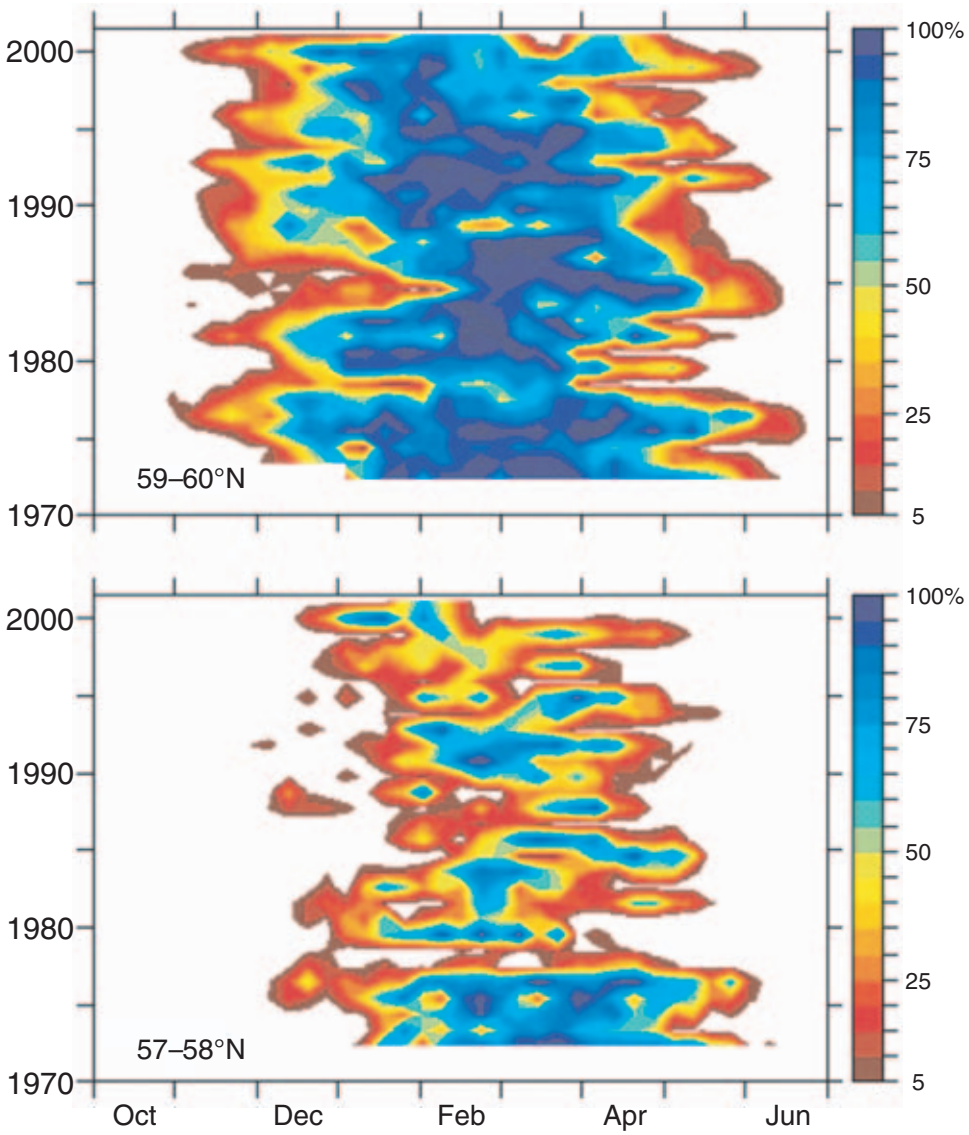

Figure 2.10: Percent ice cover for two latitudinal bands in the eastern Bering Sea. Note the decrease in ice cover in the southern region as of about 1977, whereas there is little evidence for a change in ice cover at this time in the more northerly region. From Hunt *et al.* (2002a).

shift of 1976–1977, below-normal ice cover in the eastern Bering Sea was associated with El Niño conditions, during which the center of the Aleutian Low shifted eastward, and resulted in warm air from the Pacific flowing over the southeastern Bering Sea. After the regime shift, the Aleutian Low was located even farther eastward during El Niño periods, and under these circumstances the southeastern shelf was subjected to north and east winds from the interior of Alaska, which resulted in increased ice cover.

An examination of the timing of the ice retreat and air temperature at 500 hPa (∼5 km altitude) reveals that during the last decade there has been

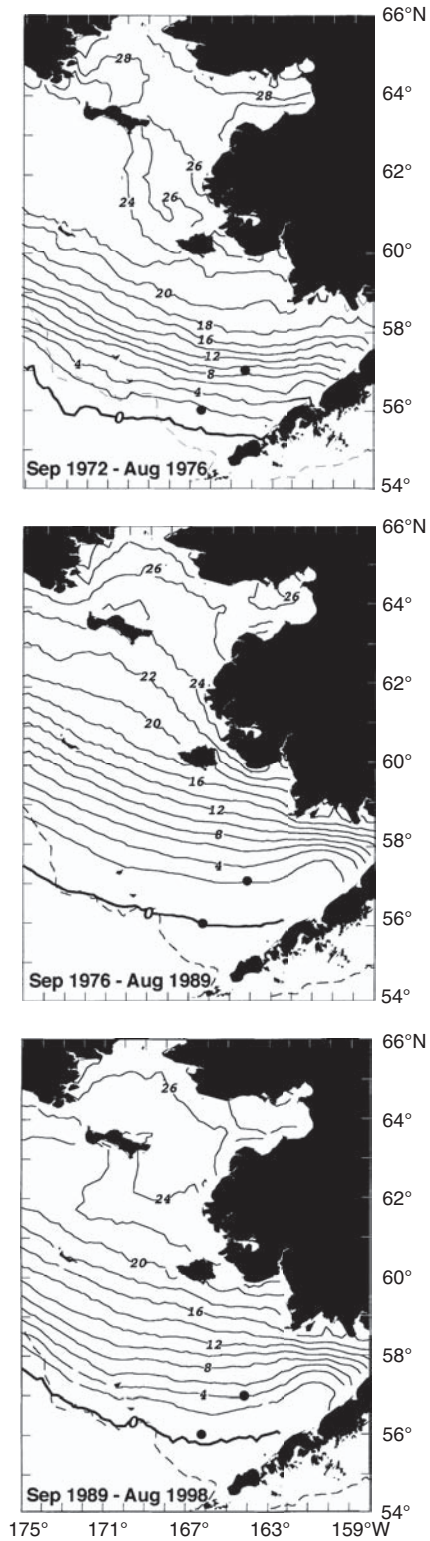

Figure 2.11: Contours of the number of weeks that >10% sea-ice cover was present over the eastern Bering Sea shelf. After Stabeno *et al.* (2001).

Table 2.1: Relationship between the timing of ice retreat and the type of spring bloom (from Hunt and Stabeno, 2002).

	Bloom Occurs at Ice Edge	**Bloom in Open Water**
Ice gone by mid March	0	7
Ice remains after late March	6	0

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.

2.3.2 Biological importance of the timing of ice retreat

In the southeastern Bering Sea, the timing of spring primary production is determined by a combination of the date of ice retreat, stabilization of the water column by solar heating, and the cessation of strong storm activity (Sambrotto *et al.*, 1986; Stabeno *et al.*, 1998, 2001; Eslinger and Iverson, 2001). The timing of the spring bloom is important because it determines the ambient water temperatures in which grazers of the bloom must forage. Data illustrative of the conditions that determine the timing of the spring bloom were obtained from Mooring 2, located in ∼72 m of water in the middle domain (Figs. 2.1, 2.12). If ice retreat comes before mid-March, there is insufficient light to support net production in the well-mixed water column (e.g., Fig. 2.12: 1996, 1998, 2000). Without ice remaining after mid March, the spring bloom is delayed until May or June, after winter winds have ceased and thermal stratification stabilizes the water column (Fig. 2.12) (Stabeno *et al.*, 1998, 2001; Eslinger and Iverson, 2001). If ice melt occurs in April or May, there is an early, ice-associated bloom (e.g., Fig. 2.12: 1995, 1997, 1999). The pattern of late ice retreats with early ice-related blooms and early ice retreats with late blooms has held since the 1970s (Table 2.1). Although wind mixing of the water plays a role in determining when the bloom will occur, it is apparent in Fig. 2.13 that the timing of the last winter storm is less important than the date of ice retreat in determining the timing of the bloom. Thus, early blooms occur in cold water and are related to ice-edge blooms, whereas late blooms occur in relatively warm water and are not related to the ice edge (Figs. 2.12, 2.14).

We also often see evidence of chlorophyll in the water under the ice during ice melt. This may be evidence of the release of ice algae or seeding of the bloom by ice algae. However, we do not know the origin of this signal, or if its species composition is the same as that of the open water bloom. This requires further investigation.

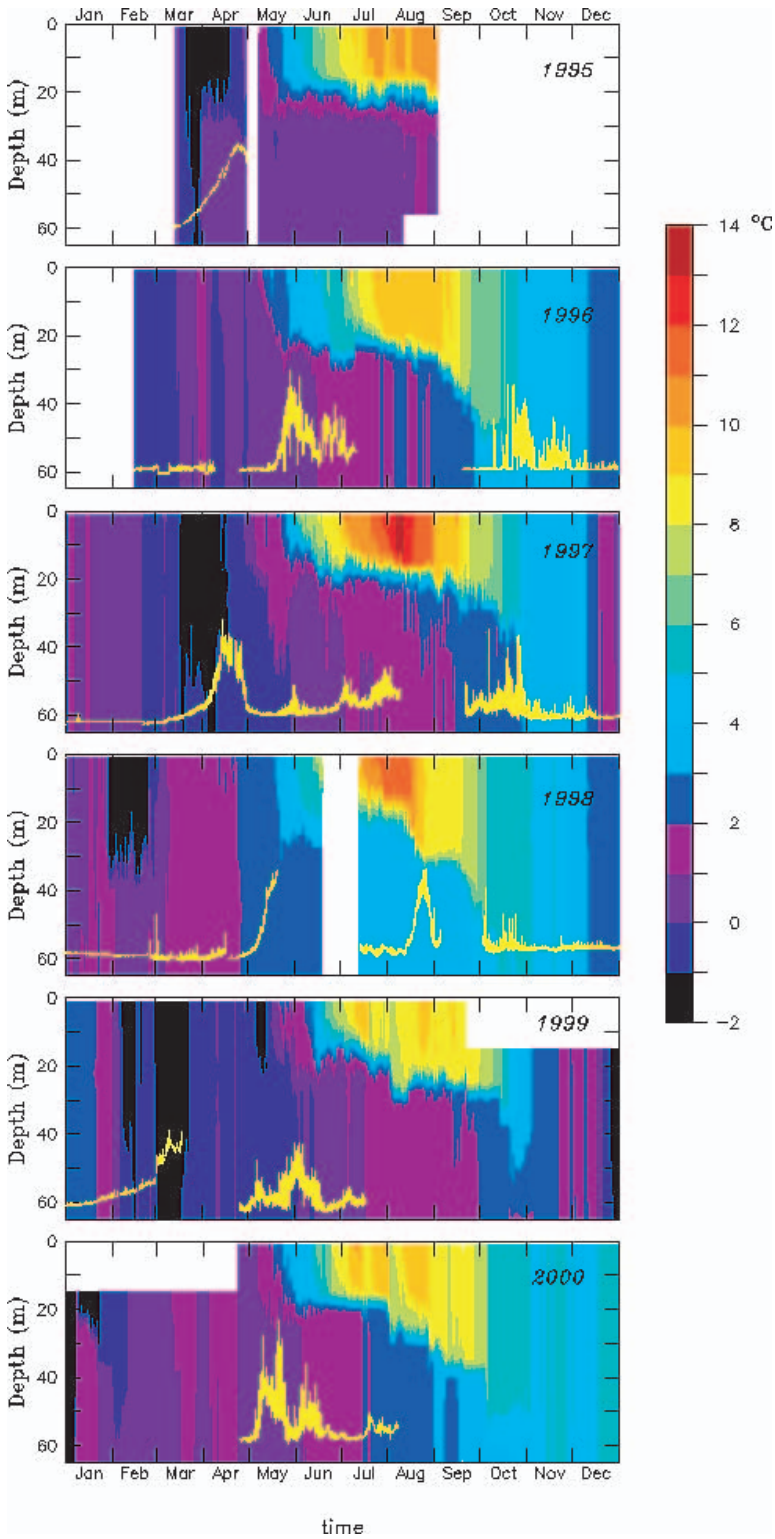

Figure 2.12: Time series of ocean temperatures and fluorescence from Mooring 2. The thin yellow line at the bottom of each panel is fluorescence scaled to the maximum each year. Temperature of <–1°C indicates the presence of melting ice. From Hunt *et al.* (2002a).

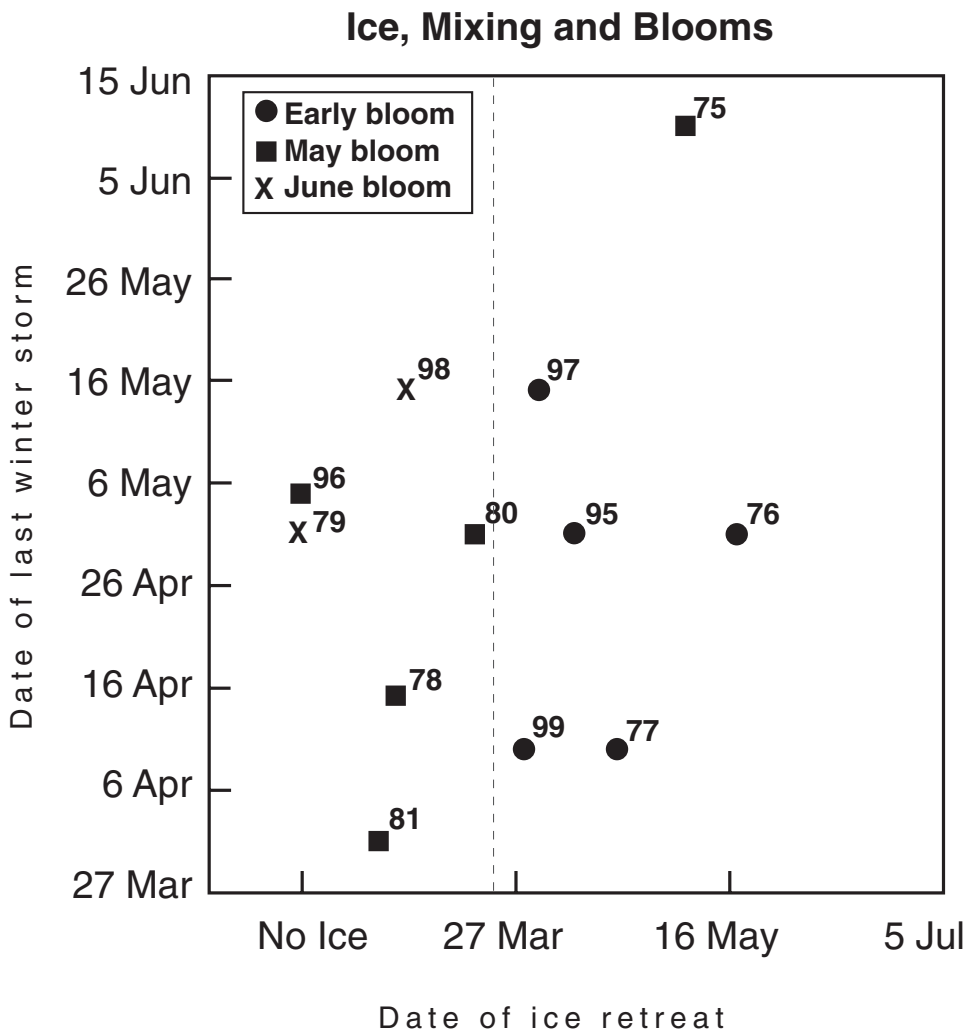

Figure 2.13: The relationship between the timing of the last winter storm, ice retreat, and the relationship of the bloom to sea ice. Note that blooms that occur to the right of the dotted gray line are associated with the ice edge. From Hunt *et al.* (2002a).

2.3.3 Cold pool formation

The bottom waters over the eastern Bering Sea shelf show considerable interannual variation in temperature. Over the northern parts of the shelf, cold, salty brine is rejected as sea ice forms in polynyas, and this dense water sinks to the bottom. Density flows to the north carry much of this salty bottom water through Bering Strait to the Arctic Ocean where it contributes to the halocline (Cavalieri and Martin, 1994; Schumacher and Stabeno, 1998).

Over the central and southeastern Bering Sea shelf, cold bottom waters are formed when sea ice melts, and the cold, fresh meltwater is mixed throughout the water column by storms (Stabeno *et al.*, 1998). These meltwaters can chill the entire water column to about –1.7°C. When the surface

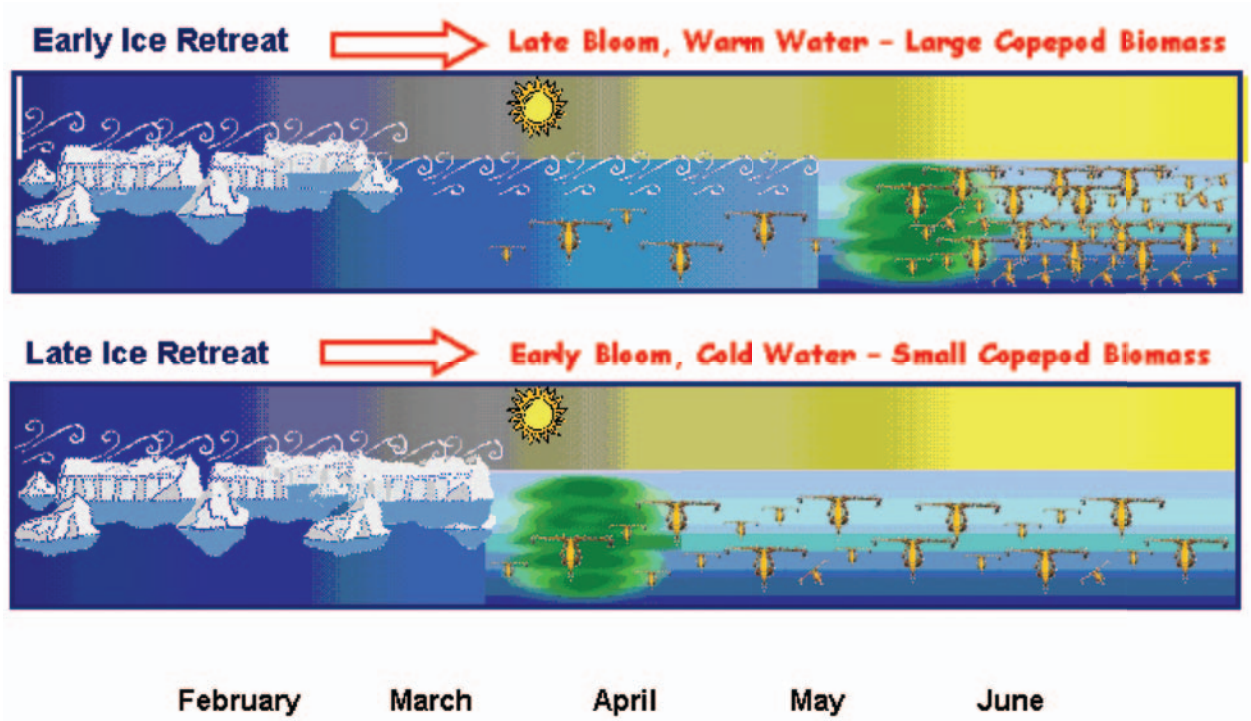

Figure 2.14: Relationship between timing of ice retreat, whether the bloom will occur in association with ice in cold water or in open, warmer water, and the potential effect of a warm water bloom on copepod production. After Hunt *et al.* (2002a).

waters are warmed by solar radiation in spring, a thermocline forms, and the cold bottom waters are largely insulated from further heating (Coachman *et al.*, 1980; Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1995). Bottom temperatures in this "cold pool" warm slightly over the summer, but may remain below 2°C until storm-induced mixing occurs in fall (Ladd *et al.*, unpublished manuscript). The extent and temperature of the southern cold pool is dependent on the amount of ice melt that occurs, and since ice is constantly melting as it is advected south, the amount of meltwater generated is a function of the duration of time that ice is present (Pease, 1980; Overland and Pease, 1982). The southern extent of the cold pool may also be influenced by the cross-shelf advection of warm water in winter (see 2.3.5, below), but the importance of advection of the warm water for cold pool limitation has not been investigated.

