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Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem

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ABSTRACT

The southeastern, middle shelf of the Bering Sea has exhibited extreme variability in sea ice extent, temperature, and the distribution and abundance of species at multiple trophic levels over the past four decades. From 1972–2000, there was high interannual variability of areal extent of sea ice during spring (March–April). In 2000, this shifted to a 5-year (2001–2005) period of low ice extent during spring, which transitioned to a 4-year (2007–2010) period of extensive sea ice. High (low) areal extent of sea ice in spring was associated with cold (warm) water column temperatures for the following 6–7 months. The ocean currents also differed between warm and cold years. During cold years, the monthly-mean currents over the shelf were largely westward, while in warm years the direction of currents was more variable, with northward flow during December–February and relatively weak flow during the remainder of the year. The types and abundance of zooplankton differed sharply between warm and cold years. This was especially true during the prolonged warm period (2001–2005) and cold period (2007–2010), and was less evident during the years of high interannual variability. During the warm period, there was a lack of large copepods and euphausiids over the shelf; however, their populations rebounded during cold period. Small crustacean zooplankton taxa did not appear to vary between and warm and cold years. For both walleye pollock and Pacific cod, year-class strength (recruitment) was low during the prolonged warm period, but improved during the following cold period. Year-class strength did not appear to vary as a function of warm and cold years during the period of high year-to-year variability. Also, recruitment of arrowtooth flounder (a predator of pollock and cod) did not appear influenced by the warm or cold years. Finally, the distribution and relative abundance of fin whales appeared to differ in warm and cold years, with fewer whales on the southeastern, middle shelf during warm years.

1. Introduction

The southeastern Bering Sea (Fig. 1) supports productive marine ecosystems and extraordinarily rich marine resources. These resources include vast numbers of marine birds and mammals, including federally protected species, and productive fish stocks, which generate more than 40% of all finfish and shellfish landings in the United States. These fisheries employ local and itinerant fishers, processors, and distributors within and outside of the region. The Bering Sea is also directly or indirectly the source of over 25 million pounds of subsistence foods used by nearly 55,000 local residents, primarily Alaskan Natives, in small rural communities. As the Bering Sea responds to variations in climate, its ability to provide resources to humans may change.

The eastern Bering Sea shelf is >500 km wide and extends northward >1000 km from the Alaska Peninsula to Bering Strait. The southeastern portion of this shelf (south of 58°N) is divided into coastal, middle, and outer subregions, or domains (Coachman, 1986). The focus of this paper is the middle shelf, south of 58°N, where the

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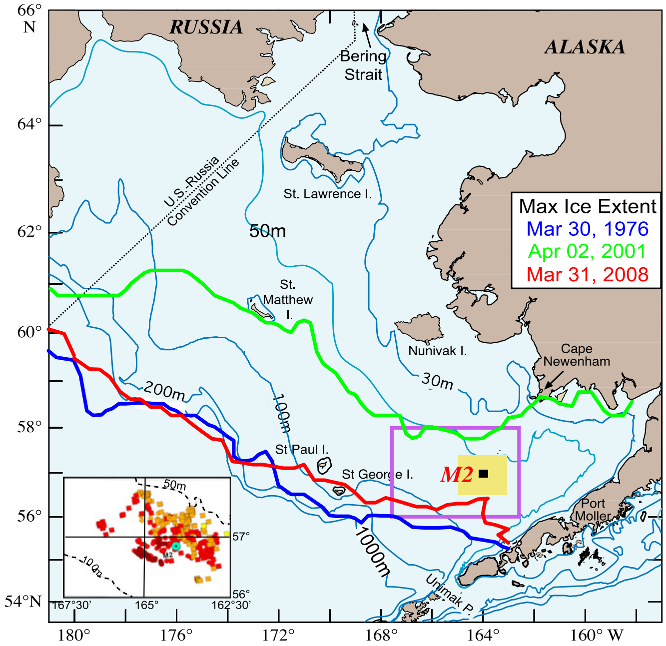

Fig. 1. Map of the eastern Bering Sea shelf. Maximum ice extent is shown for three years: 1976, one of the most extensive ice years on record; two years from our study, 2001, with very low ice extent, and 2008, with very extensive ice. The yellow box is the region for which ice statistics were calculated (Fig. 2). The inset in the lower left shows the daily positions of a North Pacific right whale tagged with satellite-transmitter from August–October 2008 and for three whales tagged for various periods during July–September 2009. In the inset, the different colors represent different months: orange is August, red is September, and brown is October. The location of M2 is indicated by a green dot. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

water depth ranges from approximately 50 to 100 m. In winter, the water column is usually well-mixed, but in summer it is characterized by a well-defined, two-layer structure. The wind-mixed surface layer is typically 20–30 m thick, while the bottom layer is tidally mixed. In warm months, the middle shelf is separated from the inshore, well-mixed coastal domain by the Inner Front, and from the offshore, outer shelf domain by the Middle Transition Zone (Kachel et al., 2002).

Physically, the middle shelf serves several functions in structuring the Bering Sea ecosystem. During summer, the bottom layer remains nutrient-rich and supplies nutrients to the euphotic zone through summer storms that deepen the surface mixed layer (Sambrotto et al., 1986). It can also provide nutrients along the Inner Front, where nutrient-rich bottom waters abut weakly stratified, nutrient-poor coastal waters (Kachel et al., 2002). Once the water column on the middle shelf stratifies (in April or May), the surface insulates the bottom layer from warming. The bottom layer warms only slightly during the summer months (Stabeno et al., 2002, 2007). Thus, the temperature of the bottom layer depends upon the temperature of the water column at the time that the two-layer structure forms. In cold years (with extensive spring ice through April) the bottom layer, or cold pool, temperature remains below 2 °C for the entire summer. In years with early ice retreat (before early March) the bottom layer temperature is often >2 °C. The cold pool acts as a cross-shelf migration barrier for subarctic fish species (e.g., walleye pollock and Pacific cod), forcing these fish to remain on the outer shelf and separating them from food sources in the middle shelf and coastal domain (Kotwicki et al. 2005; Ciannelli and Bailey, 2005). Also, in years with an extensive cold pool, populations of arctic species (e.g., Arctic cod, snow crab) may use the cold pool as a conduit to the southeastern shelf.

The maximum southerly extent of sea ice can vary among years by >100 km, and in years with extensive ice cover, the marginal sea ice zone can cover almost the entire southern Bering Sea shelf (Fig. 1). The eastern Bering Sea responds rapidly to climate change (e.g., Napp and Hunt, 2001), and as a subarctic sea, it is predicted to be sensitive to such changes (IPCC, 2007). With the continued warming of the climate, sea ice over the southern Bering Sea shelf will become less common in the spring, resulting in warmer ocean temperatures (Schumacher et al., 2003; Stabeno et al., 2006, 2012). Longer periods of continuous warm conditions will likely have profound impacts on the southeastern Bering Sea ecosystem.

The focus of this article is the middle shelf of the southeastern Bering Sea, because, with its annually varying marginal ice zone, it is the region of the Bering Sea that is most susceptible to climate change (Stabeno et al., 2012). Located at the center of this region is a biophysical mooring site (M2, Fig. 1) where data have been collected nearly continuously since 1995. Advection is weak on the middle shelf; therefore, a mooring here permits the investigation of local processes, especially during the summer (Stabeno et al., 2010). The location of the mooring was chosen in 1995 with the expectation that it would be covered by sea ice for at least a short time most years and would therefore document physical alterations to the ecosystems caused by the presence (or absence) of ice.

In this manuscript, we present an analysis of the importance of sea ice to the southeastern Bering Sea ecosystem. We then focus on the physical (temperature, salinity, currents, and vertical structure) characteristics of the ocean. A five- to six-year period of warm conditions followed by a four-year period of cold conditions provides an opportunity to study how this ecosystem might respond to a permanent shift to warm conditions resulting from climate change. We close with some examples of how sea ice and physical components affected the biological (e.g., chlorophyll fluorescence, zooplankton, fish, and whales) aspects of this shelf ecosystem.