2.3.4 Biological impacts of water temperature

The temperature of the water column beneath the surface is important for determining the rates of the physiological processes of organisms residing there. Physiological processes vary as a power function of temperature, and phytoplankton growth is less sensitive to water temperature than is zooplankton growth (see also Vidal, 1980; Vidal and Smith, 1986; Townsend *et al.*, 1994). Water temperature exerts a strong influence on the growth

rates of zooplankton, and is often thought of as more important than food availability for limiting the growth rates of small-bodied copepods (McLaren, 1963; Corkett and McLaren, 1978; Vidal, 1980; Dagg *et al.*, 1984; Huntley and Lopez, 1992). Thus, in years with warm water, Walsh and McRoy (1986) hypothesized that zooplankton would capture more of the primary production than in cold years, and the greater production of zooplankton in warm years would support the pelagic community, e.g., fish such as pollock. Thus, in the middle domain where interannual environmental variability is greatest, water temperature is likely to play a major role in interannual variation in copepod biomass (Smith and Vidal, 1984, 1986; Napp *et al.*, 2000) (See section 2.4.3 Zooplankton).

Water temperature also affects the timing of hatching and survival of pollock eggs (Blood, 2002). Modeling of hatching times based on laboratory experiments and temperatures found in the Bering Sea predicted that the hatching periods for pollock eggs could vary as much as 13 days between the warmest and coldest years encountered between 1995 and 1998. A longer incubation period means that the eggs are exposed to predation for a greater period and that there is increased risk of exposure to extreme low temperatures as the eggs in the upper water column can be subjected to temperature variations driven by short-term weather fluctuations. Malformation of pollock embryos has been reported for eggs incubated at –1°C (Nakatani and Maeda, 1984), a temperature not infrequently encountered in the shelf waters of the Bering Sea shelf in late winter and early spring (Hunt *et al.*, 2002a).

The cold pool has important effects on the distribution and survival of fish. For example, juvenile walleye pollock prefer to avoid waters <2°C (Wyllie-Echeverria, 1996). When the southern cold pool is of reduced size, these fish spread out over much of the middle domain in shelf waters not frequented by adult pollock. When the southern cold pool is extensive, the juvenile pollock move toward the warmer waters of the outer domain and shelf edge, where they are subject to increased levels of cannibalism by adult pollock that reside in these outer shelf waters (Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1995, 1996; Wyllie-Echeverria and Wooster, 1998).

2.3.5 On-shelf fluxes and nutrient replenishment

On-shelf fluxes of nutrient salts from the basin are critical for the long-term productivity of the eastern Bering Sea shelf, but the mechanisms responsible for forcing these fluxes are still not well understood. In the northern Bering Sea, it has been suggested that water from the basin and slope crosses the shelf to flow northward through Anadyr Strait and Bering Strait (Fig. 2.3) (Shuert and Walsh, 1993). Nutrients in this water would then be available to support the extraordinarily high rates of summertime production found in the Chirikov Basin and northward through Bering Strait (Springer *et al.*, 1996). This process would also provide a mechanism for the transport of large oceanic copepods onto the northern shelf, where they support immense populations of planktivorous seabirds (Springer and Roseneau, 1985; Springer *et al.*, 1987, 1989; Hunt and Harrison, 1990; Hunt *et al.*, 1990; Rus-

sell *et al.*, 1999). However, the exact connections to the Bering Sea basin remain unclear, as observations by Stabeno and Reed (1994) and model results (Overland *et al.*, 1994) suggest that the Bering Slope Current, the presumed source of water carrying nutrients and copepods to the Chirikov Basin, may turn westward south of 59°N. Rather, the source of the slope water passing through Anadyr Strait may be water that has advected onto the outer shelf episodically or through the canyons of the shelf edge as far south as Bering Canyon; these then flow along the outer shelf with increasing intensity to the north and west, and thence through Anadyr Strait (Stabeno *et al.*, 1999a).

Over the southeastern Bering Sea shelf, nutrient replenishment was initially thought to result from tidally driven diffusion (Coachman, 1986). However, more recent work shows that the coefficients required for tidally driven diffusion are larger than those present on the shelf (Stabeno *et al.*, 2001). Although mean annual current velocities over the middle shelf at Mooring 2 are weak, currents averaged over shorter periods (e.g., daily) can exceed 25 cm s^{-1}. Currents are strongest in near-surface waters (34-month mean, 1.2 cm s^{-1} at 15 m), and much weaker at the bottom (0.2 cm s^{-1} at 60 m) (Stabeno *et al.*, 2001). Currents are strongest in winter and weakest in summer. In 1998, these currents were sufficiently strong to advect organisms typical of the oceanic regime into Middle Domain waters adjacent to the Inner Front near Cape Newenham and Nunivak Island (Hunt *et al.*, 1999; Coyle and Pinchuk, 2002b). It is also hypothesized that the generally seaward movement of sea ice in winter may result in an onshore flow at depth that could contribute to replenishment of nutrients over the southeastern shelf, but this hypothesis has yet to be investigated (Schumacher and Alexander, 1999).

Mechanisms for on-shelf transport of nutrients include eddies that bring slope waters onto the shelf at least as far as the 150-m isobath (Stabeno *et al.*, 1999a; Stabeno and Van Meurs, 1999; Okkonen, 2001; Johnson *et al.*, 2004), and Reed (1998) has observed them in waters between 100 and 120 m about 20% of the time (Fig. 2.3). However, eddies are rare in water <100 m deep, and other mechanisms are required to replenish nutrients in the Middle and Inner Domains. Two regions of preferential on-shelf flow are Bering Canyon, which is just north of the Aleutian Islands near Unimak Pass, and the area west of the Pribilof Islands, where the shelf break narrows (Stabeno *et al.*, 1999a). There, acceleration of flow over the outer shelf (Coachman, 1986; Schumacher and Stabeno, 1998) results in entrainment of slope water (Stabeno *et al.*, 1999b). On-shelf flow west of the Pribilof Islands can move into the Middle Domain where it is marked by a front to the northeast of St. Paul Island (Flint *et al.*, 2002), or it may be entrained around the islands in tidal currents (Stabeno *et al.*, 1999b). Two measures of the atmospheric forcing of the ocean circulation, the wind stress curl and the wind stress along the Alaskan Peninsula/Aleutian Island chain, also exhibit substantial variability (bottom panel of Fig. 2.9), but it remains an open question whether the flow over the shelf is sensitive to these effects.

2.3.6 Stratification, mixing, and the vertical flux of nutrients

Shelf waters of the southeastern Bering Sea, although well mixed during winter by storms, stratify in late spring from solar heating (Eslinger and Iverson, 2001; Ladd *et al.*, unpublished manuscript). This stratification inhibits vertical flux of nutrients, and once the spring bloom has exhausted them from the upper mixed layer, the lack of nutrients limits new production. These nutrients can be replenished when processes break down the stratification. Sambrotto *et al.* (1986) identified the importance of summer storms as a mechanism for deepening the pycnocline and stirring nutrients into the upper mixed layer where they could be taken up by plant cells in the presence of light. Analysis of wind speed cubed, a measure of the ability of winds to mix the upper water column, shows that summer winds have declined since the early 1980s (Fig. 2.15). Ladd *et al.* identified the importance of winter conditions for determining the strength of the pycnocline, and hence the ease with which it could be eroded by storms. A second pathway for the movement of nutrients from depth to the surface layers is upward mixing in the vicinity of fronts (Iverson *et al.*, 1979a; Sambrotto *et al.*, 1986; Kachel *et al.*, 2002). For example, this upward mixing can result in regions of high productivity on the stratified side of the inner front (Hunt *et al.*, 1996a; Kachel *et al.*, 2002). These mechanisms require the availability of a pool of nutrients at depth in the vicinity of the front. In 1997, after the completion of the spring bloom, a severe storm in late May mixed the water column to depths of 65 m or more and resulted in renewed production. The result was a depletion of nutrients to 60 m or more, and a lack of availability of nutrients at the base of the inner front and at the pycnocline for mixing into the upper mixed layer (Stockwell *et al.*, 2001). This observation pointed to the importance of episodic events in structuring the ecology of shelf waters.

2.4 Biological Components of the Eastern Bering Sea Ecosystem

2.4.1 Primary production

During the past decade, we have made considerable advances in our understanding of factors influencing the timing of the spring bloom (see above, Stabeno *et al.*, 2001; Hunt *et al.*, 2002a; Hunt and Stabeno, 2002). However, we know less about the magnitude of the bloom, and whether the amount of production varies between ice-associated and open-water blooms. Alexander and Niebauer (1981) and Niebuauer *et al.* (1981, 1990, 1995) suggest that in the early 1980s the ice edge-bloom used to be as great or greater than the open-water bloom. In 1997, which had an ice-associated bloom followed by a second, open-water bloom subsequent to a mixing event in May, primary production, based on nutrient drawdown, was greater than in the early 1980s (Stockwell *et al.*, 2001).

The question of whether there has been a change in the amount of net annual new production is important. Schell (2000), using stable isotope ratios from carbon sequestered in the baleen of bowhead whales during periods of feeding in the northern Bering Sea, estimated that primary production

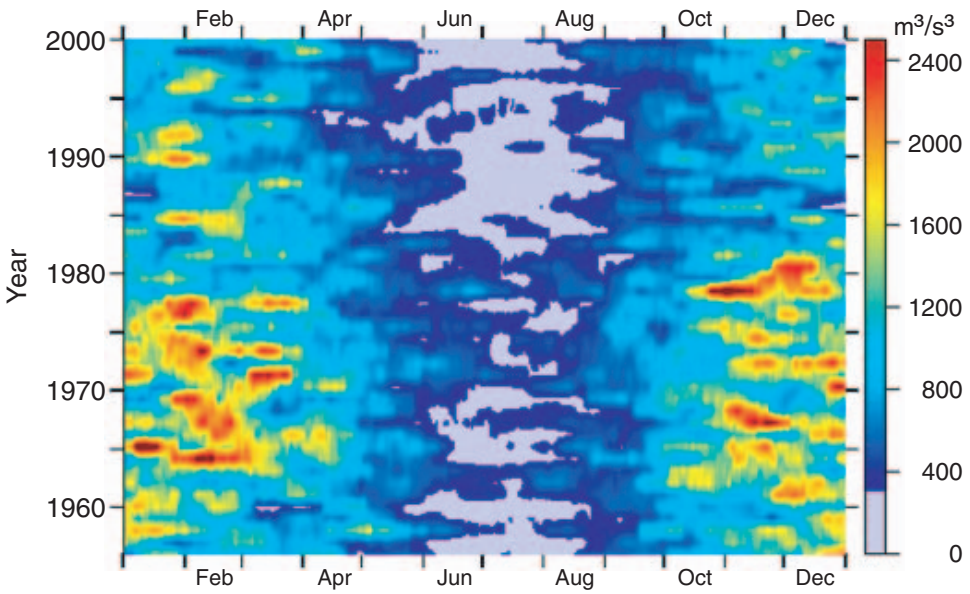

Figure 2.15: Wind speed cubed at St. Paul Island. Note that since the late 1970s, winter winds have been less strong, and in summer, there have been more periods of wind below the long-term average (those areas in light gray). From Hunt *et al.* (2002a).

in the Bering Sea had decreased by as much as 30 to 40% since 1967, with almost all of the decrease coming since 1976. Cullen *et al.* (2001) questioned whether some of this effect was the result of anthropogenic CO_2 or changes in the species composition of the phytoplankton. However, Schell (2001) provided additional information, including data from stable isotopes of nitrogen, which corroborates the earlier findings. Grebmeier and Cooper (1994, 2002), Grebmeier and Dunton (2000), and Grebmeier (1992) have found evidence for declines in sediment oxygen respiration of as high as 73% over the period 1987 to 2002, with declines in benthic biomass of 89% over a longer period. In addition, they have documented changes in the species composition of benthic bivalves and other fauna. Taken together, these studies point to a decline in production levels for the northern Bering Sea, including in the Saint Lawrence Island polynya region south of the island. These reductions in production may be related to reduced northward flow through Bering Strait (Roach *et al.*, 1995) and a consequent diminution of nutrient advection from the Bering Sea basin onto the northern shelf.

In the southeastern Bering Sea, there appears to be no clear indication of a decrease in production, though Hirons *et al.* (2001) have attempted to extend the results of Schell (2000) to the remainder of the eastern Bering Sea and Gulf of Alaska by examining stable isotope ratios in the teeth of harbor seals (*Phoca vitulina*), northern fur seals (*Callorhinus ursinus*) and Steller sea lions (*Eumetopias jubatus*). For these species, when data from teeth from both the Gulf of Alaska and the Bering Sea were combined, they found a significant decline in the δ^{13}C in sea lions and similar, though non-significant,

trends in harbor seals and fur seals. However, from their published data, it is difficult to tell whether these trends depend upon the combination of data from the Bering Sea and the Gulf of Alaska, or whether the trends would hold up within regions as well.

In contrast, in 1997, estimates of primary production in the southeastern Bering Sea, based on the reduction of nitrate over the middle and inner shelf, suggested that new production might have been between 10 and 30% greater in 1997 than in the early 1980s (Stockwell *et al.*, 2001). Estimates for production levels in 1998 and 1999, however, do not appear to differ from those of the early 1980s (Whitledge, University of Alaska Fairbanks, personal communication). In contradiction to these estimates of productivity in 1997, 1998, and 1999, sediment trap data supported the notion that productivity was higher in 1998 than 1997 (Smith *et al.*, 2002), as did data from the uptake of ammonium (Rho, 2000). However, δ^{13}C values from copepods in the 1997–1999 period were lower than found by Schell *et al.* (1998). Smith *et al.* hypothesized that this decline in δ^{13}C could be the result of diminished production, similar to that found by Schell (2000), or it could be the result of other factors. Interestingly, in the period 1997–1999, Smith *et al.* did not find a decrease in δ^{13}C in euphausiids and chaetognaths, as would have been expected if the decline in copepod δ^{13}C was the result of changes in primary productivity. Based on the sum of the above results and the high stable or increasing biomass of fish and invertebrates over the southeastern shelf (see below), it seems most unlikely that there has been a marked reduction in primary production there since the 1970s (Hunt *et al.*, 2002a).

2.4.2 Coccolithophore bloom

In the 1990s, there were marked anomalies in the species composition of phytoplankton in the eastern Bering Sea. Although diatoms typically dominate phytoplankton biomass in the eastern Bering Sea (Sukhanova *et al.*, 1999), in the late 1990s, coccolithophore blooms dominated summer phytoplankton assemblages over much of the shelf (Figs. 2.16, 2.17) (Sukhanova and Flint, 1998; Vance *et al.*, 1998; Napp and Hunt, 2001; Stockwell *et al.*, 2001). Coccolithophores are small (5–20 μm) phytoplankton surrounded by calcium carbonate plates. Coccolithophore blooms are common in the North Sea, Gulf of Maine, and coastal eastern North Pacific, and characteristically occur in nutrient depleted waters with warm, shallow mixed layers (Holligan *et al.*, 1983; Mitchell-Innes and Winter, 1987; Balch *et al.*, 1992; Townsend *et al.*, 1994). High densities of coccoliths result in a whitening of the water detectable by satellite imagery (Holligan *et al.*, 1983; Balch *et al.*, 1991; Brown and Yoder, 1993; Gower, 1997). Although coccolithophore blooms had not been documented previous to 1997 in the eastern Bering Sea, there are satellite images of "white" water from there (Brown and Yoder, 1993).

The first coccolithophore bloom (*Emiliania huxleyi*) recorded from the Bering Sea was initially observed 3 July 1997 in the middle domain (Vance *et al.*, 1998), although *E. huxleyi* cells were present in the water as early as May and June (Stockwell *et al.*, 2001). By early August, the bloom was at least 200 km wide (Tynan, 1998), and by early September it covered 2.1×10^5 km^2

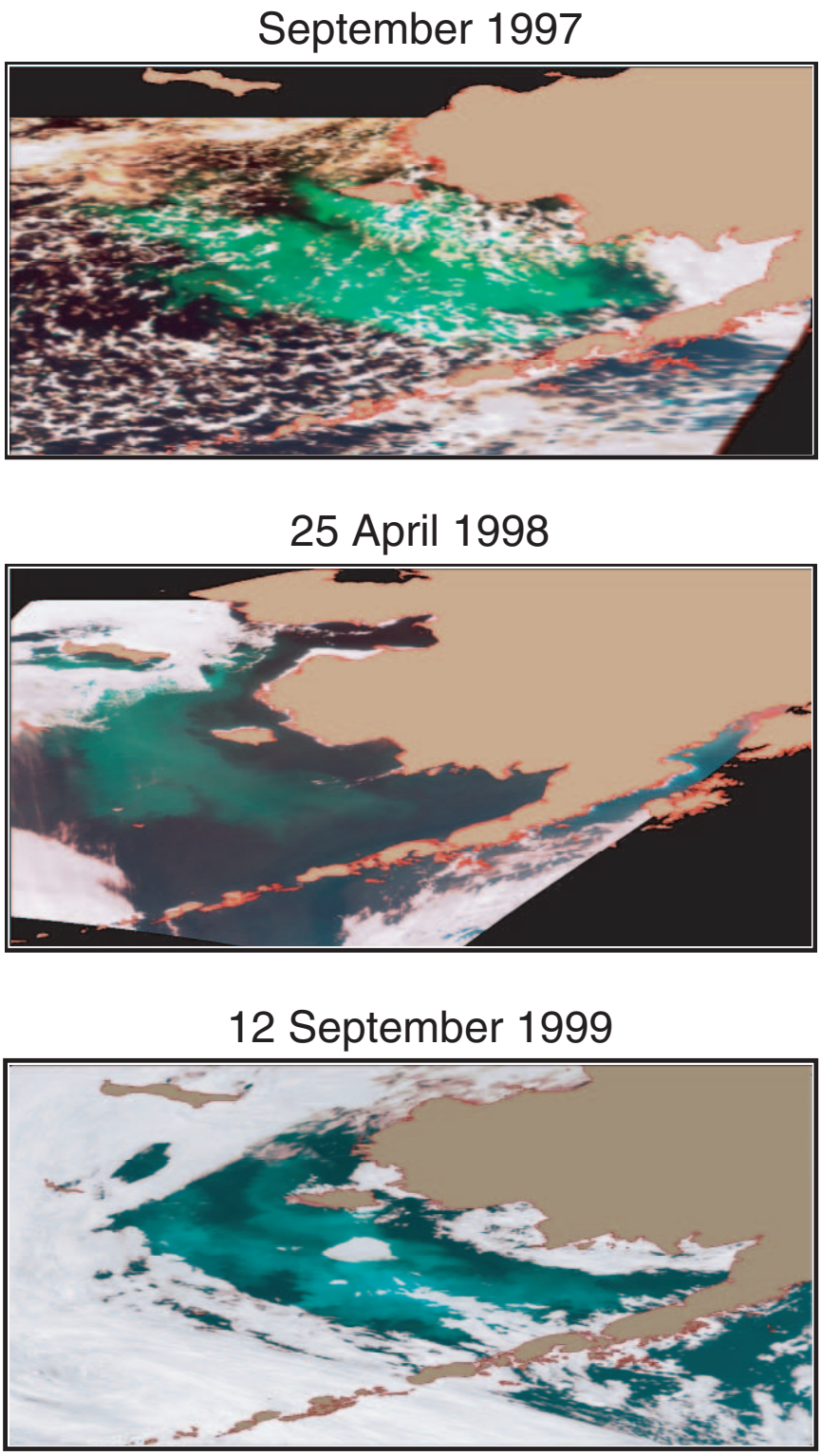

Figure 2.16: Three SeaWIFS views of the Bering Sea coccolithophore bloom.