2. Data and methods

2.1. Sea ice

Two sources of sea ice data were used. The first source was the National Ice Center (NIC, http://www.natice.noaa.gov), with data available from 1972 to 2005. The second source was the Advanced Microwave Scanning Radiometer EOS (AMSR, http://n4eil01u.ecs.nasa.gov:22000/WebAccess/drill?attrib=esdt&esdt=AE_SI12.2&group=AMSA), with data available from 2002 to 2010. These two data sets cover the entire period (1972–2010) in which high quality data of sea-ice extent and areal concentration are available.

NIC data from 1972 to 1994 are from their publically available CD of data on a 0.25° grid. Later data (1995–2005) were downloaded from their website and interpolated to the same positions. NIC data are derived from a variety of sources including the Advanced Very High Resolution Radiometer (AVHRR) aboard the Polar Orbiting Environmental Satellites (POES). AMSR data consist of daily ice concentration data at 12.5 km resolution, which are available from the National Snow and Ice Data Center (NSIDC) website.

2.2. Moorings

Moorings have been maintained at M2 almost continually since 1995 (Stabeno et al., 2010). During each deployment cycle, two to four moorings were deployed within a kilometer of each other. Moorings were recovered and redeployed twice a year, once in the spring (April/May) and again in the late summer or early fall (September/October). The main mooring was constructed of heavy chain to help protect it from loss due to sea ice and the heavy fishing pressure in the region. Data collected by instruments on the moorings included temperature (miniature temperature recorders, SBE-37 and SBE-39), salinity (SBE-37), nitrate and chlorophyll fluorescence (WET Labs DLSB ECO Fluorometer). Temperature was measured approximately every 3 m in the upper 30 m and every 5–7 m below 30 m. Currents were measured using an upward-looking, bottom-mounted, 300 or 600 kHz (Teledyne RD Instruments) acoustic Doppler current profiler (ADCP) on a separate nearby mooring. Data were collected at least hourly and all instruments were calibrated prior to deployment. The data were processed according to manufacturers' specifications.

During autumn, winter, and early spring, the shallowest instrument was at ~11 m. During late spring to early autumn (the ice-free period), the mooring at M2 included a surface toroid buoy with an aluminum tower where a full suite of meteorological variables was measured. This surface mooring permitted measurement of ocean temperature and salinity at a depth of ~1 m.

2.3. Hydrography

Conductivity–temperature–depth (CTD) data were collected on all mooring recoveries and deployments and were used for quality control of the data collected by instruments on the moorings. CTD measurements were made with a Seabird SBE 911plus system with dual temperature and salinity, oxygen (SBE-43), PAR (Biospherical Instruments QSP-200 L4S or QSP-2300) and chlorophyll fluorescence sensors (WET Labs WETStar). Data were recorded during the downcast, with a descent rate of 15 $\mathrm{m\,min^{-1}}$ to a depth of 35 m, and 30 $\mathrm{m\,min^{-1}}$ below that. Salinity calibration samples were taken on most casts and analyzed on a laboratory salinometer.

Samples for extracted chlorophyll-*a* were collected during CTD casts and filtered through glass fiber filters (nominal pore size 0.7 μm), then frozen at −80 °C until analysis. Frozen chlorophyll samples were analyzed in Seattle, Washington. Filters were extracted in 90% acetone at –80 °C in the dark for ~24 h, briefly centrifuged, and then chlorophyll concentrations were estimated by fluorometery using a calibrated Turner TD-700 fluorometer. We determined chlorophyll-*a* and phaeopigment concentration by the difference in fluorescence between the original and an acidified sample (Parsons et al., 1984).

Conversion of in vivo fluorescence to extracted chlorophyll was performed for both the moored and CTD fluorescence sensors using the nominal relationships provided by the manufacturer for each instrument during annual service. Those relationships are meant to provide a means of comparing the fluorescence from different sensors and an estimate of the amount of in situ chlorophyll. It is acknowledged that the relationships provided by the manufacturer cannot represent the range of species and physiological states of the cells found in our samples.

2.4. Zooplankton

Two different data sets were used for our analyses. The first data set is a time series of zooplankton biomass (wet weight) for the eastern Bering Sea shelf that was maintained by scientists at Hokkaido University from 1955 to 2009. Zooplankton samples were collected during summer from the T/S *Oshoro Maru* with vertical tows of a NORPAC net equipped with 0.333 mm mesh and a calibrated TSK flow meter (e.g., Anonymous, 2002). Samples from this platform were collected day and night from near bottom to the surface. The location of stations over the shelf was variable until 1995 after which a grid of stations in the southeastern Bering Sea was established (Fig. 1c in Napp et al., 2002). Only samples collected over the middle shelf (50–100 m water depth) were used in these analyses. This grid of stations was to the north and west of M2.

A time series for the abundance of individual zooplankton taxa (1998–2009) was assembled from an independent data source. These data were collected by NOAA's Ecosystems and Fisheries Oceanography Coordinated Investigations (EcoFOCI) Program. Samples were collected annually during the summer from several different vessels with double-oblique tows of paired bongo frames (60-cm frame with 0.333 mm mesh and 20-cm frame with 0.150 mm mesh). Tows extended from the surface to within 5 m of the bottom and were conducted day and night. Each net mouth contained a calibrated General Oceanics mechanical flow meter. The samples were preserved in a sodium borate-buffered 5% formalin–seawater solution and then sent to the Polish Plankton Sorting and Identification Center (Szczecin, Poland) for processing. Organisms were identified to the lowest possible taxonomic level and then enumerated. All enumerated organisms were returned to the Alaska Fisheries Science Center (AFSC) in Seattle, Washington, for quality control. Until 2006 samples were collected on the same station grid as was used by the *T/S Oshoro Maru* for the wet weight data. Beginning in 2006 the station locations varied, but were always south of 60°N.

For both data sets the means and standard errors were calculated on fourth root-transformed data before being back transformed. Replicate tows within a year range from a low of 2 or 3 to a high of 17 for wet weight and a maximum of 21 for abundance, although most years have fewer than 10 samples.

2.5. Fish

We used estimates of year-class recruitment and population abundance for walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), and arrowtooth flounder (*Atheresthes stomias*) from NOAA fisheries stock assessments (Ianelli et al., 2010; Thompson et al., 2010; Wilderbuer et al., 2010). In these stock assessments, year-class recruitment and population abundance were estimated using age-structured population models based on catch and age information from fisheries, and abundance and age information from fisheries-independent standard NOAA bottom trawl and acoustic midwater trawl surveys (Honkalehto et al., 2009; Hoff and Britt, 2011). The abundance time series ended in 2010, and fisheries data available at the time this manuscript was developed. The recruitment time series ended earlier than 2010, because the youngest fish were not available to the NOAA surveys or fisheries, and their abundance cannot be estimated until each species becomes available to be captured by standard trawls. For pollock and cod, the youngest fish available to the fisheries-independent surveys are age 1, and for arrowtooth flounder, age 2. Thus the recruitment time series ended in 2009 for pollock and cod, and in 2008 for arrowtooth flounder.

2.6. Baleen whales

To examine variability in occurrence of fin (*Balaenoptera physalus*) and humpback (*Megaptera novaeangliae*) whales, distribution and encounter rates (ER) for each species were obtained from aerial survey data during a cold (1999) and a warm (2002) year (Friday et al., 2012). Surveys were conducted in July of each year, in a region of the Bering Sea middle shelf where North

Pacific right whales (*Eubalaena japonica*) are often seen (LeDuc et al., 2001). Only sightings made while on-transect were used in the comparison, to reduce potential bias from sightings made while circling or while in transit between transects, or to and from the survey area. In addition, the seasonal occurrence and distribution of North Pacific right whales in the vicinity of M2 were obtained from passive acoustic recorders during 2000–2005 (Munger et al., 2008) and from filtered Argos satellite locations from whales tagged with location-only transmitters in the warm year, 2004 (Wade et al., 2006), and cold years, 2008 and 2009 (e.g., Zerbini et al., 2010).

3. Observations

3.1. Sea ice

To illustrate the interannual variability in ice cover near M2, we calculated time series of mean ice concentration in a box roughly 100 km on a side centered at M2 (Fig. 1). AMSR and NIC data overlap during the four-year period 2002–2005, during which time they have very similar values (Fig. 2). To span the period 1972–2010, we use both NIC and the AMSR data, using the average value in the overlap years.

The concentration of sea ice on the southern Bering Sea shelf varies on time scales ranging from daily to millennial. We focus on annual to multi-decadal scales of variability. While the southeastern Bering Sea is ice free during the summer and much of the fall, during the winter and spring, pack ice is a common feature. Typically ice appears on the southern middle shelf in mid-December, reaches a maximum in February and March and is gone by mid-May (Fig. 3).

Some years (e.g., 2000), ice came early and covered the eastern shelf in January and retreated in early February. In other years (e.g., 2002), ice only covered the northern part of the shelf. In still other years (e.g., 1976), ice arrived early and persisted well into May. Historically (1972–present), the highest concentrations of sea ice over the southern shelf were in the period 1972–1976, followed by ~25 years when the average annual concentration was moderate (Fig. 2A). From 2001 to 2006 there was a prolonged period with virtually no ice around M2. During the last four years, 2007–2010, conditions have turned very cold, with extensive ice each year.

A critical time for the ecosystem is March and April. When sea ice is present during this time there tends to be an early phytoplankton bloom (Stabeno et al., 2002, 2007, 2010) and cold ocean temperatures, which result in the cold pool extending to south of M2 (Wyllie-Echevarria and Wooster, 1998). From 1973 to 2000, there was considerable interannual variability in the amount of sea ice around M2 during March and April (Fig. 2B). This is not surprising, since M2 was chosen to be within, but near the edge of the ice field. What is surprising was that during the springs of 2000–2006, the maximum ice extent was consistently north of M2. In sharp contrast, during the springs of 2007–2010, M2 was well within the sea ice field. From 1972 to 1999, spring

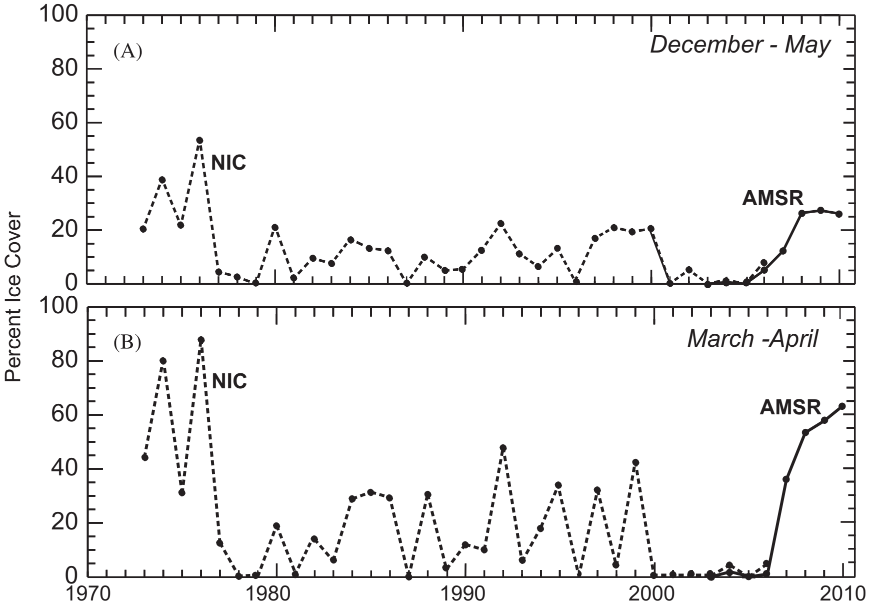

Fig. 2. The average amount of total ice cover in a 2° by 1° box (163–165°W, 56.5°–57.5°N) around M2 and shown in Fig. 1. (A) The percent of ice cover from December–May of each year, and (B) the percent of ice cover only in March and April.

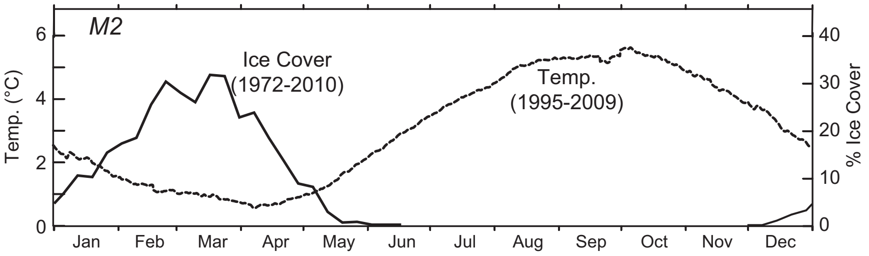

Fig. 3. Sea-ice concentration in the 2° longitude by 1° latitude box around M2 during 1972–2010 (dashed line) and mean depth-averaged temperature (solid line) at M2 during 1995–2009.

Table 1
Years categorized by sea ice and depth-averaged water temperature in the Southeastern Bering Sea.

Spring Sea ice	
1995–99	High interannual variability; low to high sea ice extent/concentration
2000–06	Low interannual variability; minimal sea ice extent/concentration
2007–10	Low interannual variability; high ice extent/concentration
Depth-averaged ocean temperature	
Cold	1995, 1997, 1999, and 2007–10
Average	1996, 2000, 2006
Warm	1998, 2001–05

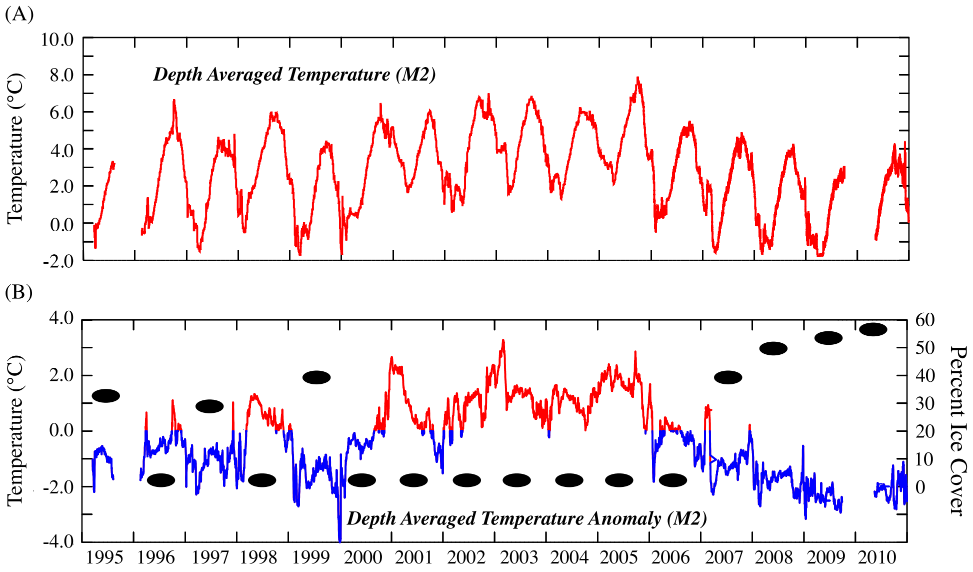

Fig. 4. Daily, depth-averaged (A) temperature and (B) temperature anomaly. The ovals in the bottom panel indicate the percent of ice coverage in March and April and are obtained from Fig. 2.

ice extent varied annually, while in the last decade, a multi-year pattern dominated the signal at M2. Thus the period 1995–2010 provides three separate periods with very different temporal patterns in the extent of sea ice: 1995–1999 high year-to-year variability; 2000–2006 low year-to-year variability with minimal ice coverage; and 2007–2010 low year-to-year variability with high ice coverage (summarized in Table 1). These patterns provide an opportunity to investigate how both the temperature (warm versus cold) and changes in the integral time scales of spring ice extent affect different trophic levels within the Bering Sea ecosystem.