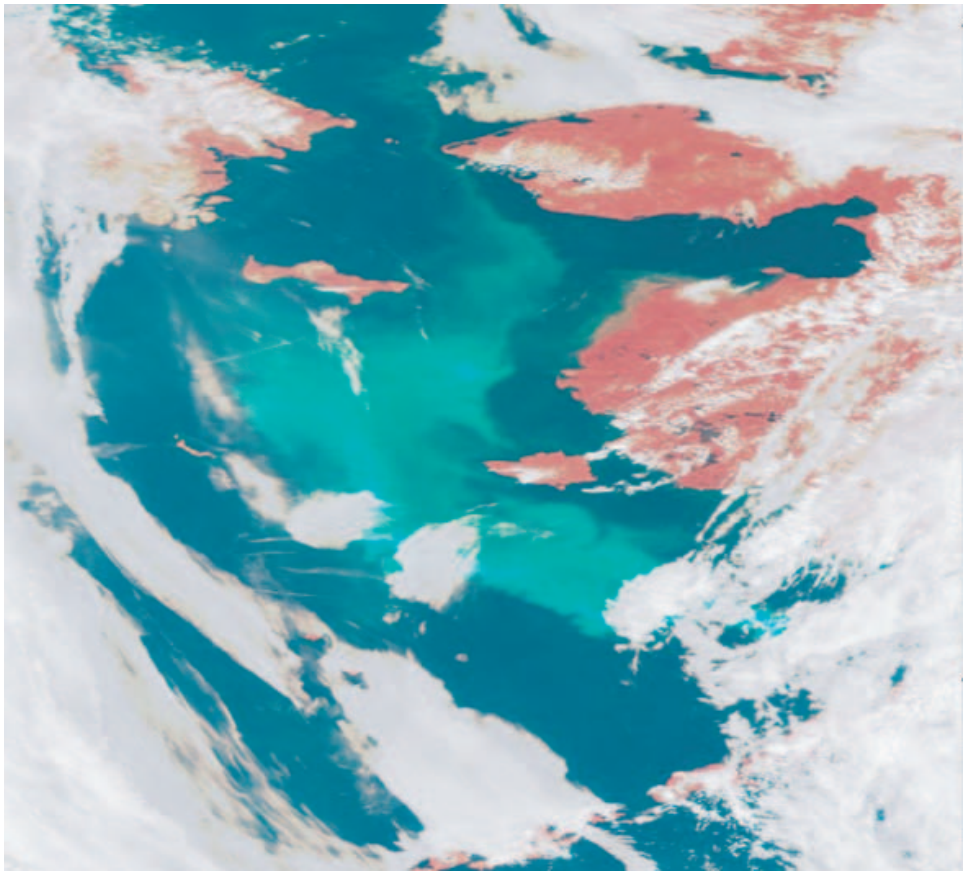

Figure 2.17: SeaWIFS false color image of the coccolithophore bloom, 24 July 1998. Note the trace of coccoliths in the water passing through Shpanberg Strait to the east of St. Lawrence island, and thence northward through the east side of Bering Strait. From Napp and Hunt (2001).

of the middle domain and parts of the inner domain (Sukhanova and Flint, 1998; Vance *et al.*, 1998; Napp and Hunt, 2001). It was apparent in SeaWiFS imagery from 18–25 September, and traces could be detected as late as October. This event was unusually large and long-lived when compared with coastal blooms of coccolithophores described previously (Table 2.2) (Holligan *et al.*, 1983; Balch *et al.*, 1991; Brown and Yoder, 1993; Gower, 1997). Most coastal blooms are on the order of 10^4 km^2, and persist less than 40 days. Concentrations of coccolithophore cells were as great or greater than those reported from the North Atlantic (Townsend *et al.*, 1994b; Robertson *et al.*, 1994).

The coccolithophore bloom greatly reduced light penetration and visibility in the water. Near Nunivak Island (Fig. 2.2), the depth of the 1% light level, often taken as the maximum limit for net photosynthesis, shoaled from between 18 and 33 m in June to between 5 and 15 m in September in the bloom (Zeeman, University of New England, personal communication). At Slime Bank (Fig. 2.1), outside the bloom, the depth of the 1% light level

Table 2.2: Comparison of large-scale *Emiliania huxleyi* blooms (after Napp and Hunt, 2001).

Characteristic	Measure	Source
Size	**km^2**	
Coastal Blooms	5–10 $\times$ 10^4	Holligan *et al.,* 1983
	5 $\times$ 10^5	Balch *et al.,* 1991
	5 $\times$ 10^5	Brown and Yoder, 1993
	5 $\times$ 10^5	Brown and Podesta, 1997
Open Ocean Blooms	5 $\times$ 10^5	Holligan *et al.,* 1983
Bering Sea 1997	2.4 $\times$ 10^5	Napp and Hunt, 2001
Duration	**months**	
Gulf of Maine, 1998	$\approx$1	Townsend *et al.,* 1994
Gulf of Maine, 1989	$\approx$1	Townsend *et al.,* 1994
NE Atlantic, 1991	1.1	Robertson *et al.,* 1994
Bering Sea, 1997	4	Napp and Hunt, 2001
Cell Density	**cells $\cdot$ ml^{-1}**	
Gulf of Maine, 1988	2.4 $\times$ 10^3	Townsend *et al.,* 1994
Gulf of Maine, 1989	1.5 $\times$ 10^3	Townsend *et al.,* 1994
NE Atlantic, 1991	1.0 $\times$ 10^3	Robertson *et al.,* 1994
Bering Sea, 1997	3.1–4.7 $\times$ 10^3	Napp and Hunt, 2001
Lith Density	**liths $\cdot$ ml^{-1}**	
Gulf of Maine, 1988	1.3 $\times$ 10^5	Townsend *et al.,* 1994
Gulf of Maine, 1989	3.0 $\times$ 10^5	Townsend *et al.,* 1994
NE Atlantic, 1991	3.5 $\times$ 10^5	Robertson *et al.,* 1994
Bering Sea, 1997	3–5 $\times$ 10^5	Napp and Hunt, 2001

remained the same (27 m) from spring until fall. Underwater videos near the Pribilof Islands documented cloudy bloom-water ranging in depth from 7 m to 44 m, and extending to the bottom in several locations (Brodeur, NOAA/NWFSC, personal communication).

The eastern Bering Sea coccolithophore bloom recurred yearly from 1997 through 2001, and in most years was comparable in spatial extent and cell density to large-scale coccolithophore blooms in other parts of the world's oceans, though of considerably longer duration (Table 2.2). New algorithms for the analysis of SeaWiFS imagery showed that the coccolithophore blooms started in February as melting began along the ice edge and then spread northward, peaking in April (Iida *et al.*, 2002). The blooms with the largest aerial extent occurred in the warm years of 1998 and 2000, whereas those in the cold years of 1999 and 2001 were smaller (Iida *et al.*, 2002).

The summer of 1997 was marked by unusually warm surface temperatures, a strong thermocline and depletion of nitrate and silicate from the surface waters (Napp and Hunt, 2001). The conditions under which the 1997 bloom commenced were similar to conditions believed to be conducive to coccolithophore blooms elsewhere (Balch *et al.*, 1992; Holligan *et al.*, 1983; Townsend *et al.*, 1994b). However, we do not know why the eastern Bering Sea blooms were initiated, or why they recurred over a several year period when there was great variability in oceanographic conditions (Stabeno and

Hunt, 2002). We also lack information on why they ceased to occur in 2002, and on their role in energy flux to the food webs of the eastern Bering Sea shelf.

2.4.3 Zooplankton

Microzooplankton are protists and metazoan organisms smaller than 200 μm that are present in the plankton (Dussart, 1965). Because they are small and individually inconspicuous, their role in the world ocean has been under-appreciated until recently. Although microzooplankton are an abundant element in the food webs of the southeastern Bering Sea, we are only just beginning to investigate their role in this ecosystem (Howell-Kubler *et al.*, 1996; Olson and Strom, 2002). For example, in April 1992, microprotozoan abundances ranged from 300 to 6233 organisms l^{-1} with a biomass of 0.58 to 9.73 μg C l^{-1} (Howell-Kubler *et al.*, 1996). These biomass levels were similar to those of other oceanic regions, and were estimated to be sufficient to meet the metabolic needs of first-feeding larval pollock, though observations to determine if pollock use this resource are not available.

Microzooplankton were an important component of the southeastern Bering Sea food webs in the summer of 1999. Within the coccolithophore bloom, 75% of the total chlorophyll *a* (Chl *a*) came from cells >10 μm (mostly the diatom *Nitzschia* spp.), and average growth rates for cells >10 μm and <10 μm were nearly equal (Olson and Strom, 2002). Within the bloom, microzooplankton grazing rates were only 28% of the growth rates of phytoplankton growth rates. In contrast, for the shelf as a whole, grazing by microzooplankton accounted for 110% of the growth of cells >10 μm and only 81% of the growth of cells <10 μm. This preferential grazing on the larger cells may help to explain the persistence of the coccolithophore bloom and is contrary to the belief that microzooplankton are constrained to diets of nannophytoplankton (Olson and Strom, 2002). These findings emphasize the need for a thorough examination of the role of microzooplankton both in the summer, for which we have evidence that they may form an important link between phytoplankton and mesozooplankton, and during the spring bloom, when their role has yet to be evaluated.

Traditionally, calanoid copepods have been believed to be the major agents of energy transfer between large-celled diatoms and upper trophic level consumers such as planktivorous fish (e.g., Hood, 1999). Although emerging data now suggest that in boreal oceans these large copepods have a large dietary component of microzooplankton (Capriulo *et al.*, 1991; Sherr and Sherr, 1992; Rivkin *et al.*, 1999), the large copepods are still important prey for fish, whales and seabirds. In the eastern Bering Sea, the copepod communities of the basin and outer shelf are dominated in spring by large species of *Neocalanus* (*N. cristatus, N. plumchrus,* and *N. fleminergi*) and *Eucalanus bungii*, and the middle and inner shelf by the smaller *Calanus marshallae, Pseudocalanus* spp. and *Acartia* spp. (Cooney and Coyle, 1982; Smith and Vidal, 1986).

The most complete time series of zooplankton abundances in the eastern Bering Sea depend on data gathered in summer by the T/S *Oshoro Maru*,

which has documented declines in zooplankton biomass from the basin between the late 1960s and the early 1990s (basin, Fig. 2.18) (Sugimoto and Takadoro, 1997). In the basin, they also found a biennial fluctuation in zooplankton biomass that was negatively correlated with the catch of Asian pink salmon (*Oncorhynchus gorbuscha*). Sugimoto and Takadoro interpreted these two patterns as indicating a bottom-up control of the zooplankton on a decadal-scale, and a top-down control on an annual scale. In contrast to the results obtained from the basin, examination of *Oshoro Maru* data from the shelf showed neither a long term trend, nor evidence of biennial cycles in summer zooplankton biomass (Fig. 2.18) (Hunt *et al.*, 2002a; Napp *et al.*, 2002). Although there was considerable interannual variation, no discernable temporal trend was detected.

For spring, two sets of studies show that the abundance of small shelf species of copepods varies with sea temperature. In 1980, the upper layer of the middle and outer shelves of the southeastern Bering Sea warmed slowly as compared to 1981 (Smith and Vidal, 1986). In May 1981, small copepods of the middle shelf were more abundant than in 1980 (Table 2.3), and *Calanus marshallae* was observed to have two generations in 1981, rather than the expected one (Smith and Vidal, 1986). In the 1990s, there was also the opportunity to compare a very cold year (1999) with two years in which water temperatures were high (1997, 1998). For species of small copepods over the inner and middle shelf areas, June abundances in 1999 were reduced by up to 90% compared to the two warmer years (Table 2.4) (Coyle and Pinchuk, 2002b). Although Smith and Vidal hypothesized that differences in predation on the copepods as well as temperature might have affected the differences in abundance between 1980 and 1981, there was no indication in the data of Coyle and Pinchuk (2002b) that chaetognaths were responsible for the declines in copepod abundance observed in 1999. Coyle and Pinchuk (2002b) provide compelling evidence that, even on a station-by-station basis, there was a strong relationship between the numbers of copepods present and integrated water temperatures (e.g., Fig. 2.19). They estimated that secondary production of calanoids in spring 1999 was about 3–4% that which occurred in the warm years of 1997–1998. Interestingly, by August–September, there were no consistent significant differences in the biomass of small copepods between 1999 and the two warmer years (Coyle and Pinchuk, 2002b).

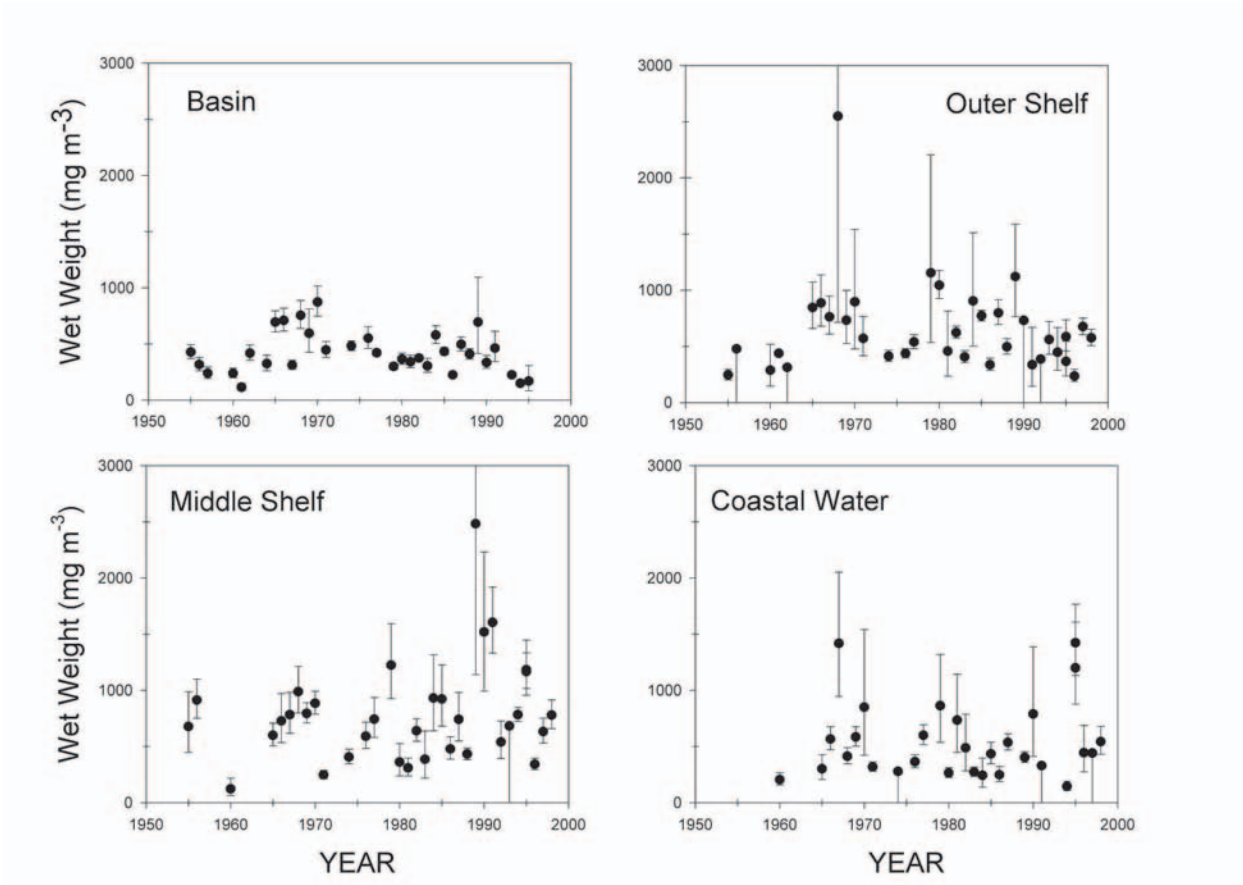

Figure 2.18: Changes in zooplankton biomass in the deep basin and in the outer, middle, and coastal domains of the southeastern Bering Sea sampled by the Oshoro Maru summer cruises. Data from 1994 to 1997 from Sugimoto and Tadokoro (1998). Data from 1995 to 1999 from Dr. N. Shiga (unpublished). Means with standard errors. From Hunt *et al.* (2002a).

Table 2.3: Responses of calanoid copepods to interannual variation in water temperature during the spring bloom in the Bering Sea. Copepod data are numbers m^{-3} from the middle shelf in May 1980 and 1981.

Variable	Year 1980	Year 1981	Difference
Onset of Bloom	25 April	5 May	
Termination of Bloom	28 May	29 May	
Temperature (°C) Prior to Bloom—top 20 m	0.97	3.04	2.07
Temperature During Bloom—top 20 m	2.22	5.06	2.84
Acartia spp. All copepodids	18.9	8.5	–55%
Arcatia spp. Adult males and female	9.4	2.8*	–70%
Pseudocalanus spp. All copepodids	83.1	308.5*	+270%
Calanus marshallae All copepodids	31.7	30.6*	–3.5%
Calanus marshallae Adult females	0.1	0.8*	+700%
Metridea pacifica All copepodids	1.6	20.3*	+1169%
Oithona spp.	269.6	233.4	–13.4%

* = difference significant $p < 0.05$. Data from Smith and Vidal (1986).

Table 2.4: Responses of calanoid copepods to interannual variation in water temperature during the spring bloom in the Bering Sea. Copepod data are numbers m^{-3} from the middle shelf and inner shelf in June 1997, 1998, and 1999.

Variable	Year 1997	Year 1998	Year 1999	Change in 1999 from mean of 1997 + 1998
Onset of Bloom	Mid April	Early May	Late March	
Temperature during June, integrated water column °C	3.76	3.45	0.32*	3.29
Acartia spp.	961	711	64*	–92%
Pseudocalanus spp.	1168	893	240*	–77%
Calanus marshallae	34	72	3.7*	–93%
Calanoid nauplii	616	626	322*	–48%
Oithona similis	99	219*	28	–82%
Chaetognaths	43	12*	28	+1.8%

* = difference significant $p < 0.05$. Data from Coyle and Pinchuk (2002b) and Hunt *et al.* (2002a).