3.2. *Mooring observations—temperature and fluorescence*

The moorings at M2 show the evolution of temperature over the middle shelf of the Bering Sea for the last 16 years. Depth-averaged temperatures had a strong seasonal signal (Fig. 4A). Average temperature reached a minimum in April as the sea-ice typically began its retreat, and a maximum in late September or early October (Fig. 3). Average temperatures increased ~1.2 °C per month from mid-April through late August. The interannual variability, however, was large, and the maximum temperature each year was related to initial temperatures in spring (Fig. 4A). Cold temperatures in spring resulted in cooler temperatures in late summer (and vice versa). When ice was present, the depth-averaged temperature was usually near −1.76 °C. When ice retreated, temperatures often quickly increased by ~1 °C due to advection. In years with extensive, late ice (e.g., 2009 and perhaps 1995), the summer maximum depth-averaged temperatures were below 4 °C. In years with little ice (e.g., 2002, 2005) maximum depth-averaged temperatures could reach 7–8 °C.

Subtracting the annual mean (1995–2009, Fig. 3) from the depth-averaged temperature (Fig. 4A) yields the depth-averaged temperature anomaly (Fig. 4B). The warm period (2001–2005) and the cold period (2007–2010) are distinct with the temperature anomaly related to the presence/absence of sea ice in March and April. Years with sea ice in the March and April tended to have below-average temperatures. Years without ice had either average or above average temperatures throughout the year. One reason that some of the years with little sea ice in the March–April were cooler than others was due to presence of ice (resulting in colder ocean temperatures) in February, or even in January (e.g., 2001, 2006).

At M2, most of the vertical stratification is due to temperature (Ladd and Stabeno, 2012; Stabeno et al., 2010), so an examination of temperature alone is sufficient for describing the structure of the water column (Fig. 5). The extensive ice in 2007–2010 was reflected in the very cold temperatures measured at M2. In most years, the water became well mixed after the retreat of sea ice, although there were exceptions (e.g., 1999, 2009). Hence, there usually was not a freshwater lens that initiated stratification in the spring over the southern shelf. In years without ice, water temperatures remained generally above 1.5 °C. In some years, stratification began as early as April (e.g., 1995), but more typically it occurred in May. The two-layer structure persisted through October and sometimes into November (e.g., 2008). In years with extensive ice, the surface temperatures were cold, but so were bottom temperatures. In years with little ice in March or April, the surface temperatures

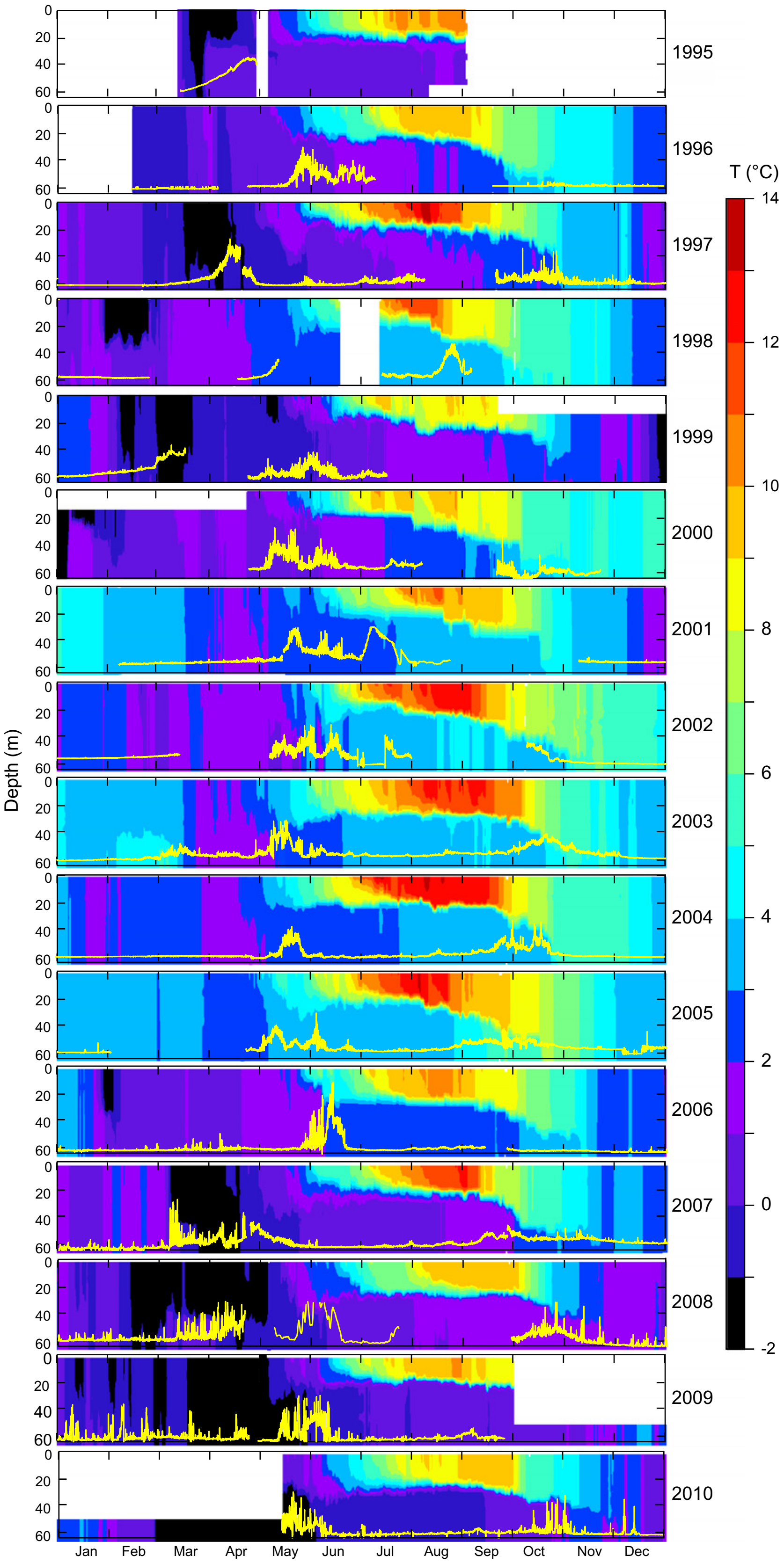

Fig. 5. Evolution of water column temperature measured at M2 during the last 16 years. Instruments typically were at every 3 m in the upper 30 m and every 5–7 m in the bottom 40 m. When temperatures were below −1 °C (black), ice was present at the mooring site. The yellow lines are normalized fluorescence from the fluorometers at ∼11 m.

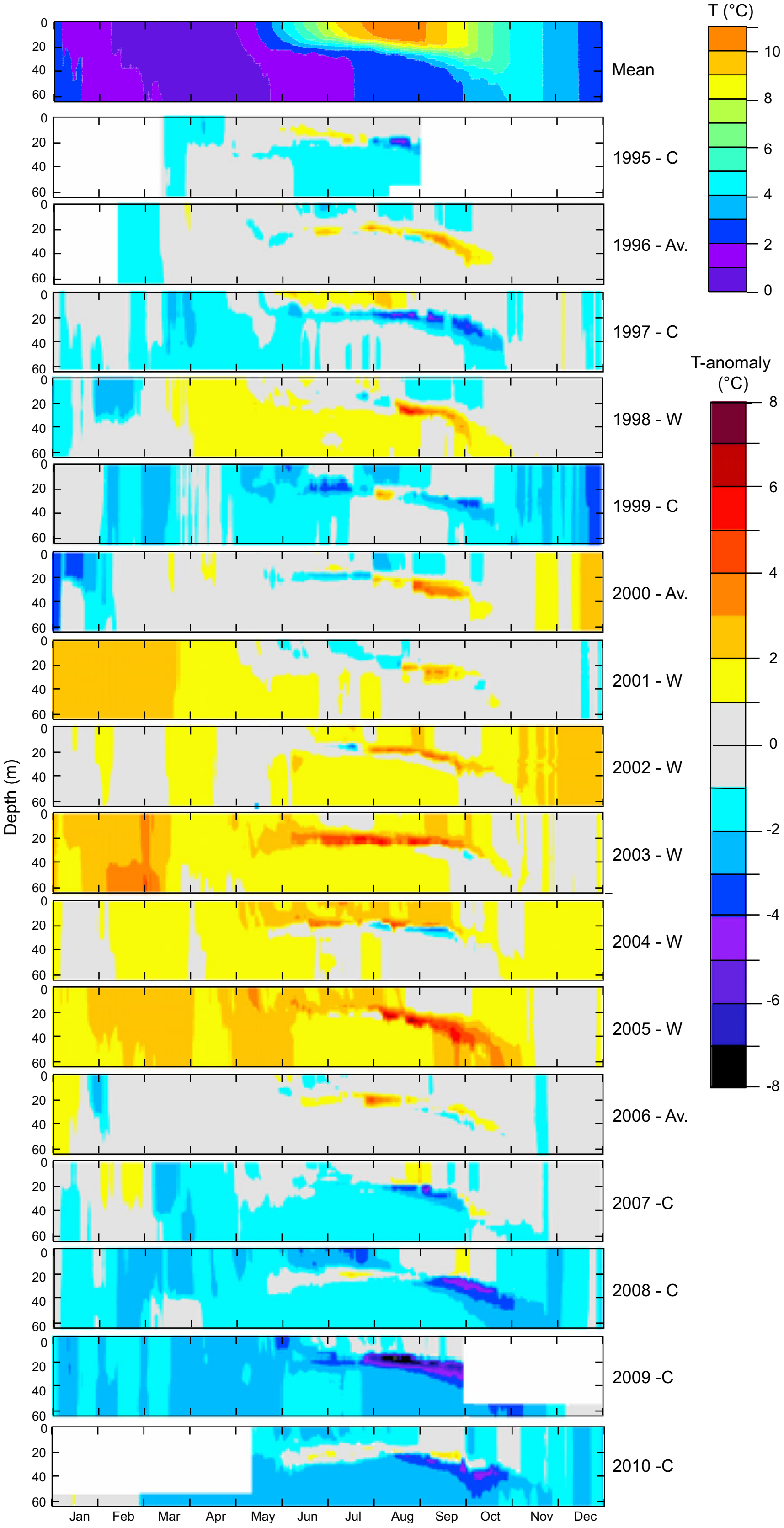

Fig. 6. The average (1995–2009) annual signal of temperature structure at M2 (top panel) and the water column temperature anomaly for each year (1995–2010). The average annual temperature structure (top panel) was subtracted from data shown in Fig. 5 to derive the anomaly. The top color scale refers to the mean temperature and the bottom color scale refers to the 16 annual temperature anomly panels. The labels W, C or Av, to the right of the years indicate warm, cold or average temperatures, respectively.

may have been warmer than average, but bottom temperatures were also warmer than average. Noting this, it is not surprising that the magnitude of vertical stratification over the southern shelf is unrelated to the extent of sea ice (Ladd and Stabeno, 2012).

During years with ice in mid-March or later, a phytoplankton bloom occurred at the site underneath the ice (Fig. 5). In some years (e.g., 2007) this was the only spring phytoplankton bloom. In other years (e.g., 1998, 2008) a later bloom occurred in May or sometimes June. In years without sea ice after mid-March, the spring bloom was delayed until solar heating stratified the water column. In years when sea ice persisted past mid-March, the bloom occurred in cold water (−1.5–2.0 °C), while in years without ice after mid-March the bloom occurred in relatively warm water (5–8 °C). The high variability in fluorescence at 11 m in the winters of 2007–2009 is mimicked by the fluorescence records at ∼30 m (not shown). Since sea ice was present over the mooring (indicated by black in the temperature contours), the high variability in fluorescence probably indicates the phytoplankton were ice algae, blooming underneath the ice and falling to the bottom; this high variability is not seen in blooms in May or June. The high fluorescence observed underneath the ice in our time series can occur when the ice was advancing, retreating or largely stationary. In addition to the blooms in spring, there often was a fall phytoplankton bloom (e.g., 2002–2005, 2008) when September and October storms introduced nutrients to the euphotic zone.

If the mean annual signal (Fig. 6, top panel) is subtracted from the water-column temperature (Fig. 5), we obtain the water-column temperature anomaly (Fig. 6). Using this plus the information in Fig. 4B, the years were divided into three categories: cold (1995, 1997, 1999, 2007–2010); average (1996, 2000, 2006); and warm (1998, 2001–2005). During the spring of each of the cold years, there was significant ice cover, while during the spring of the warm years there was little ice cover (Fig. 2). With the removal of the seasonal temperature signal, the differences in mixed-layer depth are clearly visible during the summer. For instance, in 1996, there were warm temperatures immediately below the surface indicating that the surface mixed layer was deeper than average (Fig. 6). A similar pattern occurred in 1998, 2000–2003, and 2005. In other years (1997, 1999, 2007, 2008, and 2009) there was a colder-than-average layer below the long-term mixed layer, indicating that the mixed layer was shallower than usual or mixing in late summer and early fall was delayed. These patterns indicate that the depth of the mixed layer remained constant for at least several weeks and often persisted from May to September.

3.3. Winds and currents

It is not surprising that the atmospheric pressure patterns differed markedly during warm and cold years (Fig. 7), since it is atmospheric forcing that largely controls the extent of sea ice over the Bering Sea shelf (Pease, 1980; Stabeno et al., 2007). During the recent warm period (2001–2005), the spring wind anomalies (derived from the pressure field in Fig. 7A) were out of the south, resulting in less sea ice. In contrast, during the recent cold period (2007–2010), the spring wind anomalies were out the northwest (Fig. 7B).

To investigate the annual pattern of the winds near M2, the data were divided into four periods or seasons: "winter" (December–February); "summer" (June–August); "spring" (March–May); and "fall" (September–November). The data can also be divided into warm and cold years as defined in Table 1. Average winds are strongest in the "winter" and weakest in "summer" (Table 2). During the "winter" and "summer", the wind speeds during the warm years did not differ greatly from those during the cold years.

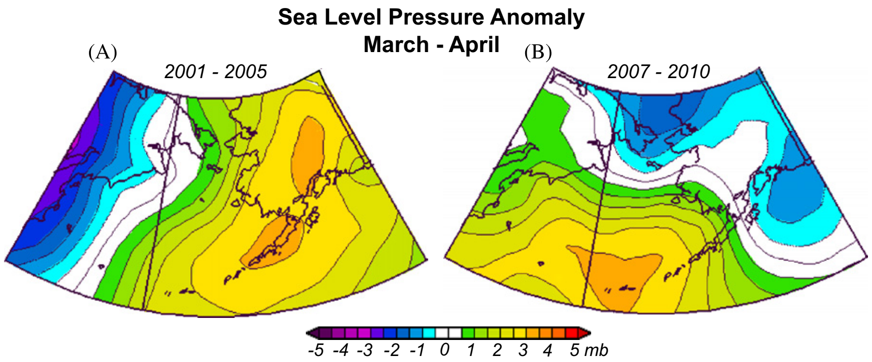

Fig. 7. Sea level atmospheric pressure anomalies. (A) The period of warm years (2001–2005) and (B) the period of cold years (2007–2009). The climatology used to create the anomalies was 1968–1996.

Table 2
The mean seasonal near-surface current and wind velocities for the warm years and for the cold years. The mean *U* and *V* components are given ± the standard error. The units for speed and direction (Dir.) are cm s^{-1} and (°T), respectively.