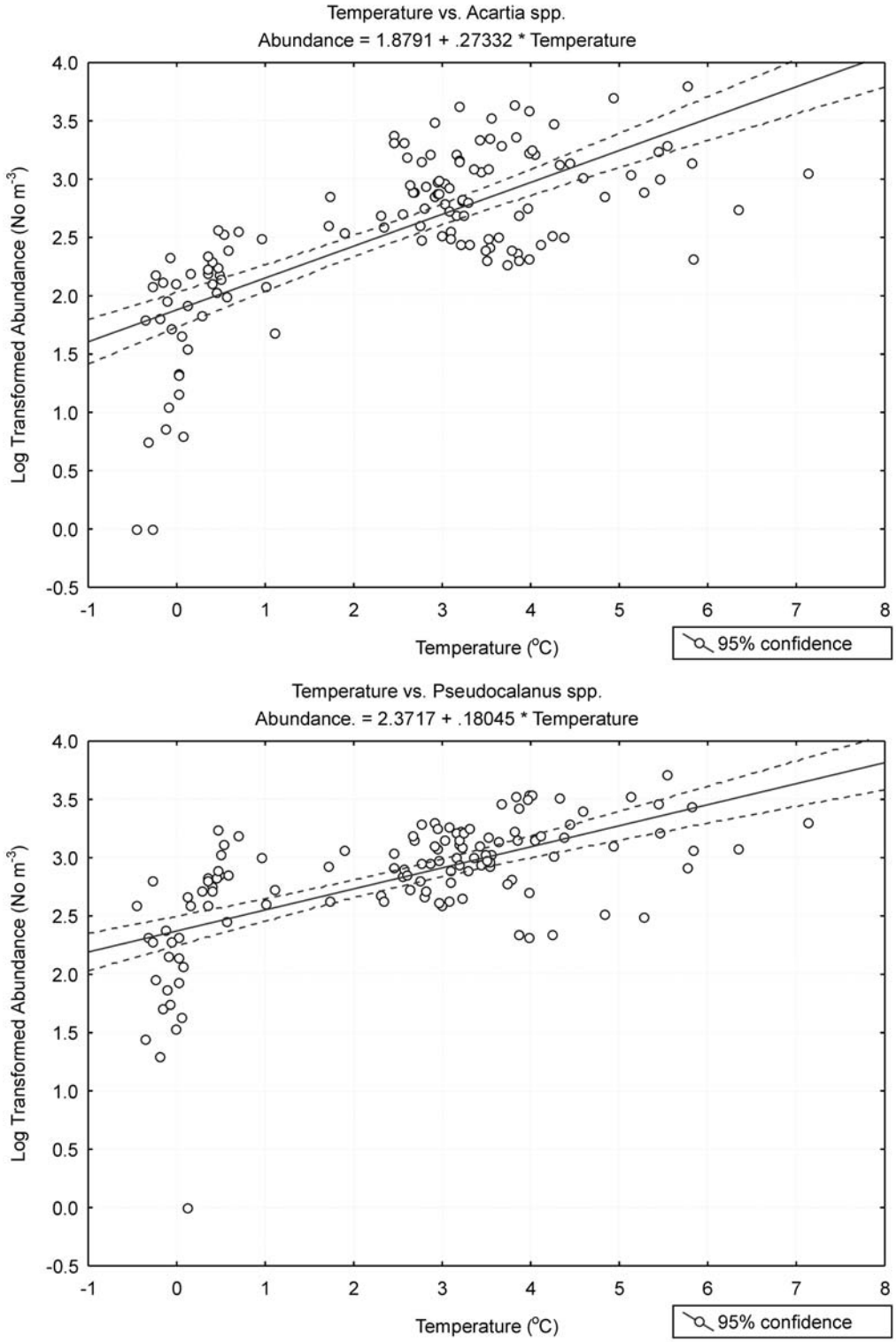

Figure 2.19: June abundances of *Acartia* spp. (top) and *Pseudocalanus* spp. (bottom) in relation to the integrated water temperatures at the stations where they were collected 1997–1999. Dashed lines are 95% confidence intervals around the regressions. Coyle, unpublished data.

Table 2.5: Comparison of acoustically determined euphausiid biomass among the years 1997, 1998, and 1999, mean and 95% confidence interval.

	June 1997	**June 1998**	**June 1999**
Transect location	**Mean g m^{-2} (95% Cl)**	**Mean g m^{-2} (95% Cl)**	**Mean g m^{-2} (95% Cl)**
Port Moller, Line A	2.3 (1.94–2.57)	0.77 (0.54–0.99)	17.27* (13.27–21.27)
Port Moller, Line C	2.98 (2.36–3.61)	0.34 (0.25–0.44)	15.76* (14.60–17.46)
Port Moller, Line E	No Data	0.73 (0.62–0.83)	5.29* (4.30–5.65)
Cape Newenham, Line C	1.91 (1.14–1.70)	5.50* (4.71–6.22)	2.75 (1.59–3.91)
Nunivak Island, Line C	1.58 (1.46–1.70)	2.38 (2.26–2.49)	6.82* (5.91–7.72)
Nunivak Island, Line E	1.25 (1.13–1.36)	1.93 (1.62–2.19)	5.64* (4.89–6.02)

* = Statistically significant at $p < 0.05$. Data from Coyle and Pinchuk (2002a).

The effect of temperature on euphausiids appeared to be the inverse of its effect on copepods; in 1999, the acoustically measured biomass of adult euphausiids on the inner and middle shelf was significantly higher than in 1997–1999 (Table 2.5) (Coyle and Pinchuk, 2002a). However, Coyle and Pinchuk point out that this difference may be related to a delay in euphausiid breeding in the cold year, which would result in more adults remaining in the water column when they were sampled in June than in a warm year when most adults would have spawned and died prior to June. Coyle and Pinchuk (2002a) noted that there were significantly higher densities of euphausiid eggs and larvae present in 1999 (the cold year) compared to the warm years of 1997 and 1998. Coyle and Pinchuk (2002a) concluded that there were no significant differences in the biomass of euphausiids over the inner and middle shelf in 1997 and 1998 compared to earlier periods for which data were available. However, if euphausiid spawning is completed in early spring and there is a reduced availability of late spawning adults in summer, this change in the timing of availability could have a negative impact on predators, such as short-tailed shearwaters (*Puffinus tenuirostris*) that depend on euphausiids for a significant portion of their diet (Baduini *et al.*, 2001a,b; Hunt *et al.*, 2002b).

In the last three decades, gelatinous zooplankton, in particular large scyphomedusae, have gone through a remarkable increase in biomass and then crash (Fig. 2.20) (Brodeur *et al.*, 1999a, 2002). The cause (or causes) of the outbreak of jellyfish is not known, though it has been hypothesized that changing climate and ocean temperatures may have been the trigger (Brodeur *et al.*, 1999a). It has also been hypothesized that a decrease in forage fish over the southern portion of the shelf in the early 1980s may have contributed to the jellyfish increase by releasing them from competition (Brodeur *et al.*, 2002). Currently, there are no hypotheses to explain why they suddenly decreased. At the Pribilof Islands, the dominant scyphozoan, *Chrysaora melanaster*, was estimated to consume about one third of the standing stock of crustacean zooplankton and 4.7% of their annual production. Additionally, these jellyfish were estimated to consume about 3% of the standing stock of age-0 pollock in the vicinity of the Pribilof Islands (Brodeur *et al.*, 2002).

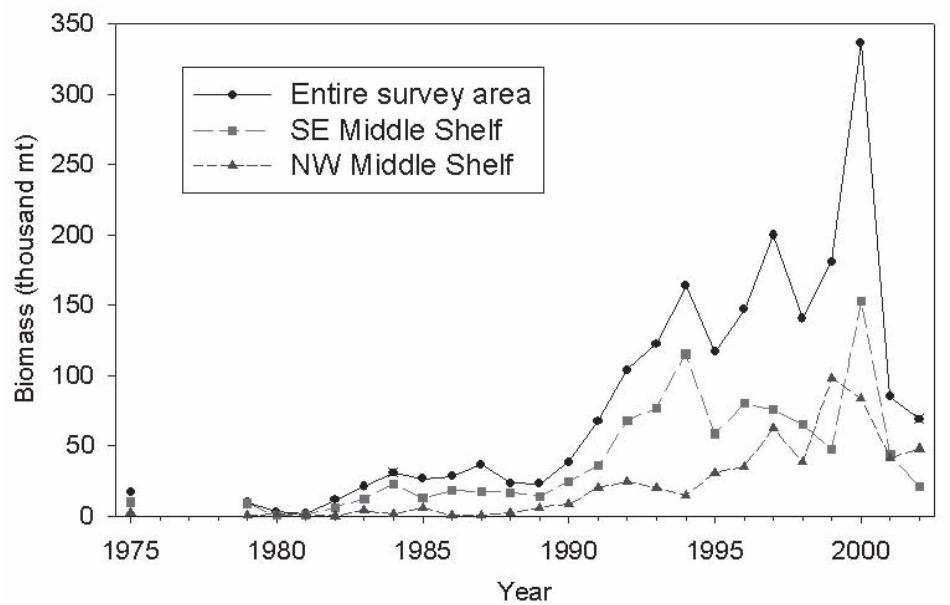

Figure 2.20: Biomass of large medusae in the National Marine Fisheries Service bottom trawl surveys of the southeastern Bering Sea. Data courtesy of G. Walters and R. Brodeur.

2.4.4 Fish

During the late 1970s and early 1980s, several stocks of groundfish and non-crab invertebrates showed strong changes in biomass in the eastern Bering Sea (Conners *et al.*, 2002). Conners *et al.* identified three sites that had been surveyed consistently since about 1965 using comparable gear. Patterns of change in biomass for all species combined were similar across these three areas (Fig. 2.21), and timing of changes in both commercially exploited and non-exploited species were similar. Pacific cod and several species of flatfish showed changes of 300 to 600 percent, whereas the biomass of Greenland turbot decreased by 90 percent (Fig. 2.22). These changes resulted in a marked shift in the species composition of ground fish and benthic invertebrates in shelf waters. Conners *et al.* noted that the timing of the change in CPUE in the trawls was consistent with the timing of the major regime shift of 1976–1977, and that there was little evidence of responses to the later, weaker, regime shifts in 1989 and 1998.

The female spawning biomass of the pollock stock increased strongly in the 1980s because of the growth and survival of the strong year classes that started in 1972 (Fig. 2.23). The biomass continued to be above the long-term average during the 1990s because of the strong year-classes that followed the exceptionally strong 1989 year-class. The increases were apparently due to a combination of favorable ocean conditions and the conservative fishery management practices put in place by the North Pacific Fishery Management Council. The stock showed fluctuations as the young recruits grew in size and were taken by the fishery or died through natural mortality (Fig. 2.22).

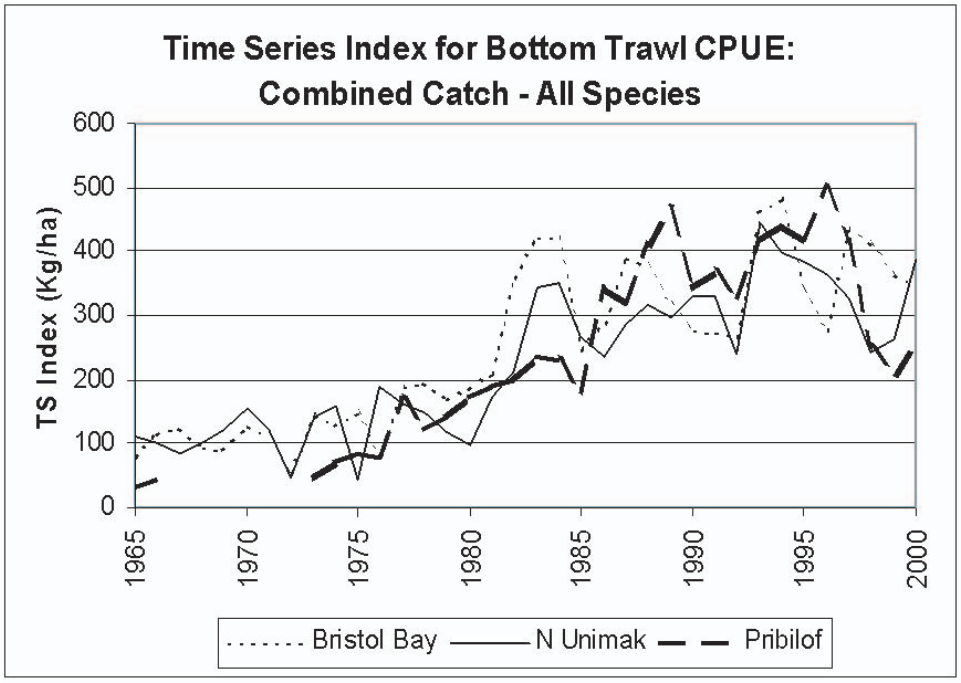

Figure 2.21: Time series of bottom trawl surveys in three regions of the southeastern Bering Sea that have been consistently surveyed with similar gear since the mid-1960s. From Conners *et al.* (2002).

Year-class success represents an annual estimate of productivity and survival for a species. During the period from 1963 to 2001, year-class strength of walleye pollock in the eastern Bering Sea varied from a low of 3.6 billion age-1 fish in 1963 to a high of 66.0 billion in 1978 (Fig. 2.23). Hollowed and Wooster (1995) classified years into those warmer and colder than the long-term mean for the North Pacific Ocean from 1946 to 1990. They found that during a warm period, the year-class strength of many stocks of groundfish were stronger, while during a cool period, the same stocks showed weaker year-class strength. Exceptionally strong year classes of pollock occurred in 10 years (Fig. 2.23, Table 2.6). There were two or three banner year classes per decade with intermediate years showing average to weak year classes (NPFMC, 2000).

Other species of groundfish in the eastern Bering Sea showed the same general pattern as walleye pollock of increase in biomass during the early 1980s due to strong year classes following the 1976–1977 climate regime shift. As examples (Fig. 2.22), Pacific cod (*Gadus macrocephalus*), yellowfin sole (*Limanda aspera*), northern rock sole (*Lepidopsetta polyxystra*), Alaska plaice (*Pleuronectes quadritubeculatus*), flathead sole (*Hippoglossoides elassodon*), arrowtooth flounder (*Atheresthes stomias*) and Greenland turbot (*Reinhardtius hyppoglossoides*) follow this pattern (NPFMC, 2000). These trends were due to the increased productivity that was manifest as year-class success (Fig. 2.23).

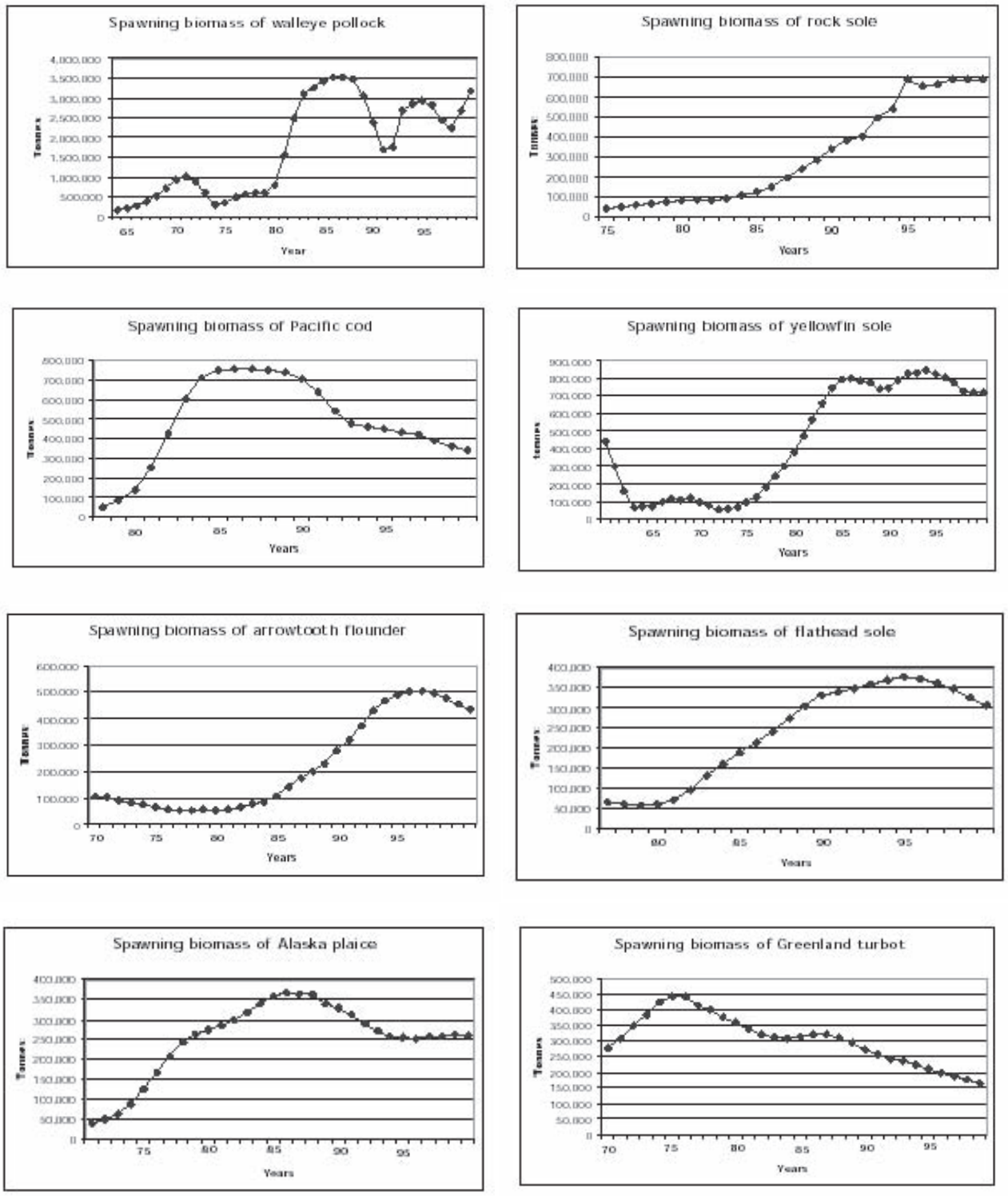

Figure 2.22: Spawner biomass of selected ground fish in the eastern Bering Sea. Data from NPFMC SAFE (2000).

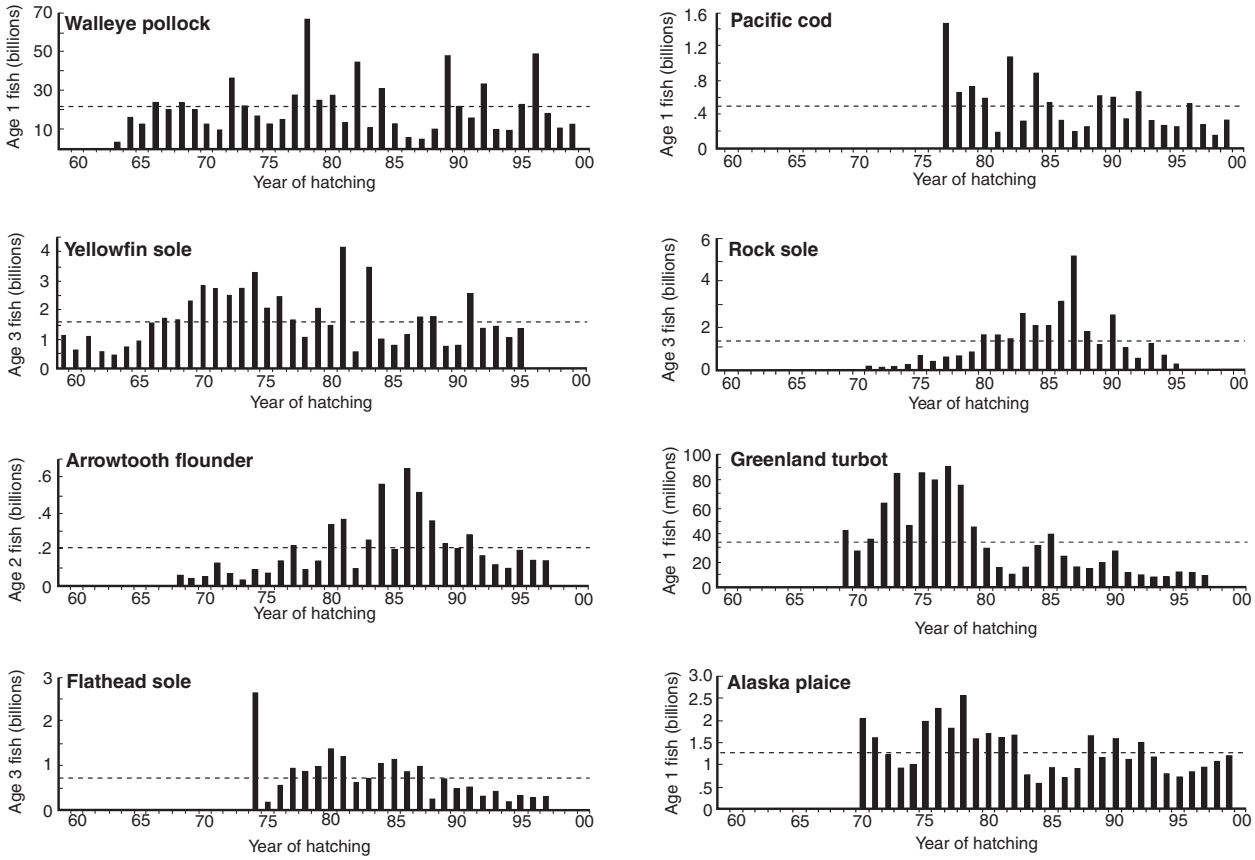

Figure 2.23: Year-class strength for selected species of groundfish in the eastern Bering Sea. Data from NPFMC SAFE (2000).