	December–February		March–May		June–August		September–November	
	Current (cm s^{-1})	Wind (m s^{-1})	Current (cm s^{-1})	Wind (m s^{-1})	Current (cm s^{-1})	Wind (m s^{-1})	Current (cm s^{-1})	Wind (m s^{-1})
Warm years (1998, 2001–2005)								
U	−0.3 ± 0.3	−2.8 ± 0.3	0.2 ± 0.2	−0.8 ± 0.4	0.5 ± 0.3	0.5 ± 0.4	−0.9 ± 0.4	1.2 ± 0.6
V	1.4 ± 0.4	−0.8 ± 0.4	−0.2 ± 0.3	−0.1 ± 0.7	−0.1 ± 0.3	0.6 ± 0.3	−0.5 ± 0.5	−0.3 ± 0.7
Speed, Dir.	1.4, 347°	2.9, 254°	0.3, 135°	0.8, 262°	0.5, 101°	0.8, 40°	1.1, 241°	1.2, 93°
Cold years (1995, 1997, 1999, 2007–2010)								
U	−1.7 ± 0.5	−2.1 ± 0.5	−2.1 ± 0.3	−0.3 ± 0.4	−0.4 ± 0.3	0.9 ± 0.3	−1.8 ± 0.2	0.9 ± 0.4
V	−0.2 ± 0.3	−1.8 ± 0.3	−0.2 ± 0.3	−1.6 ± 0.5	−0.8 ± 0.3	0.7 ± 0.4	−0.5 ± 0.3	−1.6 ± 0.6
Speed, Dir.	1.7, 263°	2.8, 230°	2.1, 264°	1.6, 191°	0.9, 207°	1.1, 52°	1.9, 254°	1.8, 150°

During "spring" and "fall", however, the winds were significantly stronger during cold years than during warm years. During each of the four "seasons", the direction of the winds during the cold years were more southward than during the warm years (Table 2). While the differences were small in "winter" (230° versus 254°) and "summer" (52° versus 40°), they were pronounced in the two transition seasons (191° versus 262° in the "spring", 150° versus 93° in the "fall"). So, during "spring", the winds were almost due southward in the cold years and almost due westward in the warm years. Similarly, during "fall", the winds were southeastward during the cold years and almost due eastward during the warm years.

The currents at M2 vary seasonally, with weaker flow during late spring and summer, and stronger flow during the remainder of the year (Fig. 8). These monthly mean currents differ from those reported in Stabeno et al. (2007), mainly because there are marked differences between the currents during warm and cold years, and with the longer time series there are more cold years than reported earlier. To study how currents varied, the data were divided between warm and cold years as presented in Table 1. Surface currents in warm years were northward in December–February, weak during March–August, and westward during September–November. A similar pattern held for both the shallow and near-bottom flow, although the deeper currents were consistently weaker. In cold years, the near-surface flow was largely westward, except during June–August when currents were southward, but relatively weak. During the cold years, the near-bottom flow was much weaker than the near-surface flow, and the direction also differed. So, the flow during cold years was more baroclinic than during the warm years.

To obtain better statistics, the near-surface current data were divided into the same time periods as the winds (Table 2). Three differences between warm and cold years are clear. In the cold years, the currents had a significant westward component during each "season". During the warm years, there was a significant northward component in the currents during "winter". Finally, currents during the cold years tended to be stronger, particularly during "spring".

3.4. Some implications of the physics on the ecosystem

3.4.1. Zooplankton

Time series of zooplankton wet-weight biomass show both strong interannual variation and a correspondence between biomass and the longer periods of warm and cold (Fig. 9). In the middle shelf domain, total wet weight biomass showed a long-term decline, which began in the late 1980s and early 1990s, and reached minimal values during the warm period of 2001–2005. The exact timing of an apparent long-term decrease is difficult to pinpoint in these data due to the high interannual variability during the period 1989–1991. The biomass during 1989–1991 was distinctly higher than the three years proceeding or following that period. Interestingly, this period of high biomass and variability coincided with low total ice cover around M2 (Fig. 2).

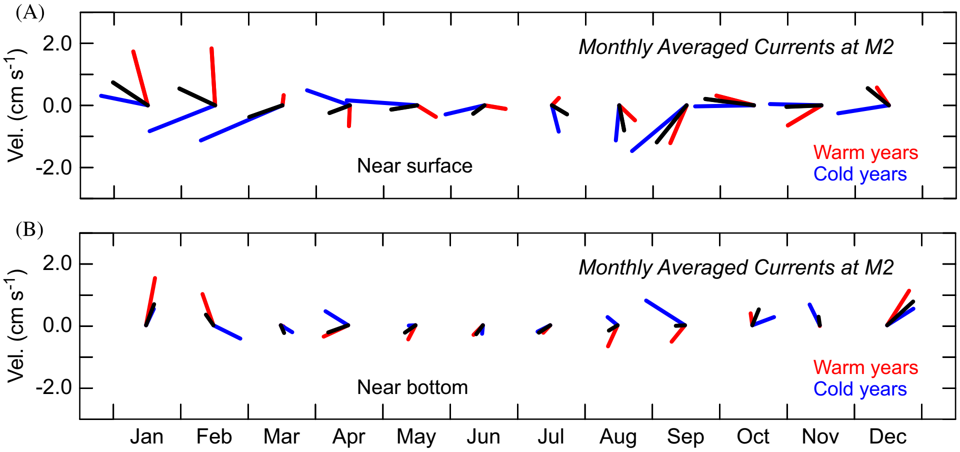

Fig. 8. Monthly mean currents in warm (red) years (1998, 2001–2005) and cold (blue) years (1995, 1997, 1999, 2007–2010). The black lines indicate the average over all available data (1995–2010). The top panel (A) shows near surface current velocity, and the bottom panel (B) shows near bottom current velocity.

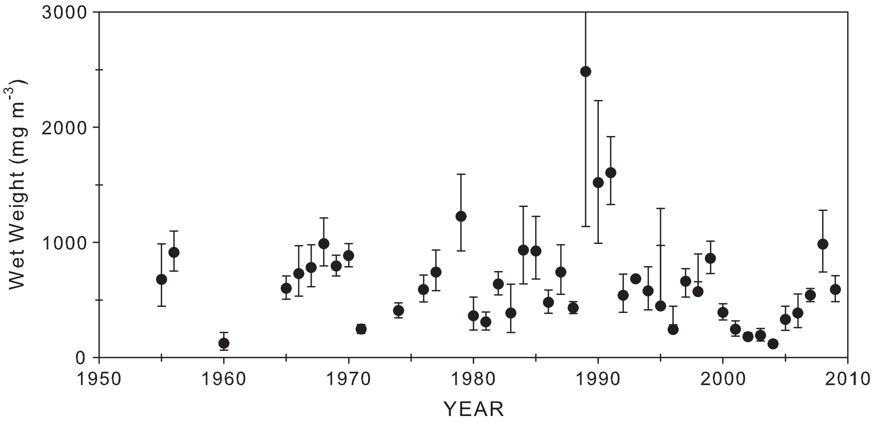

Fig. 9. Time series of zooplankton biomass from the middle shelf of southeastern Bering Sea shelf. Shown are the mean and standard error of zooplankton wet weight.

The biomass in 2000 was distinctly lower than that of 1997–1999 and appears to be the first low biomass year during the recent warm period. The subsequent increase in zooplankton biomass may have begun in 2005, the last warm year or in 2006 a year of average water temperatures. The median biomass during the recent warm years was less than half that during the cold years (218 in 2000–2005 versus 566 mg m^{-3} in 2006–2009).