Table 2.6: Strong year classes (≥20% above the mean from 1975 to 1999) and weak year classes (≤20% below the mean) by species in the Bering Sea. Years not shown had average year classes (mean ±20%). Data from NPFMC, 2000.

Group	Strong Year Classes	Weak Year Classes
Group A		
Walleye Pollock	77, 78, 79, 80, 84, 89, 92, 96	75, 76, 81, 83, 85, 87, 88, 91, 93, 94, 98, 99
Alaska Plaice	75, 76, 77, 78, 79, 80, 82, 88, 90	83, 84, 85, 86, 87, 94, 95, 96, 97
Yellowfin Sole	75, 76, 79, 81, 83, 91	78, 82, 84, 85, 86, 89, 90, 94
Flathead Sole	77, 79, 80, 81, 84, 85, 87	75, 76, 88, 90, 91, 92, 93, 94, 95, 96, 97
Pacific Cod	77, 78, 79, 82, 84, 89, 92	81, 83, 86, 87, 88, 91, 93, 94, 95, 97, 98, 99
Group B		
Rock Sole	80, 81, 83, 84, 85, 86, 87, 88, 90	75, 76, 77, 78, 79, 91, 92, 94, 95
Arrowtooth Flounder	80, 81, 83, 84, 86, 87, 88, 91	75, 76, 78, 79, 82, 93, 94, 96, 97
Greenland Turbot	75, 76, 77, 78, 79	81, 82, 83, 86, 87, 88, 89, 91, 92

Two alternative recruitment patterns seem to have emerged. There are those species that show strong year classes in the late 1970s and early 1980s, and there are species with a delayed run of strong year classes beginning in the late 1980s and continuing through the early 1990s (Table 2.6). Both patterns show a reduction of year-class strength in the late 1990s. Fishes with strong year-class productivity in the late 1970s and 1980s include Pacific cod, yellowfin sole, flathead sole, and Alaska plaice. Fishes without strong recruitment in the 1970s, but having strong year classes in the 1980s, are rock sole and arrowtooth flounder (Fig. 2.23). Greenland turbot are unique in that they had strong year classes in the late 1970s, but not in the 1980s and 1990s. There are years that stand out as being characterized as having coincident strong or weak year classes among eight species of groundfish (Table 2.6). The years during which over half of the species had strong year classes were 1977 (5/8), 1979 (6/8), and 1984 (5/8). Two years had weak year classes for over half of the species, 1986 (5/8) and 1994 (7/8).

An important difference between walleye pollock and other groundfish is the continued high biomass levels of walleye pollock in the Bering Sea in the 1990s, which contrasts with patterns of decline for many other economically important species (Fig. 2.22). Walleye pollock is unique in its continued production of young through the decade of the 1990s (Fig. 2.23, Table 2.6).

The pattern of changes in biomass available to the fisheries has followed the availability of recruits, not the catch of the fishery. However, these stock changes greatly affected the fishery landings and sustainable yields. The most notable series of stock increases came after the 1976–1977 regime shift that resulted in favorable ocean conditions north of the state of Washington. During the 1980s, simulations showed that wind-driven surface currents in the southeastern Bering Sea were mostly eastward, and flatfish as well as pollock enjoyed high levels of recruitment (Wilderbuer *et al.*, 2002). However, in the 1990s, surface currents were westerly (seaward), and flatfish recruitment was weaker. For the flatfish, this would have resulted in advection to favorable nursery grounds (Wilderbuer *et al.*, 2002); for pollock,

advection into Bristol Bay would result in separation of larvae and juveniles from cannibalistic adults (Wespestad *et al.*, 2000).

The late 1970s and early 1980s were also a period of major change in the management of the fisheries. In 1977, the extended fishery jurisdiction of the United States and Canada came into force. International fishing was severely curtailed and fishery management became progressively more conservative. There was a transition period of "joint venture" fishing during the late 1970s and early 1980s, after which only domestic fishing was allowed. Also, because of the cooperative interaction between the International Pacific Halibut Commission and the North Pacific Fishery Management Council, the catch of cod and flatfish has been conservative. Thus, fishery takes have affected the total biomass of groundfish in the eastern Bering Sea, and patterns in change appear to be driven by ecological determinants of recruitment.

Another group of species that are of great importance to both the commercial sector and to subsistence users are the Pacific salmon. The world's largest runs of wild sockeye salmon (*Oncorhynchus nerka*) occur in Bristol Bay (USGS, 2004), and important runs of other species occur in most of the drainages of western Alaska. Several of the runs showed remarkable increases in the 1970s (e.g., Yukon River chum [*O. keta*] and Bristol Bay sockeye), but returns from these and other stocks in western Alaska plunged precipitously in the late 1990s (Fig. 2.24). The reasons for these declines are not apparent, but the most likely hypotheses focus on ocean survival (Kruse, 1998). In recent years, the ocean ecology of salmon in the eastern Bering Sea has received little attention, and we have few data on their impact on the ecosystem there (e.g., Nishiyama, 1974), nor on factors that might affect their ocean ecology. Work recently begun by the North Pacific Anadromous Fish Commission (the BASIS program, NPAFC, 2001), will begin to remedy this lack of information by completing an international survey of Bering-Aleutian salmon.

In addition to work on the commercially important groundfish and salmon species, there have also been significant gains in our knowledge of the distribution, abundance, and ecology of forage fishes. These fish include both small species, such as sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*), smelts, and mesopelagic groups such as Myctophids (lanternfish) and Bathylagidae (deep-sea smelts), as well as the young of larger species such as age-0 and age-1 walleye pollock. These species are eaten by large fish, including Pacific cod, Pacific halibut (*Hippoglossus stenolepis*) and walleye pollock, and are also important components of the diets of marine mammals and seabirds. Brodeur *et al.* (1999b) summarized data collected in 1987 in a joint program with Russian colleagues that resulted in a pair of surveys that covered most of the Bering Sea. They found that age-0 and age-1 pollock were more abundant on the eastern shelf than elsewhere in the Bering, that herring and capelin were most abundant on the northern and western shelves. They also compared the distribution of various species, as sampled in the National Marine Fisheries Bottom Trawl Surveys, in a warm year (1987) and in a cold year (1986). They found that

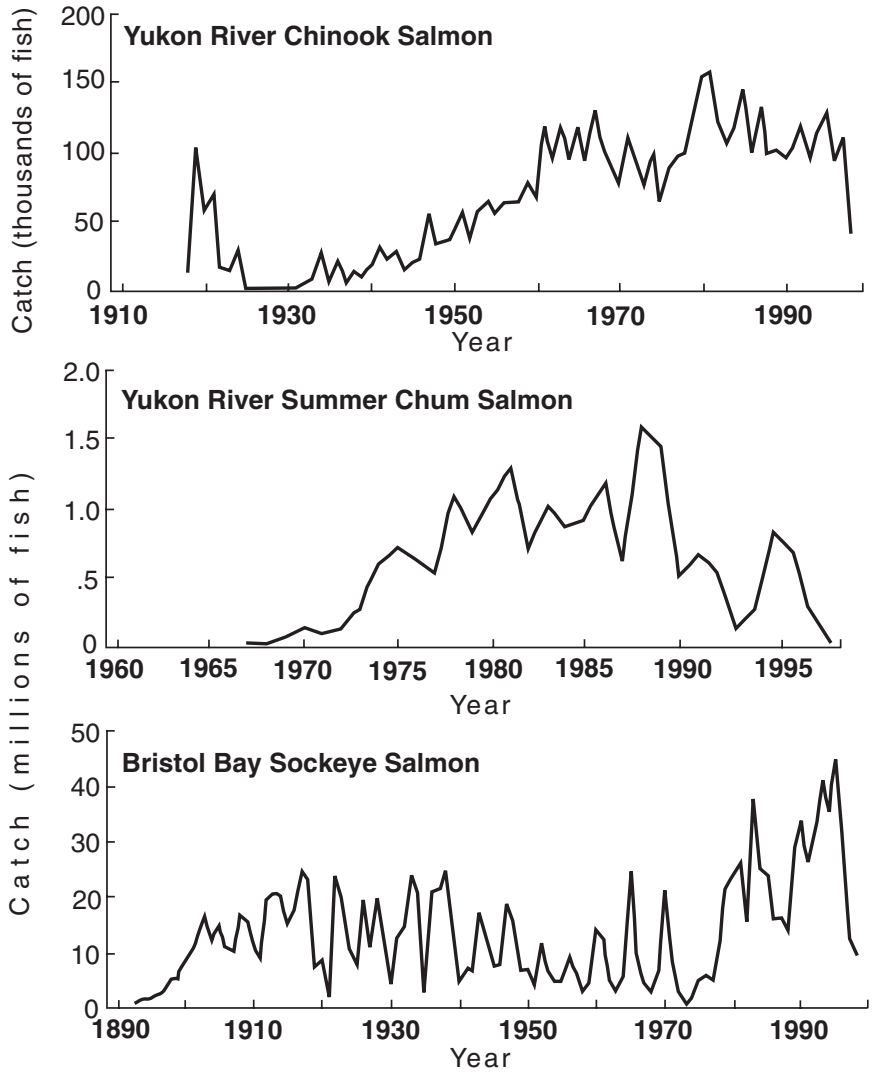

Figure 2.24: Time-series for three western Alaska salmon runs. From Kruse (1998).

some forage fishes, such as age-1 pollock, avoided regions with cold bottom temperatures, whereas others did not (e.g., capelin).

A group of little-studied forage species that deserve particular attention are the mesopelagic fish and squid, which are important forage for upper trophic level consumers including large fish, marine mammals, and seabirds. Many mesopelagic species migrate into the upper mixed layer each night to forage on euphausiids and copepods, returning to depth during the day. This behavior provides a mechanism for rapid downward transport of production from the upper ocean. One species, *Stenobrachius leucopsarus*, perhaps the ecologically most important, may have a biomass of 21 million tons in the North Pacific sub-arctic gyres (including the Bering Sea and the Sea of Okhotsk) (Beamish *et al.*, 1999a). Sinclair *et al.* (1999) assembled data on

mesopelagic fishes and squids from the Bering Sea to provide a description of the species composition, distribution, and relative abundances of members of this important fauna. They noted that, of the squids, members of the families Gonatidae and Cranchiidae appeared in the highest numbers in both trawl surveys and predator diets, while of the fishes, Myctophidae and Bathylagidae were most common. Sinclair and Stabeno (2002) sampled basin waters near the edge of the southeastern Bering Sea shelf. They found unexpectedly high concentrations of biomass, driven primarily by the deep-sea smelt *Leuroglossus schmidti*. Their work revealed a new species of gonatid, a range extension for the snailfish (*Paraliparis paucidens*), and new size records for several species of fish and squid. Discoveries of this nature demonstrate that this ecologically important group of organisms has been neglected. Given their large biomass compared to that of most fish species, we must devote more effort to learning about them. Because of mesopelagics' strongly dial cycles of behavior, study of their ecological role will require examination of trophic relations both during the daylight and at night.

The waters around the Pribilof Islands have been thought to provide a uniquely productive habitat for juvenile pollock because of the potential for enhance production associated with frontal processes there. During the 1990s, several projects examined the ecology of age-0 walleye pollock there. These are referenced in Section 2 (Pribilof Islands) of this report and will not be discussed here.

2.4.5 Marine mammals and seabirds

Dramatic population declines of pinnipeds and seabirds in the eastern Bering Sea and Gulf of Alaska since the mid 1970s contrast with their stability elsewhere in the North Pacific Ocean. Previous studies have proposed a combination of natural (climatic) and anthropogenic (fisheries) factors that may have altered the structure of the food web in the eastern Bering Sea (Piatt and Anderson, 1996; NRC, 1996; Merrick, 1997; Springer, 1998; Anderson and Piatt, 1999; Hunt *et al.*, 2002a) and thus affected population stability of apex predators. Although the mechanisms of change unique to the Bering Sea are not fully understood (Hunt and Byrd, 1999; Hunt *et al.*, 2002a), changes in the populations of marine birds at the Pribilof Islands are likely the result of declines in prey availability, as there is little evidence that these seabird species are subject to significant levels of predation.

Marine mammal populations. Approximately 80% of the world population of northern fur seals (*Callorhinus ursinus*) breeds on the Pribilof Islands where population estimates have been conducted since the turn of the century, and with consistent methodology for the past 60 years (York and Hartley, 1981). There are currently an estimated 800,000 animals remaining from an estimated population of 2 million as recently as the 1950s. The species is listed as depleted under the Marine Mammal Protection Act (NMFS, 1993). Unlike most other apex predators in the Bering Sea, the pattern of decline among northern fur seals is one of steady to severe reductions in population numbers followed by some years of stability (Fig. 2.25). A steep decline began in the mid 1970s that was the effect of either reduced pup

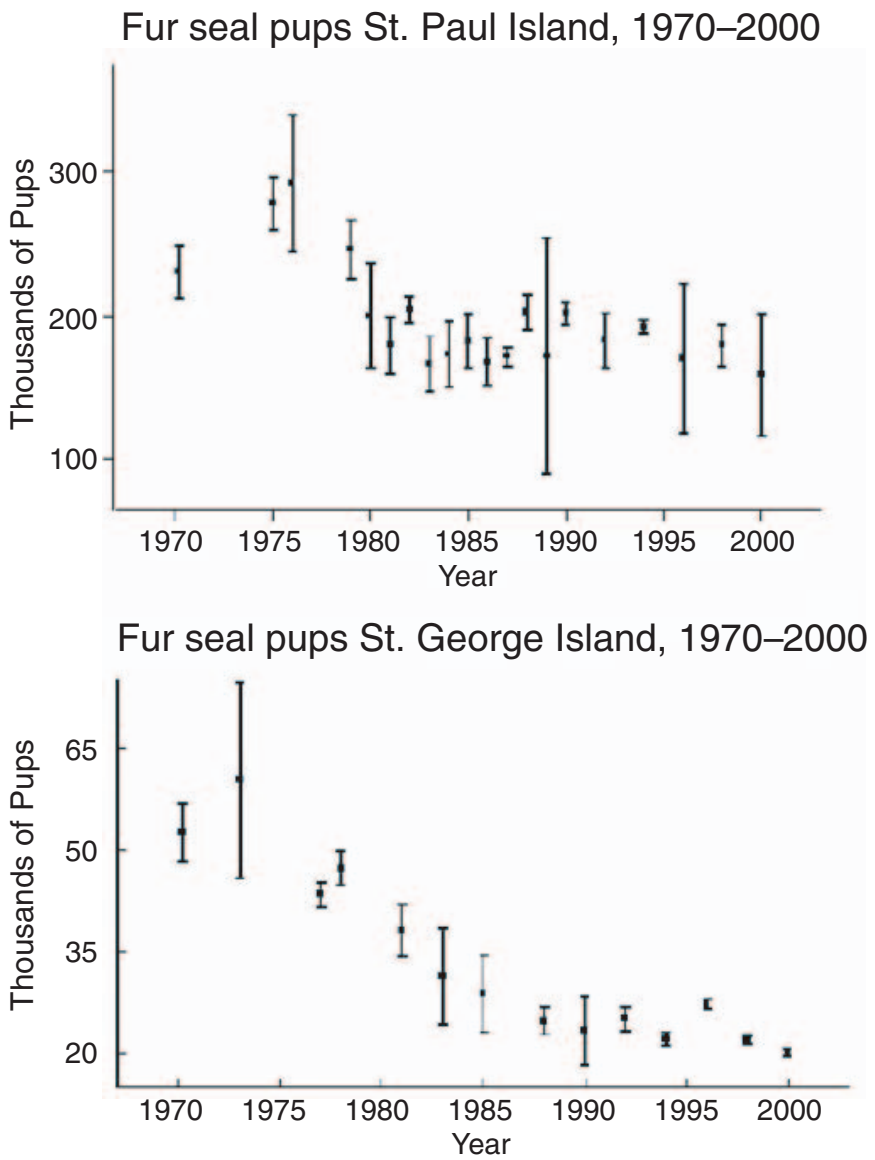

Figure 2.25: Time series of pup counts at St. Paul Island and St. George Island, Pribilof Islands. From NMFS (2002).

production or decreased juvenile survival during their pelagic phase (York and Kozloff, 1987). Declines continued into the mid-1980s, after which the St. Paul Island population remained stable at 33% of its 1970s population, while the smaller population of St. George Island stood at 60% of its 1970s level and continued to decline incrementally into the 1990s (York *et al.*, 2000; Loughlin *et al.*, 1994). The most recent population count in 2002 indicates that an annual decline of 5% has been occurring on both islands since 1998 (NMFS, 2002).

Steller sea lions (*Eumetopias jubatus*) currently are divided into two stocks. The western stock ranges from 144°W in the Gulf of Alaska westward

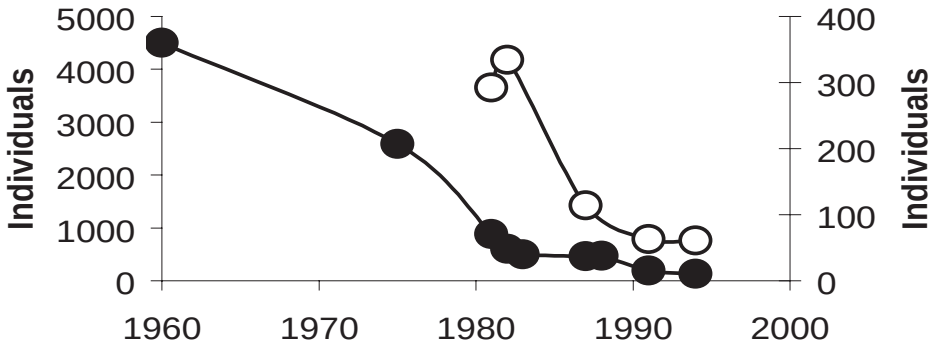

Figure 2.26: Changes in the number of adult (left scale, filled dots) and pup (right scale, open dots) Steller sea lions counted on Walrus Island, Pribilof Islands. Data from National Marine Fisheries Service, National Marine Mammal Laboratory, Seattle, Washington. From Hunt *et al.* (2002a).

across the Aleutian Island chain and includes Walrus Island in the Pribilof Island group. After a continual population decrease of 5% per year since the 1970s, the monitored portion of the stock in the Gulf of Alaska and along the Aleutian Islands chain showed an increase of 5% between 2001 and 2002. The population of Steller sea lions on Walrus Island (Pribilof Island group) has been in steady decline since the 1960s and is considered a nearly extinct rookery (Fig. 2.26). The western stock of Steller sea lions is currently listed as endangered under the U.S. Endangered Species Act. The causes of the decline in the western stock of Steller sea lions remain controversial (NRC, 2003).