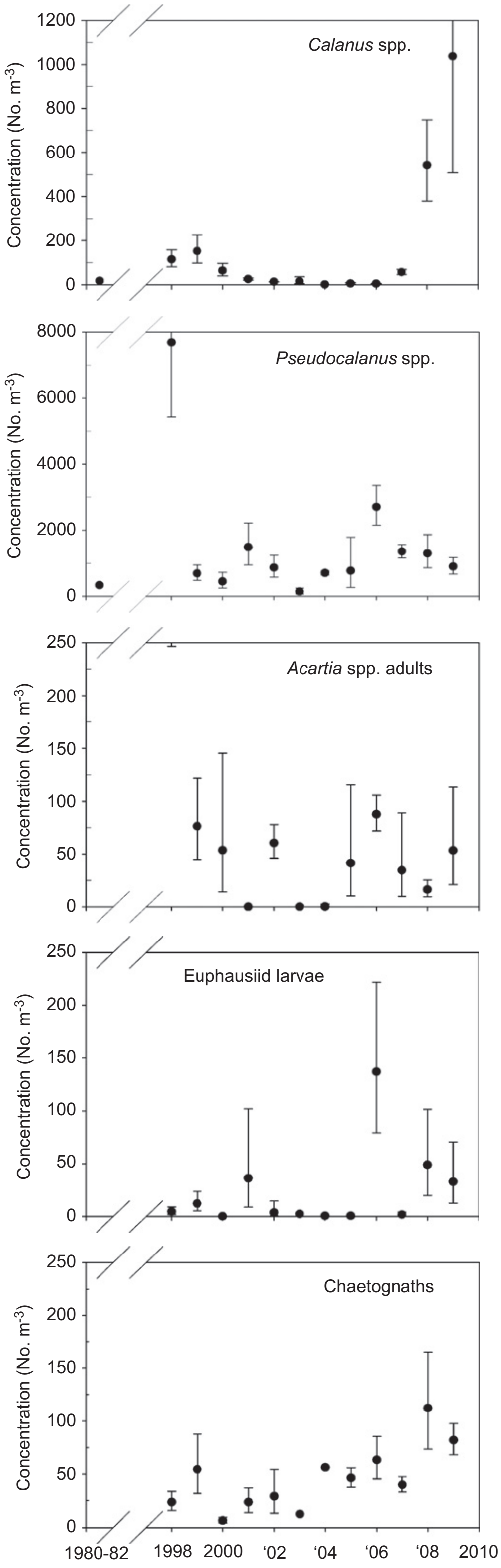

Fig. 10. Time series of zooplankton abundance for selected taxa from the middle shelf domain of the Southeastern Bering Sea. Shown are the mean and standard error. Values prior to 1998 are from PROBES data reports (e.g. Smith et al., 1982).

Individual plankton taxa from the middle shelf exhibited a variety of patterns (Fig. 10). For example, the largest copepod of the middle shelf, *Calanus*, showed a strong correspondence to the multi-year pattern (low in warm years; abundant in cold years), while the small copepods, *Pseudocalanus* spp. and *Acartia* spp. adults, had great variation among years, but no apparent response to the shift from large interannual variability in temperature to longer sustained period of warm and cold. Lack of a patterned response in *Acartia* may be due to low sample sizes in some years (e.g., 2002 and 2004). Euphausiid larvae (nauplii, calyptopae, and furcilia) had high concentrations during the transition year (2006) with relatively high, but decreasing concentrations in 2008 and 2009. These concentrations were much higher than in the warm years. *Chaetognaths* had elevated concentrations in 1999 and 2006–2009, but those values were comparable to those measured in some of the warm years, 2004 and 2005.

3.4.2. Fish

Walleye pollock, Pacific cod and arrowtooth flounder are important pelagic species in the Bering Sea (Aydin et al., 2007). We compared modeled stock-assessment estimates of year-class recruitment and population abundance for these three species to the depth-averaged temperature measured at M2 (Fig. 11).

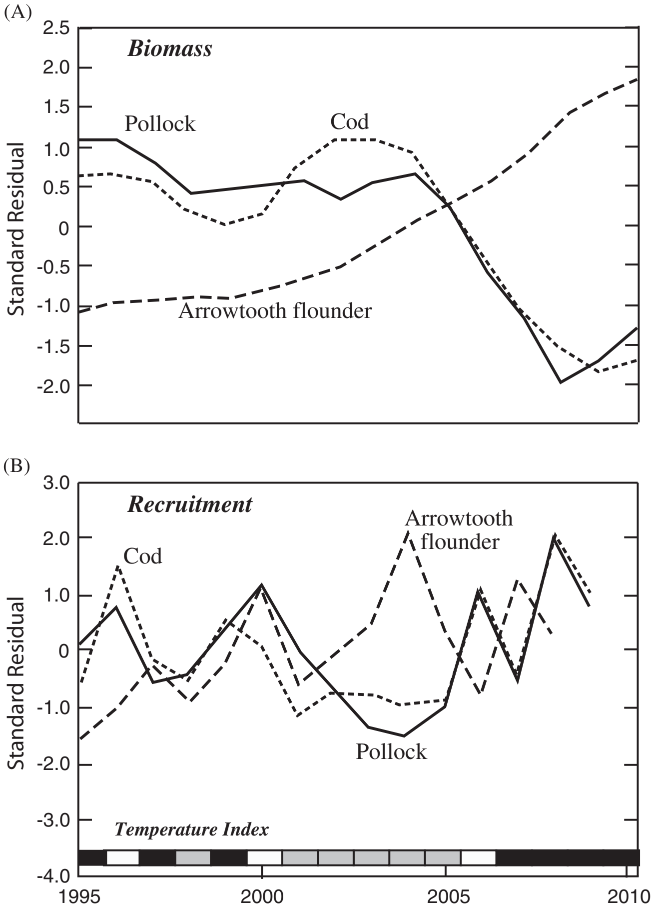

Fig. 11. Shown are the standard residuals of total abundance (A) and year class recruitment (B) of walleye pollock, Pacific cod and arrowtooth flounder for 1995–2010. The standard residuals are defined as the anomaly from long-term mean, standardized by the square root of the mean square error (Neter et al. 1985). The bar at the bottom of panel B indicates whether the year was warm (gray), average (white) or cold (black).

Pollock, cod and arrowtooth flounder are multi-age species, which grow rapidly when young and recruit to the fishery when they are 3–5 years old. As a result, biomass will increase a few years following the appearance of a strong year class.

Recruitment of pollock and cod was below average during the warm years of 2001–2005 (Fig. 11), with standard residuals from the long-term mean averaging −0.92 and −0.90, respectively. In subsequent years when temperatures cooled (2006–2009), recruitment of pollock and cod was higher with standard residuals averaging 0.82 and 0.92, respectively. The values from the warm and cold periods are significantly different (two-sample t-test with $\mathrm{df}=7$, $p=0.016$ for pollock, and $p=0.006$ for cod). The most likely cause of the turnaround was increased abundance of their prey, large copepods (Fig. 10 and Coyle et al., 2011) and euphausiids (Ressler, 2012).

In contrast to the multi-year warm (cold) period with its associated reduced (increased) pollock and cod year-class abundance, the period of high year-to-year variation (prior to 2000) did not show this relationship. During 1995–2000, temperature varied from year-to-year as did year-class abundance, but not in the clear inverse pattern seen for 2001–2009. During 1995–2000, pollock recruitment standard residuals averaged −0.05 (cold years), 0.95 (average years) and −0.43 (warm years). These differences were not significant (ANOVA, $\mathrm{df}=5$, $p=0.10$). Cod recruitment standard residuals averaged −0.07 (cold years), 0.80 (average years), and −0.54 (warm years). These differences were, also, not significant (ANOVA, $\mathrm{df}=5$, $p=0.38$). Arrowtooth flounder recruitment oscillated during 1995–2008, but showed no apparent relationship with temperature. Their standard residuals averaged −0.12 (cold years), −0.25 (average years), and 0.22 (warm years). These differences were not significant (ANOVA, $\mathrm{df}=13$, $p=0.79$). Recruitment estimates are not yet available for arrowtooth flounder in 2009 and 2010 and for pollock and cod in 2010. Once available, these estimates will provide additional information on these species responses to stanzas of cold years.