Populations of large cetaceans in the eastern Bering Sea were greatly reduced by commercial whaling that continued through about 1970 (NRC, 1996). In contrast to declines in pinniped and seabird populations (see below), populations of large baleen whales, which were almost extirpated in shelf waters of the eastern Bering Sea by the 1960s (NRC, 1996; Merrick, 1997), may be increasing. Although in the mid 1970s it was rare to encounter any large cetacean over the eastern Bering Sea shelf (Leatherwood *et al.*, 1983; Brueggerman *et al.*, 1987), since the 1980s, whales have been encountered over shelf waters with increasing frequency (Baretta and Hunt, 1994). Significant numbers of large cetaceans are now present in shelf waters during summer (Tynan, 1999; Moore *et al.*, 2000, 2002).

Pinniped diets. The composition of the diet of northern fur seals in the Bering Sea has been inferred from material obtained from stomachs of animals shot at sea, from stomach contents and vomits of animals on land, and most recently from analysis of hard parts remaining in scats (feces) (Sinclair *et al.*, in preparation). Although not completely comparable because of differences in the likelihood of detection of different dietary items, the time series for fur seals provide evidence of significant changes in the composition of their diets over the past forty years (see Hunt *et al.*, 2002a for a review of earlier work). Most significantly, in the 1960s, cold-water species such as capelin and Greenland turbot were important, whereas by

the 1980s, these had disappeared from fur seal diets at the Pribilofs, and diets were dominated by pollock ≤2 years of age.

During the 1990s, analyses of scats on St. Paul and St. George Islands revealed that fur seals there take at least four species of squid and approximately 30 species of fish. Primary prey (those species that occurred with a frequency of 10% or higher on either island, in any single year) included the four species of squid and five species of fish. On St. Paul Island, only walleye pollock ranked above 10% for all sample years combined. In all years combined on St. George Island, pollock, salmon, and the gonatid squid *Gonatopsis borealis/Berryteuthis magister* ranked as primary prey items. Since 1988, the number of northern fur seals on the Pribilof Islands consuming squid has decreased, while the number consuming walleye pollock (*Theragra chalcogramma*) and northern smoothtongue (*Leuroglossus schmidti*) on both islands, and Pacific salmon (*Salmonidae*) on St. George Island has increased (Fig. 2.27). While northern fur seals have relied primarily on juvenile pollock (ages-0 and -1) and to a lesser degree age-2+ since the 1980s (Sinclair *et al.*, 1994, 1996; Antonelis *et al.*, 1997), in the 1990s, there has been an increase in the use of age-3+ pollock, and possibly a decrease in the consumption of age-0 pollock, particularly on St. Paul Island (Fig. 2.28). Over the decade of the 1990s, fur seals on St. George have had a somewhat higher consumption of age-3+ pollock compared to those on St. Paul Island, which is in line with the greater densities of adult pollock around St. George Island relative to St. Paul (NMFS, 1993).

Adult fur seals are typically specific to summer feeding locations (Robson, 2002) depending upon the rookery of their birth; adult females from St. George Island can be generally characterized as off-shelf feeders compared to those from St. Paul Island (Sinclair *et al.*, 1996; Goebel, 2002). Off-shelf feeding is indicated by consumption of salmon, northern smoothtongue, and the Gonatid squid *Gonatopsis borealis/Berryteuthis magister*.

Scats collected from Steller sea lions on Walrus Island in 1994 (n = 43) and 2001 (n = 44) contained 11 species (or taxonomic groups) of fish prey that ranked above 10% in frequency of occurrence (FO) in one or both years. Irish Lord (*Hemilepidotus hemilepidotus*), Pacific cod, walleye pollock, and rock sole ranked above 10% FO in both sample years. With the exception of salmon, all the species consumed by Steller sea lions on Walrus Island are demersal or semi-demersal in habit. Both juvenile and adult pollock were present in Steller sea lion scats with an emphasis of age 5+ in year two.

Seabird populations. During the 1970s and early 1980s, the abundance of piscivorous seabirds breeding at the Pribilof Islands declined (Figs. 2.29, 2.30) (Decker *et al.*, 1995; Springer, 1998; Dragoo *et al.*, 2001). Kittiwake (*Rissa* spp.) and common murre (*Uria aalge*) declines were especially severe on St. Paul Island during the 1970s and 1980s. During that time, common murres became more abundant on St. George Island. It is unclear why population declines in murres were more severe on St. Paul Island than on St. George Island.

Schmutz (Appendix 1 in Sinclair *et al.*, in preparation) partitioned the causes of kittiwake and murre population changes on the Pribilof Islands between reproductive success (productivity) and other factors that include

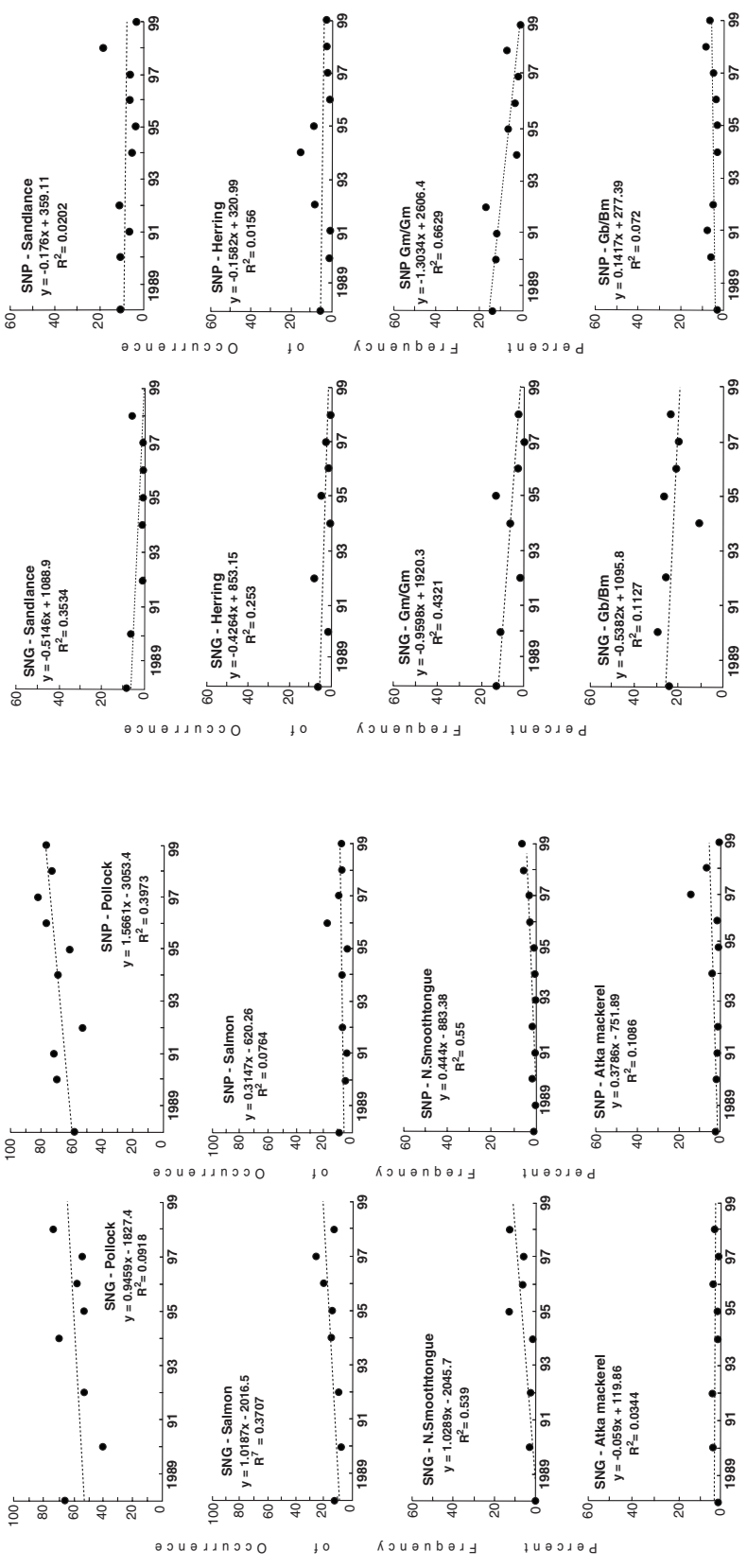

Figure 2.27: Changes in prey composition for northern fur seals on the Pribilof Islands in the late 1980s and 1990s. Gm/Gm: "shelf squid," one or both of two species *Gonatus middendorffi* and/or *G. madokai*. Gb/Bm: "slope squid" *Gonatopsis borealis* and/or *Berryteuthis magister*. SNP = St. Paul and SNG = St. George. From Sinclair *et al.* (in preparation).

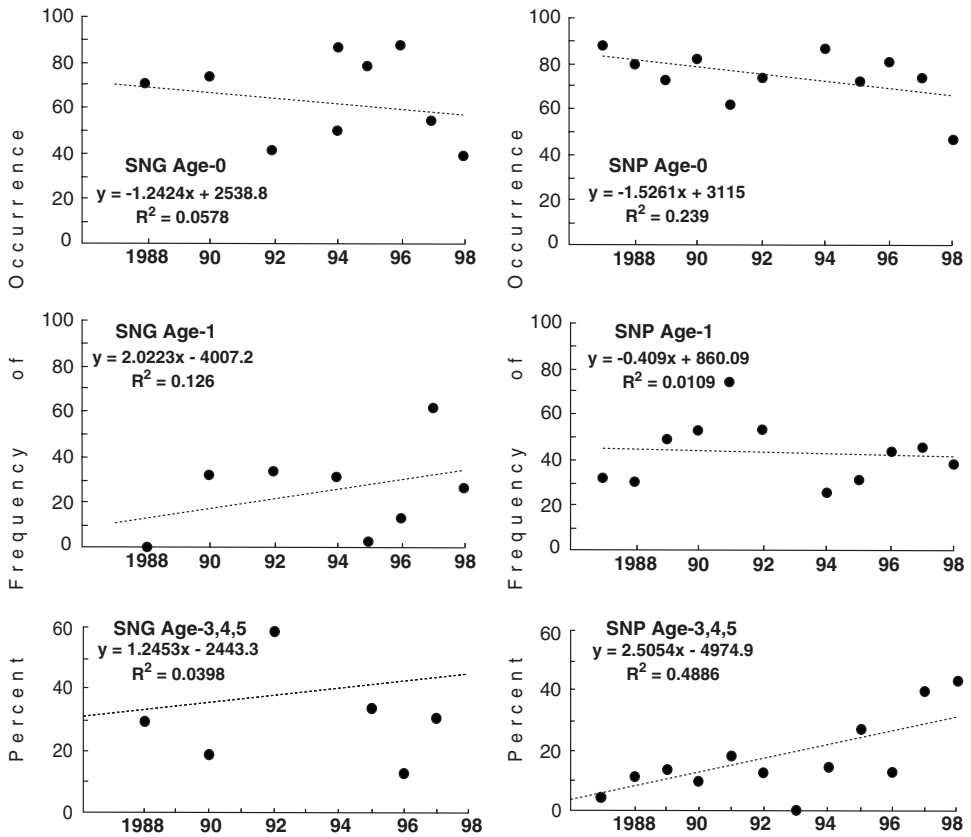

Figure 2.28: Changes in the age composition of walleye pollock in the diets of northern fur seals on the Pribilof Islands in the late 1980s and 1990s. Data from Sinclair *et al.* (in preparation).

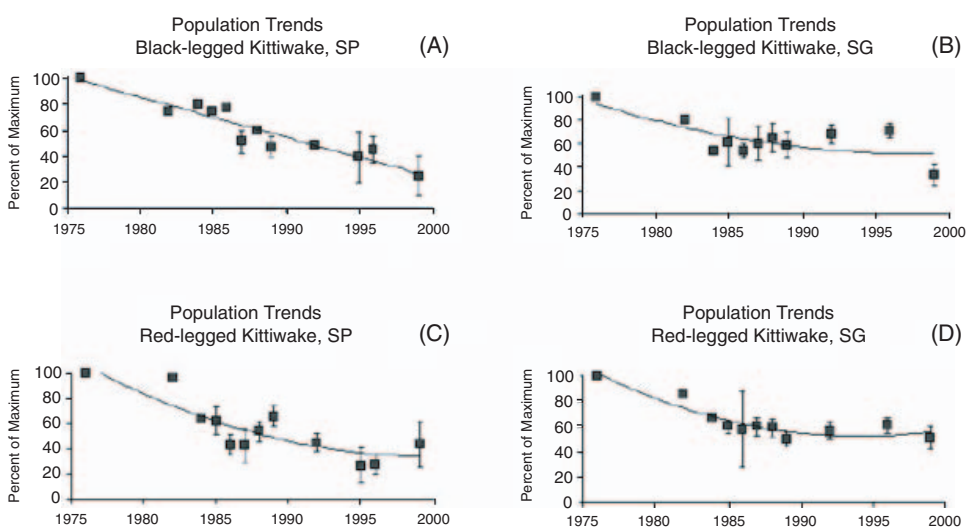

Figure 2.29: Population trends in black-legged kittiwakes and red-legged kittiwakes on the Pribilof Islands. From Dragoo *et al.* (2001).

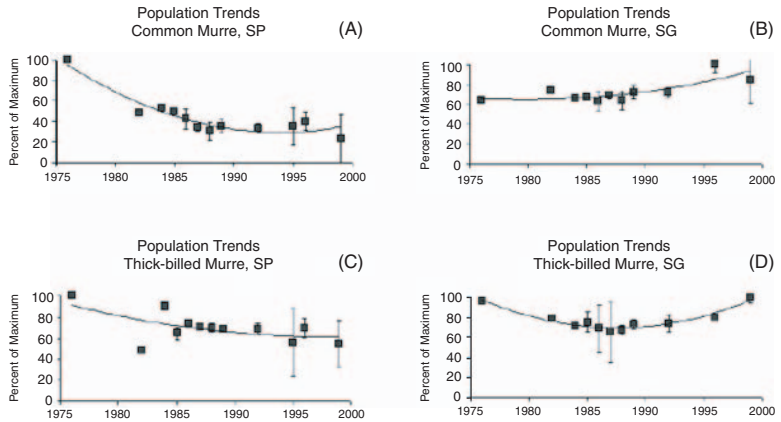

Figure 2.30: Population trends of common and thick-billed murres on the Pribilof Islands. From Dragoo *et al.* (2001).

post-fledging mortality and emigration. He found that for the four species of kittiwakes and murres, productivity accounted for one-third (34%) of the variation in population change. The majority (66%) of variation in population growth rate was attributable to mortality and emigration, but distinction between these two demographic processes was not possible for most species due to lack of data. However, other survival and population data for the geographically restricted red-legged kittiwake (*Rissa brevirostris*) indicated that, for this species, variations in survival have likely been a principal demographic force.

Marine bird diets. Sampling of marine bird diets has shown that there are consistent, significant differences in diet components between seabirds nesting on St. George and St. Paul islands, and that, since the mid 1970s, there have been significant changes of diet components for seabird species nesting on St. George and St. Paul islands (Sinclair *et al.*, in preparation). During the 1970s and 1980s, black-legged kittiwakes (*R. tridactyla*) and common and thick-billed murres (*U. lomvia*) used more invertebrates (e.g., euphausiids, squid) on St. George than on St. Paul Island. Similarly, during the 1990s, the proportion of black-legged kittiwake and thick-billed murre diets consisting of invertebrates was higher on St. George than on St. Paul Island. During the 1970s and 1980s, there were also differences in the proportions of four species of forage fishes used (Sinclair *et al.*, in preparation). Capelin composed a higher proportion of kittiwake diets on St. Paul Island than on St. George Island. Sand lance were a larger proportion of murre diets on St. George Island than on St. Paul Island. During the 1990s, all four seabird species took a higher percentage of gadids on St. Paul Island than they did on St. George Island.

The differences in diets between the islands are important. They indicate that kittiwakes and murres on St. George have had access to a wider variety of prey, in particular, invertebrates including squids and euphausiids, than seabirds on St. Paul Island. And, seabirds on St. Paul Island have been more dependent on juvenile gadids and capelin than birds on St. George Island

where seabirds apparently had more ready access to a wider variety of forage fishes including sand lance and myctophids.

During the 1970s and 1980s, gadids (mainly walleye pollock) were the primary component of black-legged kittiwake, common murre, and thick-billed murre diets. Red-legged kittiwakes took mainly lanternfish. There was a significant decline between the 1970s and 1980s in the proportion of gadids in kittiwake diets on St. Paul, but not St. George Island (Fig. 2.31), and in thick-billed murre diets on St. George Island. Likewise, the diet of red-legged kittiwakes during the early season contained a higher proportion of gadids during the 1970s than they did during the 1980s.

Seabird reproduction in an ecosystem context. Sinclair *et al.* (in preparation) evaluated the spatial scale at which causal factors appeared to have influenced demographic parameters in Pribilof Islands' seabirds. If population declines were related to processes that operate on large (regional) spatial scales, such as prey availability over the shelf, then seabird reproductive success and colony attendance should have been correlated between St. Paul and St. George Islands. If populations responded to processes that operated on small (local) spatial scales, such as prey availability associated with oceanographic features near an island, then seabird demography should have differed between the islands. Because colony attendance and reproductive success of black-legged kittiwakes and red-legged kittiwakes were correlated between populations on St. Paul and St. George Islands, as were interannual variations in the diets of these species on the two islands, Sinclair *et al.* (in preparation) concluded that population dynamics in kittiwakes were influenced by processes that occurred over large spatial scales (shelf-wide), rather than at the local (island) level. In contrast, for both common and thick-billed murres, interannual variability in colony attendance, and reproductive success in thick-billed murres, were not correlated between islands, suggesting that the sizes of populations of two murres were influenced by factors that operated on a local scale.

At about the time of the 1976–1977 regime shift, and concurrent with the declines in piscivorous pinnipeds and seabirds at the Pribilof Islands, there were significant decreases in the biomass of age-1 walleye pollock on the Bering Sea shelf (Brodeur *et al.*, 1999b; Hunt *et al.*, 2002a; Sinclair *et al.*, in preparation). In some areas, abundance decreased by as much as 95% (Springer, 1992; Sinclair *et al.*, 1996; Brodeur *et al.*, 1999b; Hunt *et al.*, 2002a). Likewise, there is evidence for significant declines in the abundance of capelin, an important forage fish for seabirds (Hunt *et al.*, 1996a). Because seabirds whose populations declined had diets consisting primarily of age-1 pollock (Springer, 1992; Decker *et al.*, 1995; Hunt *et al.*, 1996c, 2002a), and the proportion of these declined in their diets, it was hypothesized that declines in the abundance of age-1 pollock and other forage fishes reduced the foraging success and, consequently, reproductive success and population size of kittiwakes and murres at the Pribilof Islands (Hunt and Byrd, 1999). A shift from use of age-1 to age-0 pollock during this period (Hunt *et al.*, 1996b) would have been particularly challenging, as age-0 pollock are both smaller (about 2 g) than age-1 pollock in spring (about 19 g) and of lower energy density (about 2% fat vs. about 5% fat) (Iverson *et al.*, 2002).

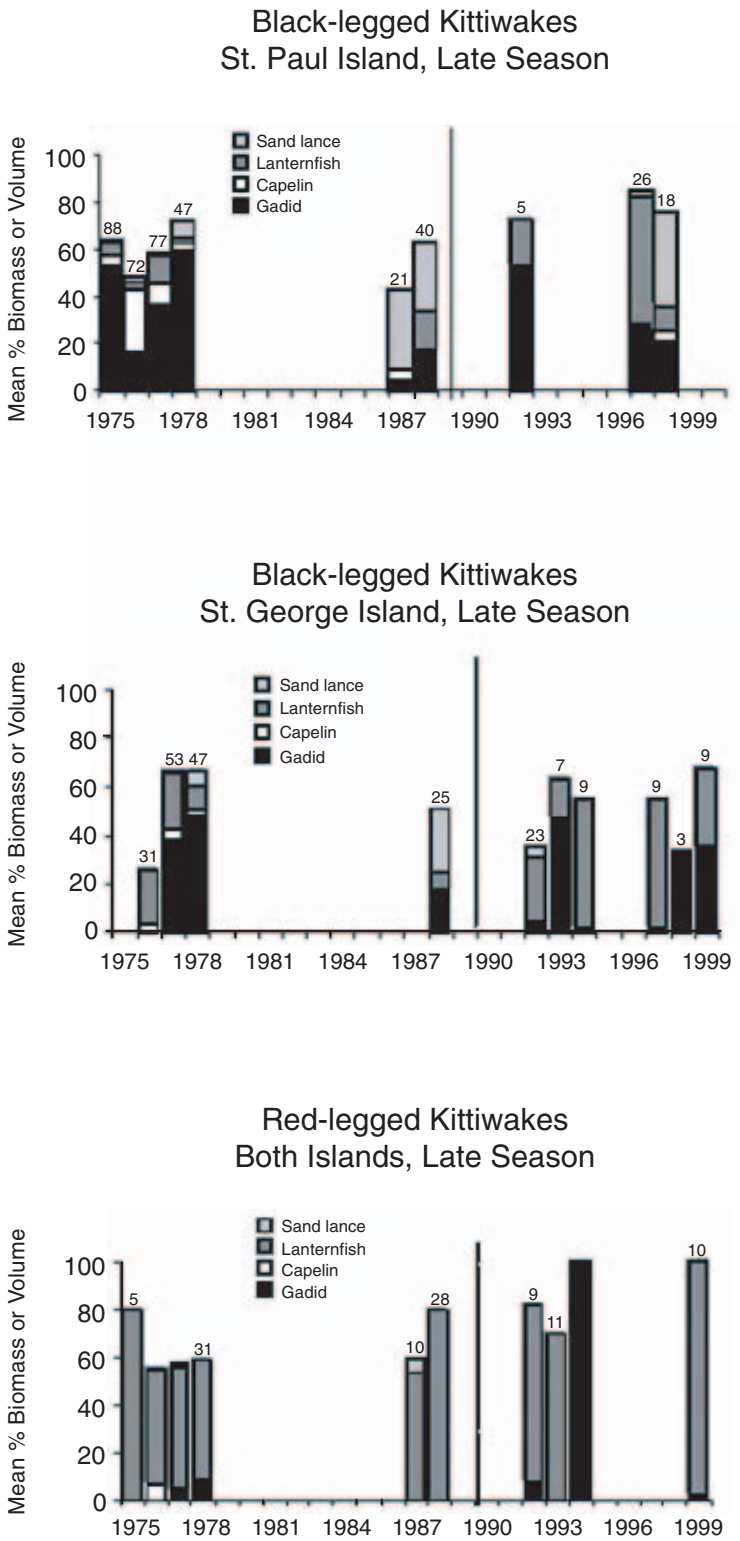

Figure 2.31: Changes in the species composition of the diets of black-legged and red legged kittiwakes at the Pribilof Islands, 1975–1999. Data from Sinclair *et al.* (in preparation).

The decreases in at least black-legged kittiwakes may be related to an increase in adult pollock on the shelf and competition with these fish for age-1 pollock and other forage fish. The biomass of adult (age 3+) walleye pollock on the Bering Sea shelf increased during 1976–1999 ($r^2 = 0.30$, $P = 0.006$, $n = 24$), with the steepest increase in their biomass occurring during 1979–1982 (Sinclair *et al.*, in preparation). The annual variability in reproductive success in black-legged kittiwakes was negatively correlated with the biomass of adult walleye pollock on the Bering Sea shelf ($r = -0.68$, $p < 0.001$) (Livingston *et al.*, 1999; Hunt and Stabeno, 2002; Sinclair *et al.*, in preparation). There was no correlation between reproductive success in red-legged kittiwakes ($r = -0.35$, $p = 0.160$), common murres ($r = 0.18$, $p = 0.626$), or thick-billed murres (St. Paul: $r = -0.419$, $p = 0.136$; St. George: $r = 0.19$, $p = 0.440$) and the biomass of adult walleye pollock on the shelf (Sinclair *et al.*, in preparation).

Prey availability and seabird mortality at the Pribilof Islands. Although Sinclair *et al.* (in preparation) found little correlation between juvenile pollock abundance on bottom trawl surveys and seabird reproductive success on an interannual basis, changes in the availability of young pollock (and possibly other prey) to seabirds during the late 1970s probably *did* result in poor foraging conditions for seabirds. Inter-colony comparisons suggest that seabird productivity at the Pribilof Islands is limited by the availability of food. For example, since the mid 1970s, the long-term (1976–1999) mean reproductive success of black-legged kittiwakes on St. Paul Island is 0.28 chicks $nest^{-1}$ $year^{-1}$, and on St. George Island, it is 0.22 chicks $nest^{-1}$ $year^{-1}$. In contrast, mean reproductive success over the same period for black-legged kittiwakes at Cape Lisburne, northern Bering Sea, is 0.80 chicks $nest^{-1}$ $year^{-1}$, and in some areas, black-legged kittiwakes raise two or more chicks per year. At the Pribilofs, kittiwakes raise at most one (Dragoo *et al.*, 2001). Likewise, reproductive success is also low among murres at the Pribilof Islands relative to murres at other colonies in the North Pacific. Since the mid 1970s, common murres on St. Paul Island fledged an average of 0.53 chicks $nest^{-1}$ $year^{-1}$, and, on St. George Island, the average is 0.52 chicks $nest^{-1}$ $year^{-1}$. In contrast, common murres at Cape Thompson, in the northern Bering Sea, fledged an average of 0.70 chicks $nest^{-1}$ $year^{-1}$. At Kodiak Island (E. Amatuli), in the Gulf of Alaska, they fledged an average of 0.71 chicks $nest^{-1}$ $year^{-1}$ (Dragoo *et al.*, 2001). The ability of kittiwakes and murres at other colonies to consistently raise more young than they do at the Pribilof Islands suggests that competition for food is greater around the Pribilofs or foraging conditions around the Pribilofs are poor relative to other regions in the Bering Sea.

If prey availability to seabirds at the Pribilof Islands is relatively low during the breeding period, as suggested in the preceding discussion, reproduction may be an especially stressful time for Pribilof seabirds. Kitaysky and colleagues (1999a,b, 2000, 2001a) demonstrated the exacerbating effect that a limited food supply can have on acute stress to seabirds during the reproductive phase. Kitaysky *et al.* (1999b) found that adult black-legged kittiwakes breeding at a colony in Cook Inlet, Alaska, had elevated corticosterone levels during reproduction, and that stress levels were nega-

tively associated with food availability near the breeding colony (Kitaysky *et al.*, 1999b). In addition, corticosterone concentrations in birds increased throughout the breeding season, indicating that stress can become increasingly severe for seabirds as they progress from the egg-laying to the chick-rearing periods (Kitaysky *et al.*, 1999b). Using captive kittiwakes, Kitaysky *et al.* (1999a, 2001a) showed that food scarcity and food of poor nutritional quality increased circulating concentrations of a stress-response hormone, corticosterone, in black-legged and red-legged kittiwake chicks. Corticosterone indicates catabolic activity of metabolic pathways, signaling reliance by seabirds on endogenous energy reserves.

Increasing levels of corticosterone in plasma may affect not only the behaviors of the birds involved, but also their probability of survival. Kitaysky *et al.* (2000) showed experimentally that adult black-legged kittiwakes with elevated levels of corticosterone had significantly lower probability of returning to their colonies over the 2 years subsequent to implantation of corticosterone than did birds with shame operations. These results support the hypothesis that when adults have to work hard to raise chicks, either because food may be in short supply (Kitaysky *et al.*, 2000), or because the begging of hungry chicks forces them to work harder (Kitaysky *et al.*, 2001b), adult survival may be compromised (Golet *et al.*, 1998; Golet and Irons, 1999; Kitaysky *et al.*, 2001b). In the laboratory, Kitaysky *et al.* (2003) showed that young red-legged kittiwake chicks with elevated levels of corticosterone resulting from implants were less able at learning to find food than were birds that were shame-operated. Here the implication is that young kittiwakes that have had less food than optimal while growing may have difficulty learning to feed themselves once fledged and independent. These birds would be exceptionally vulnerable to starvation during the first few months of independence. There is considerable evidence that young seabirds have a more difficult time catching prey than adults. Learning deficits imposed by lack of adequate feeding in the nest and the consequent high stress levels would exacerbate this situation.

Thus, mortality among seabirds at the Pribilof Islands may have varied with the abundance of prey near the islands and may have been most severe during the post-breeding period, when deaths were difficult to observe. By that time, adults would have spent a considerable amount of energy on reproduction and fledglings would have had to learn to forage for themselves or perish. Storm activity is also greater during the post-breeding period (i.e., autumn), and inclement weather can have both direct and indirect implications for chick survivorship and adult mortality, as stormy weather impairs foraging by some seabirds. At the Pribilof Islands, Braun and Hunt (1983) found that in black-legged kittiwakes on St. Paul Island, chick loss due to ejection of second-hatched young by an older sibling happened more often than expected by chance during inclement weather. Work by others has shown that these behaviors result from the older chick being unable to satisfy its nutritional needs (Mock *et al.*, 1990; Irons, 1992).

Inability to obtain adequate prey has also affected migrant, non-breeding species in the Bering Sea. Each year millions of short-tailed shearwaters (*Puffinus tenuirostris*) migrate from Australia to the Bering Sea to forage

over the inner shelf. The evolution of this annual trans-equatorial migration implies that usually extraordinary amounts of prey must be readily available to these birds in the Bering Sea. During summer and fall of 1997, possibly as many as 10% of the 16 million short-tailed shearwaters present in the southeastern Bering Sea died (Vance *et al.*, 1998; Baduini *et al.*, 2001a,b). Between 1 August and 1 September, reports of moribund and dead shearwaters came from both sides of the Alaska Peninsula, the Aleutian Islands as far west as Adak, Bristol Bay, the Bering Sea north to Cape Anadyr (Russia), and the eastern Chukchi Sea. At least several hundred thousand shearwaters washed ashore. Compared with previous large-scale seabird die offs in the Bering Sea (Bailey and Davenport, 1972; Oka and Maruyama, 1986; Hatch, 1987; Piatt and Van Pelt, 1997), the 1997 event in the southeastern Bering Sea was probably one or two orders of magnitude larger (10^5–10^6 vs. 10^4 birds dying). Apparently they were unable to obtain sufficient of the usual prey, euphausiids, in 1997. In 1998, shearwaters were again emaciated, but few died, perhaps because the summer was windier, and they needed less energy to fly between places where food was obtainable. Their diets also shifted, with a greater proportion of fish and zooplankton being taken than was true in the same region in earlier years (Hunt *et al.*, 2002b).

In spring 1998, shearwaters had lower body masses than in spring 1997. Because the seasonal progression of stratification, bloom, and euphausiid mating occurred earlier in 1997, foraging for shearwaters arriving in May 1997 was apparently good, and birds were fat in June. In contrast, in 1998, the seasonal progression was late, and euphausiids were only beginning to form mating swarms in June. Consequently, shearwaters did not put on the level of fat reserves seen in June 1997. Perhaps because euphausiid mating came early in 1997, by late July, few near-surface swarms of mating euphausiids were available to shearwaters. If we are correct in our assessment that euphausiid maturation was delayed in 1999, and that the biomass of euphausiids was large compared to 1997, then swarms should have been available late into the summer and late-season body mass of shearwaters should be high. In the cold spring of 1999, euphausiids were abundant well into summer (Coyle and Pinchuk, 2002a), and shearwaters gained mass through the summer. Thus, it appears that temperature, through its affects on the timing of the availability of prey, may have important impacts on the survival of top predators.

2.5 What Controls Recruitment of Walleye Pollock?

Walleye pollock dominate the biomass of the eastern Bering Sea ecosystem and the trophic guilds in which they participate (Schumacher *et al.*, 2003). They are harvested in greater quantity than any other species of fish or shellfish, and made up >65% of the total groundfish biomass harvested during the 1980s (Napp *et al.*, 2000). Pollock, because of their vast numbers, are a nodal species for the Bering Sea, i.e., they are an integral part of the food chain for lower and higher trophic prey and predators. Thus, in any examination of the ecosystems of the eastern Bering Sea, factors that influ-

ence the abundance, distribution, and ecology of walleye pollock are of key importance for understanding the function of the ecosystem as a whole.

Walleye pollock were not always so abundant. In the early 1960s, their populations were small by comparison with those of the 1980s and 1990s. The reason for their initial increase in the mid to late 1960s is not known, but one hypothesis is that the increase was a result of a trophic cascade that occurred when large, plankton-eating whales and Pacific Ocean perch (*Sebastes alutus*) were harvested to "commercial extinction" in the late 1960s and early 1970s, thereby releasing vast amounts of zooplankton from consumption (Merrick, 1997; NRC, 1996). This newly available zooplankton resource then fuelled the expansion of the pollock population. The removal of the whales may also have released age-0 and age-1 pollock from predation pressure, as fin (*Balaenoptera physalus*) and minke (*B. acutorostrata*) whales would have most likely consumed young pollock along with zooplankton.

During the 1970s and early 1980s, the biomass of walleye pollock first declined and then increased explosively. In the mid 1970s, excessively high harvest rates imposed by the foreign fishing fleets caused the stock to decline. This foreign fishery ceased as of the establishment of the 200-mile Exclusive Economic Zone in 1977. In 1978, pollock produced an enormous year-class that numbered 63.5 billion age-1 fish in 1979 (NMFS, 2002). As these fish grew to adult size, their biomass came to dominate the eastern Bering Sea ecosystem. The reasons for this second spurt in population growth are not known. It is possible that this was a continuation of the ecological release of the pollock population subsequent to the removal of the whales and fish with which they are believed to have competed for prey. An alternative, but not mutually exclusive, hypothesis for this population growth is that the strong year classes of 1977 and 1978 were the result of the 1976–1977 regime shift that resulted in earlier ice retreat and warmer water temperatures in spring, conditions favorable for zooplankton production that would have provided abundant prey resources for growing pollock (Francis *et al.*, 1998; Hunt *et al.*, 2002a). Indeed, there is a general acknowledgment that warm years are conducive to enhanced pollock recruitment (Bulatov, 1995; Hollowed and Wooster, 1995; Bailey *et al.*, 1995, 1996; Quinn and Niebauer, 1995; Walsh and McRoy, 1986; Blood, 2002). The cessation of the foreign fishery did not cause the strong year class of 1978. The increase was driven by exceptional early survival and recruitment. Had the fishery continued into the mid 1980s, there might not have been as great a growth in pollock biomass, but the 1978 year class still would have been exceptional.

Throughout the 1980s, the biomass of walleye pollock in the eastern Bering Sea remained high, though between 1990 and 1998 there was a substantial decline (Fig. 2.32) (NMFS, 2002). During the 1980s, there were three strong year classes, and during the 1990s, there were two (Table 2.6; Fig. 2.32). It is these strong year classes, as they matured, that sustained the biomass of the stock and its ability to support commercial fisheries. Understanding of the determination of year-class strength is a key to understanding much of what occurs in the southeastern Bering Sea marine ecosystem. Section 4 of this report discusses some factors in detail.

Table 2.7 lists several hypotheses that have been put forward as expla-

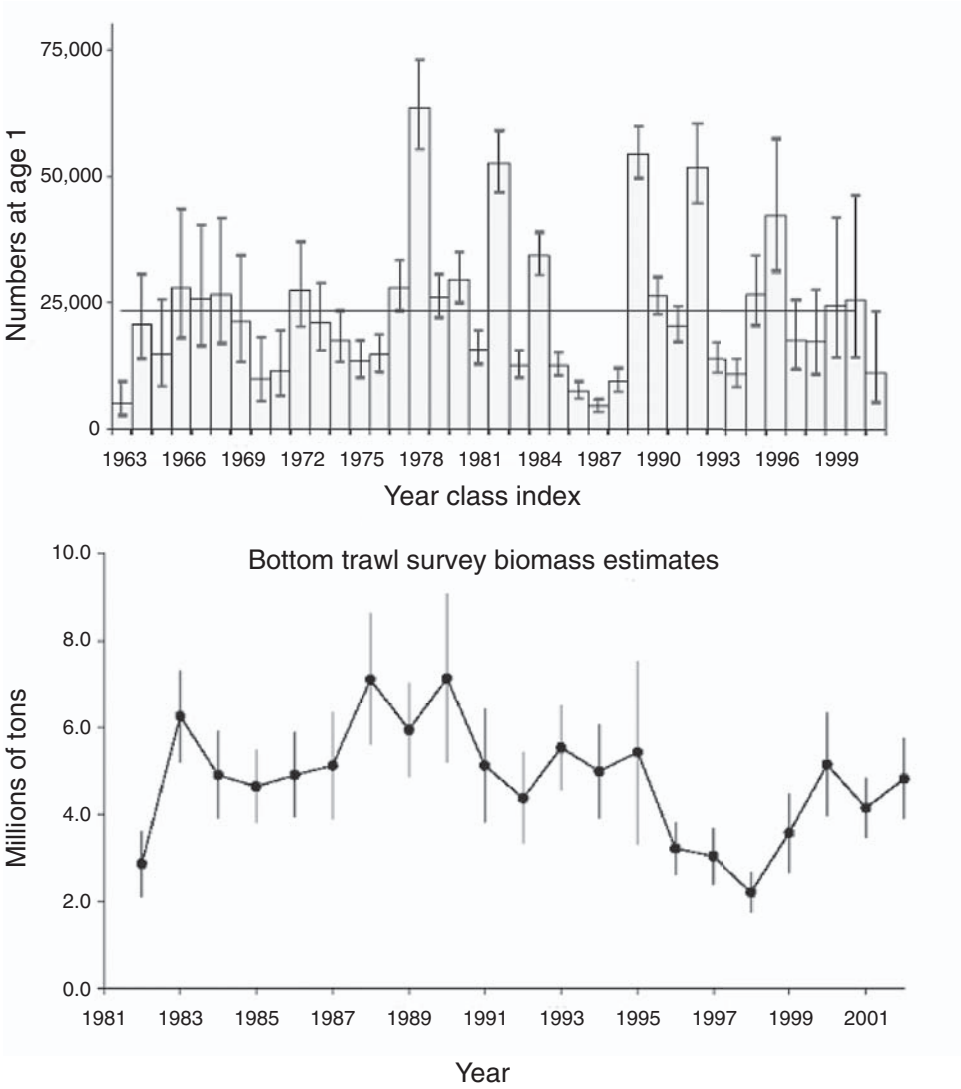

Figure 2.32: Top: year class strength of walleye pollock; **Bottom:** biomass of pollock on the eastern Bering Sea shelf (NPFMC, 2002).

nations for variation in pollock year-class strength. They can be divided into four groups. Group A focuses on the importance of primary or secondary production for the survival of young pollock; Group B focuses on the importance of cannibalism and mechanisms that result in the separation of adult and juvenile pollock; Group C hypothesizes that variation in risk of predation and variation in the abundance of zooplankton are causal, and Group D relates survival of young pollock to variation in the amount of turbulence when feeding. Ladd *et al.* (ms) have modeled the amount of mixing across the seasonal pycnocline expected during each summer over the past decades, and a preliminary comparison of their results with the distribution of strong and weak year classes in Table 2.6 suggests that variations in primary production forced by summer entrainment of nutrients is not likely a

good predictor of year-class strength in pollock. The abundance of small shelf copepods does vary significantly with integrated water temperature (Tables 2.3 and 2.4), and if prey is a limiting factor in pollock year-class strength, then this remains a viable hypothesis. Cannibalism is recognized as a major source of mortality for young pollock (Dwyer *et al.*, 1987; Wespestad, 1994; Balykin, 1996; Livingston and Lang, 1996; Wespestad and Quinn, 1996; Livingston and Methot, 1998; Lang *et al.*, 2000; Livingston and Jurado-Molina, 2000), and mechanisms for separating vulnerable individuals from cannibalistic older fish, such as on-shelf advection (Wespestad *et al.*, 2000), are likely to be of importance, regardless of what other factors are at play. For instance, Cooney *et al.* (2001) found that in Prince William Sound, adult pollock would feed on large *Neocalanus* copepods in spring if the copepods were abundant, but if not, the adult pollock would prey upon juvenile salmon and herring. Finally, variations in the amount of turbulence may influence foraging success of larval pollock by either enhancing the encounter rate with food particles at intermediate rates of turbulence, or depressing foraging success with either too much turbulence or insufficient turbulence (Megrey and Hinckley, 2001). Most of these hypotheses remain to be tested in the field, and it is likely that some combination of them together will provide the key to understanding the occurrence of strong year classes.

It is also likely that, as pollock populations wax and wane, the mechanisms responsible for population control will shift. Hunt *et al.* (2002a) hypothesized that under environmental conditions in which zooplankton were scarce, such as during a prolonged series of cold springs, walleye pollock populations would be controlled from the bottom-up because there would be insufficient zooplankton for larval or juvenile pollock (Fig. 2.33). In contrast, in years when pollock populations were large, cannibalism would exert strong top-down control on the population, as it apparently does at present. In periods under top-down control, large year classes could still occur, but to do so there would have to be some mechanism to promote separation of the young fish from the adults (e.g., Hypotheses 3 and 4, Table 2.7). When there is a switch from a period of years with cold springs to warm springs, one can expect large year classes, as there should be plentiful zooplankton and low risk of cannibalism, while during a switch from a prolonged period of warm springs to cold springs, year-class strength might be expected to be low because of both bottom-up and top-down effects.

The distributions and abundances of adult and juvenile pollock (age-0 and age-1) have important impacts on other elements of the eastern Bering Sea ecosystem. Juvenile pollock are a major source of prey for not only large piscivorous fishes such as adult pollock, Pacific cod and arrowtooth flounder, they are also staples in the diets of several species of marine birds and pinnipeds, such as northern fur seal, harbor seal, and Steller sea lions (see above). There is evidence for a negative relationship between the reproductive success of black-legged kittiwakes on St. George Island and the biomass of adult pollock on the eastern Bering Sea shelf (Livingston *et al.*, 1999; Hunt and Stabeno, 2002; Sinclair *et al.*, in preparation). During the period of population decline in the 1990s, northern fur seals at St. Paul

Table 2.7: Hypotheses for explaining variation in year-class strength of walleye pollock in the eastern Bering Sea.

	Hypothesis	Citations	Tests
A.	**Production-Based Hypotheses**		
1.	Decreases in wind mixing negatively influence post-bloom primary production.	Sambrotto *et al.* (1986) Hunt *et al.* (2002a) Springer, this report, Part 4	Compare wind mixing in years with strong and weak year classes; Ladd *et al.* (unpublished manuscript). Probably no significant relationship with summer mixing. Determine if there is strong coupling between spring and summer primary production, zooplankton abundance, and pollock year-class strength.
2.	Late ice retreat results in cold water blooms and reduced zooplankton production.	Stabeno *et al.* (1998) Hunt *et al.* (2002a) Hunt and Stabeno (2002)	Compare zooplankton abundances in years with early and late ice retreat; Coyle and Pinchuk (2002b) show significant differences. Determine if zooplankton abundance limits age-0 or age-1 pollock survival.
B.	**Cannibalism-Based Hypotheses**		
3.	When the cold pool is large, age-1 pollock move to the shelf edge where adults abound.	Dwyer *et al.* (1987) Ohtani and Azumaya (1995) Wyllie-Echeverria (1995)	Compare cold pool size in years with strong and weak year classes.
4.	Favorable winds in early spring may transport eggs, larvae, and small age-0 pollock deep onto the shelf, thus separating them from adults.	Wespestad *et al.* (2000)	Compare wind forcing in years with strong and weak year classes.
C.	**Mixed Production/Cannibalism Hypothesis**		
5.	Adult pollock switch prey types such that when zooplankton are scarce in spring, they increase cannibalism.	Cooney *et al.* (2001)	Since zooplankton are less abundant in cold years, compare the amount of cannibalism in years with cold and warm spring temperatures.
D.	**Mixing Process Hypothesis**		
6.	Intermediate levels of turbulence are required for optimal foraging conditions.	Megrey and Hinckley (2001)	Compare turbulence levels in years with strong and weak year-classes.

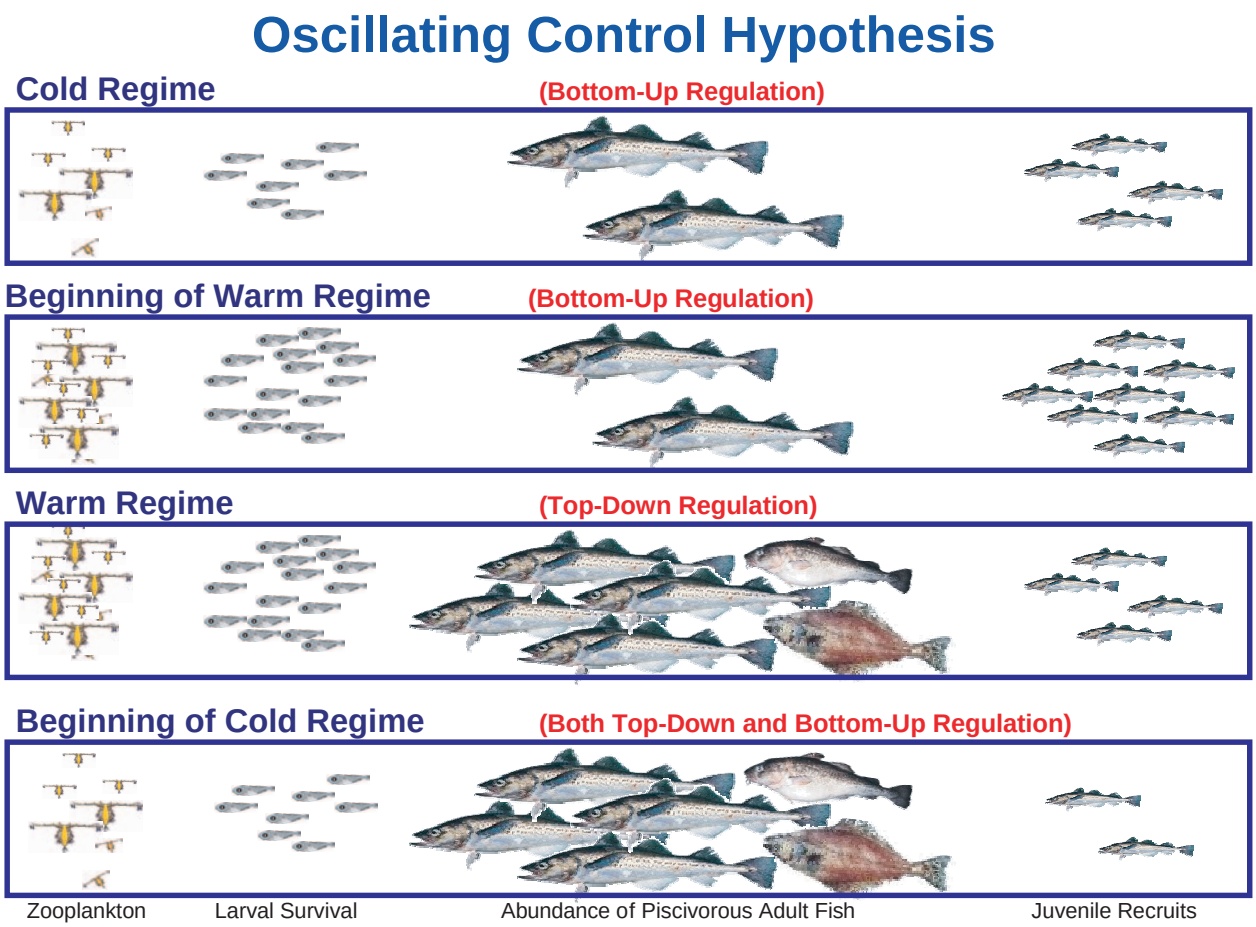

Figure 2.33: Schematic of the function of the Oscillating Control Hypothesis. For an explanation, see text. (From Hunt *et al.*, 2002a).

Island reduced their use of age-0 and age-1 pollock, sand lance, and slope squids, but increased their use of age-3, -4, and -5 pollock. It is difficult to know the causes of these shifts in fur seal diets.

The distribution of age-1 pollock may be affected by not only water temperature (Hypothesis 3, Table 2.7), but also their exposure to predation, either through removals, or through behavioral responses to the presence of predators (Sogard and Olla, 1993). Displacements of juvenile pollock from surface waters will make them unavailable to predators such as kittiwakes that are restricted in their foraging to the very surface of the water column, while displacements in the horizontal from the vicinity of rookeries and colonies will diminish their value to central place foragers as a function of the distance travelled from the central place. After the biomass of adult pollock increased near the Pribilof Islands, the biomass of age-1 pollock there dropped precipitously (Hunt *et al.*, 2002a, Fig. 2.12). There remains a need to understand the role that adult pollock play in determining not only the abundance, but also the distribution of forage fishes, including age-1 pol-

lock, and their availability to upper trophic level predators including marine mammals and seabirds.

2.6 Summary of Advances

Many of the important advances in our understanding of the coupling of regional atmospheric processes, physical processes in the Bering Sea, and biological responses to these forcing mechanisms have been the subjects of recent review (Stabeno *et al.*, 2001; Overland *et al.*, 2002; Schumacher *et al.*, 2003). Among these advances in our knowledge are:

2.6.1 Marine climate

1. A new understanding of the importance of warm-season climate (Overland *et al.*, 2001; Bond and Adams, 2002).

2.6.2 Basin and slope waters

1. An improved understanding of the function of the Aleutian North Slope Current and the Bering Slope Current (Reed and Stabeno, 1999; Stabeno *et al.*, 1999a; Johnson *et al.*, 2004), and their potential importance to fish (Reed, 1995);

2. Documentation of eddies over the slope (Schumacher and Stabeno, 1994; Okkonen, 2001) and along the outer shelf (Reed, 1998) and their importance as habitats for fish and for the transport of small pollock onto the shelf (Schumacher and Stabeno, 1994);

3. Development of a model that resolves eddies and suggests that the source of eddies in the southeastern Bering Sea basin is in the Bering Slope Current (Hermann *et al.*, 2002).

2.6.3 Shelf waters

1. Discovery of mean flows across the shelf (Reed and Stabeno, 1996; Reed, 1998), which for short intervals in summer can result in replenishment of salts and transport of oceanic zooplankton to the Inner Front (Stabeno *et al.*, 2001; Coyle and Pinchuk, 2002b);

2. A clarification of the role of the timing of ice retreat for the timing and fate of the spring bloom (Stabeno *et al.*, 2001; Hunt *et al.*, 2002a; Hunt and Stabeno, 2002);

3. Understanding of the relative importance of winter and warm season conditions for determining the timing and strength of spring stratification and the potential for summer mixing across the pycnocline (Ladd *et al.*, unpublished manuscript);

4. An understanding of the temporal and spatial variability of the Inner Front and its role in nutrient fluxes from depth (Kachel *et al.*, 2002);

5. A greater appreciation for the role of water temperature in the distribution of fish, especially pollock (Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1996; Wyllie-Echeverria and Wooster, 1998), the hatching time of pollock eggs (Blood, 2002), and the population dynamics of zooplankton (Coyle and Pinchuk, 2002a, b);

6. A greater appreciation for the role of episodic events in structuring the ecosystem;

7. A new hypothesis concerning the role of wind-forced transport for the survival of juvenile walleye pollock (Wespestad *et al.*, 2000).

2.6.4 Biological components of the ecosystem

1. Evidence that the net annual primary production in the northern Bering Sea may be declining (Schell, 2000; Grebmeier and Cooper, 1994; Grebmeier and Dunton, 2000), whereas in the southeastern Bering Sea, increases in standing stocks of fish and non-crab benthic invertebrates do not suggest a decline in production (Conners *et al.*, 2002);

2. Commencement of research on the role of nanno- and microplankton, including coccolithophores, in the marine ecosystem of the southeastern Bering Sea (Howell-Kubler *et al.*, 1996; Olson and Strom, 2002);

3. Re-examination of the *Oshoro Maru* zooplankton time series shows no evidence for a significant decline in zooplankton biomass within samples stratified by the domain in which they were collected (Hunt *et al.*, 2002a; Napp *et al.*, 2002);

4. Immense increases in the biomass of large jellyfish and then a rapid decline to levels seen in the early 1980s (Brodeur *et al.*, 1999a, 2002);

5. Observations of responses of crustacean zooplankton to variations in water temperature, including apparent shifts in the timing of breeding in shelf euphausiids (Coyle and Pinchuk, 2002a), and the abundance of small shelf copepods (Coyle and Pinchuk, 2002a; Napp *et al.*, 2002);

6. Determination that large cetaceans are now encountered more frequently in shelf waters than in the 1970s, and that substantial numbers are present over the shelf (Baretta and Hunt, 1994; Moore, 2000);

7. Progress in developing understanding of climate effects on flatfish recruitment (Wilderbuer *et al.,* 2002);

8. Progress in defining multiple hypotheses concerning the control of year-class strength in walleye pollock (Table 2.7; Section 4 of this report);

9. Improved understanding of the foraging habits and diets of marine birds, northern fur seals, and Steller sea lions at the Pribilof Islands; the potential relationships between the abundance of adult pollock over the shelf and the reproductive success of black-legged kittiwakes at the Pribilof Islands (Sinclair *et al.*, in preparation);

10. Evidence that sub-lethal food stress during the breeding season can lead to elevated levels of corticosteroids, and possibly elevated levels of post-breeding season mortality in seabirds (Kitaysky *et al.*, 1999b, 2001a, 2002);

11. Development of a mechanistic explanation of how variations in climate could cause shifts in the mechanisms controlling walleye pollock populations (Oscillating Control Hypothesis, Hunt *et al.*, 2002a).

2.7 Areas of Research Requiring More Attention

Although a great deal of progress in understanding the forcing mechanisms and the ecosystem responses of the southeastern Bering Sea has been made since the early 1990s, there are still many unanswered questions that demand attention if we are to provide good stewardship for the resources of the Bering Sea shelf. Answers to these questions go beyond academic value; we need to understand the processes and mechanisms that determine how changes in global climate and the associated physical forcing affect the flow of energy to upper trophic level organisms including commercially valuable fish and shellfish, marine mammals, and seabirds. Below are listed a number of questions that require attention.

1. How do atmospheric forcing mechanisms influence the distribution and transport of salts, heat, nutrients, and organic matter in the eastern Bering Sea?

   (a) How does atmospheric forcing influence the distribution, abundance, and magnitude of eddies?

   (b) How does atmospheric forcing affect cross-shelf flow? Do the mechanisms whereby climate affects cross-shelf flow vary seasonally? What are the time scales of primary importance?

   (c) How does one scale up and down between large-scale atmospheric processes and the biological processes critical to the production regimes of the eastern Bering Sea?

2. How is the timing and magnitude of cross-shelf flux controlled?

   (a) What are the relative contributions of summer and winter cross-shelf fluxes for renewal of nutrients on the eastern Bering Sea shelf?

   (b) What is the relative importance of flow up canyons, movement in eddies, and other mechanisms of cross-shelf flux?

   (c) What is the relative importance of nutrients provided by wintertime on-shelf advection and nutrients that have been remineralized by benthic processes? Are the estimates provided by Sambrotto *et al.* (1986) still useful?

3. How do different patterns in the formation, thickness, extent, and meltback of sea ice influence the ecosystems of the eastern Bering Sea shelf?

(a) How does the pattern of ice melt-back affect the timing and type of phytoplankton bloom? Do these mechanisms work in similar ways in the southern and northern Bering Sea?

(b) Do open-water blooms occur in the northern Bering Sea? If so, are they as important as the ice-related blooms?

(c) Are ice-related blooms shorter and more intense than open-water blooms? When both are potentially present, which is likely to fix more carbon?

(d) How do ice formation and melt-back interact with cross-shelf advection of warm water in winter to determine the temperature and extent of the southern cold pool?

4. What controls the amount and fate of primary production?

   (a) Has primary production decreased over the southeastern Bering Sea shelf?

   (b) For the cold-adapted species of the Bering Sea, are zooplankton growth and production more sensitive to temperature than phytoplankton productivity, as is assumed in the hypothesis of Walsh and McRoy (1986)?

   (c) Does significantly more phytoplankton sink to the bottom in cold years than in warm years, as hypothesized by Walsh and McRoy (1986)?

   (d) How do the nanno- and microplankton affect the flow of energy in the southeastern Bering Sea? Are they directly or indirectly important prey for either larval or juvenile walleye pollock?

   (e) How do coccolithophores affect energy flow in the southeastern Bering Sea? Why did they suddenly bloom, and then as suddenly disappear after blooming consecutively for 5 years?

5. What controls the biomass and productivity of upper trophic level organisms?

   (a) How do plankton predators such as chaetognaths, ctenophores, and larger jellyfish affect the flow of energy in the eastern Bering Sea? Why did the population of large jellyfish increase and then crash? Are they significant competitors or predators on juvenile pollock and other forage fish?

   (b) How does temperature affect the role of chaetognaths, ctenophores and larger jellyfish as predators of crustacean zooplankton?

   (c) How can one account for the simultaneous increase of round-fish, flatfish, and non-crab invertebrates over the shelf of the southeastern Bering Sea (Conners *et al.*, 2002)?

   (d) How variable is the abundance of mesopelagic fish and squids in the eastern Bering Sea? What are the ramifications of this variability for their use by commercially valuable fish, marine mammals and seabirds?

6. How can we translate information about Bering Sea ecosystems into products useful to those who are managing the fisheries of the eastern Bering Sea?

   (a) What factor or factors control year-class size in walleye pollock? The most promising hypotheses, such as those listed in Table 2.7, need to be tested systematically.

   (b) There is a need to test the underlying assumptions and predictions of the Oscillating Control Hypothesis (Hunt *et al.*, 2002a). In particular, are zooplankton grazers closely coupled with phytoplankton in any season, and does this coupling affect their availability to larval or juvenile pollock? Likewise, are larval or juvenile pollock closely coupled to zooplankton in any season?

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