3.4.3. Baleen whales near M2

Four species of baleen, or filter-feeding, whales occur regularly around M2 in summer and autumn (Wade et al., 2006; Friday et al., 2012). North Pacific right whales prey primarily upon large copepods (Baumgartner and Mate, 2005), while fin, humpback, and minke whales consume large pelagic zooplankton and forage fishes, such as juvenile pollock, capelin, and sand lance (Aydin et al., 2007). To examine variability in occurrence of fin whales with temperature, their distribution and encounter rates (ER) were obtained from aerial survey data during a cold (1999) and a warm (2002) year. There were 18 sightings for a total of 60 fin whales seen in 1999, compared to five sightings of 26 whales in 2002 (Fig. 12). Group and individual encounter rates were 7–12 times higher in the cold year compared to the warm year (Table 3). There were too few data to support a comparison for right, humpback or minke whales. While these data are not definitive, they do suggest that fin whales occurred in greater numbers on the Bering Sea middle shelf in cold years than warm years, presumably because of higher prey availability.

Although critically endangered with a population thought to number only in the tens of individuals (Wade et al., 2010), North Pacific right whales have been seen or heard near M2 since sampling began (Wade et al., 2006; Munger et al., 2008). Visual sampling began in 1997, and acoustic sampling by instruments deployed on M2 started in 2000. As an example, four whales tagged with satellite transmitters in July and August 2008 and 2009 spent 4–7 weeks within a 100 km of M2, probably feeding (inset, Fig. 1). A similar pattern was reported for a single right whale tagged near M2 in August 2004 (Wade et al., 2006). Meanwhile, the calls of right whales, recorded in bouts from May through December in 2000–2005, suggest North Pacific right whales either reside in or pass through the middle shelf of southeast Bering Sea over this eight-month period (Munger et al., 2008). Of note, in 2006 the period and rate of right whale call detections were similar to that described above, occurring after the seasonal maximum in the acoustic-signal of copepod biovolume at M2 (Stafford et al., 2010).

4. Summary and discussion

4.1. Physics and primary production

The southeastern Bering Sea shelf ecosystem varies greatly among years. An informative way to categorize the years is by temperature (warm, cold, or average). Extensive sea ice in spring

Table 3
Comparison of group and individual encounter rates (ER) for fin whales on the Bering Sea middle shelf in cold (1999) and warm (2002) years. CV is the coefficient of variation.

	1999	2002
Fin whale		
Group mean ER (× 100 km)	1.9607	0.2720
Group ER CV	2.0386	2.4092
Number of groups	18	5
Individuals mean ER (× 100 km)	6.8104	0.5769
Individuals ER CV	2.1716	2.3509
Number of individuals	60	26

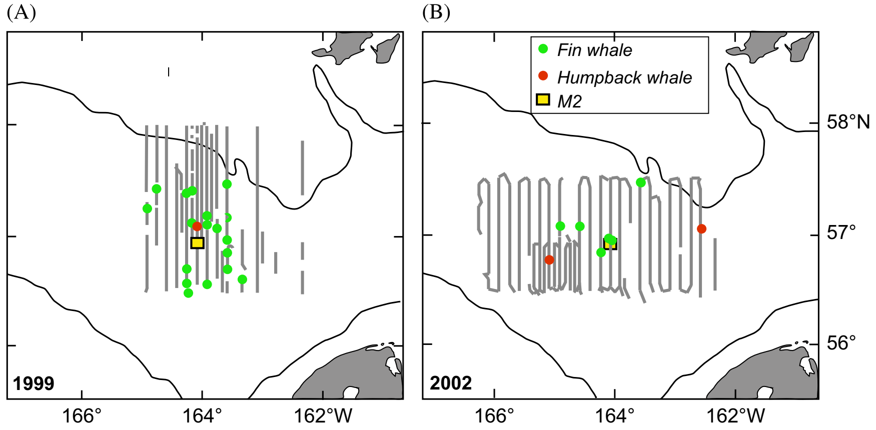

Fig. 12. Distribution of fin whales on the Bering Sea middle shelf in July of (A) a cold (1999) and (B) a warm (2002) year.

results in cold ocean temperatures that persist until the following November or December. Thus, a year with extensive sea ice over the southern shelf in spring is characterized as cold, and one with little or no ice in spring is characterized as average or warm. These are characteristics of the southeastern shelf and not necessarily applicable to the northern shelf.

Winds are the primary mechanism controlling the amount of sea ice over the southeastern Bering Sea shelf. While in the "winter", the wind velocity did not differ significantly between warm and cold years, in the "spring" (March–May) there were significant differences in the direction of the winds. The spring winds during the cold years were out of the north, advecting ice southward. These southward winds were likely cold, preventing large scale melting of the sea ice. So, "spring" winds in the cold years supported extensive sea ice near M2. In contrast in the warm years, "spring" winds were weaker and out of the east, and so less likely to maintain ice over the southern shelf.

Monthly mean currents were markedly different in warm and cold years. The northward currents at M2 during warm years could reduce the amount of sea ice on the southern shelf, both by advecting it northward and by introducing relatively warm water from along the Alaska Peninsula northward into the vicinity of M2. The occurrence of strong, cold winds out of the north, however, could easily overcome the relatively weak northward currents and transport ice southward. The westward flow of water from the coastal domain during cold years would introduce colder water to the middle shelf, thus reinforce the cooling caused by the southward advection of ice. One question that arises is: what role does such a relatively weak current play in the advection of zooplankton, larval fish, salinity, and nutrients on the shelf?

In years with significant ice after mid-March, there was an early (March–April) phytoplankton bloom. This was accompanied during some years by a second bloom in May or June, resulting from an injection of new nitrogen into the upper-water column (Stabeno et al., 2010, 2012). While the presence/absence of spring ice determines the temperature of the southeastern shelf, the sea ice does not determine vertical stratification. So it is not expected that there will be differences in summer mixing, because stratification and mean wind speed did not differ significantly between warm and cold years during summer. Noting this, it is not expected that the nutrient supply to the euphotic zone during summer will differ between warm and cold years.

The timing of the spring bloom and the temperature of the water may be critical in determining which habitat receives most of the primary production (e.g., benthic, pelagic). Walsh and McRoy (1986) hypothesized that blooms occurring in warm water would be consumed by copepods, whose foraging and growth increase in efficiency with temperature (Huntley and Lopez, 1992), whereas blooms occurring in cold water would not be effectively grazed by copepods, and would fall to the bottom to support a benthic food web. We now know that macrozooplankton ingestion removes a small fraction of the spring production and that the microzooplankton are the major consumers of primary production in this and many other high latitude shelf ecosystems (e.g., Strom et al., 2007; Sherr et al., 2009). Regardless of the source of phytoplankton mortality, where the net primary production ends up is very relevant (e.g., Hunt et al., 2002, 2008) and may be one of the most important distinguishing features between the northeastern and southeastern Bering Sea shelf (Grebmeier et al., 2006; Stabeno et al., 2012).

4.2. Zooplankton

The types and abundances of organisms over the shelf differed sharply between the warm and cold years. The lack of *Calanus* spp. over the shelf during the summer was marked during the warm period (2001–2005); since then their numbers have increased during the cold period. This was also true for adult and juvenile euphausiids (Coyle et al., 2008; Ressler, 2012), although we could not detect a strong signal in the concentrations of euphausiid larvae (Fig. 10). The mechanisms responsible for low concentrations of large crustacean zooplankton (e.g., copepods and euphausiids) during warm years are not clear, although there are several hypotheses. One possibility is bottom-up control. A match–mismatch condition (a failure of food availability at a critical time) may have existed that reduced growth and survival of *Calanus* (Baier and Napp, 2003) and euphausiids during the warm years. Another possibility is that strong predation pressure from pollock, and other planktivores reduced the concentrations observed during mid-summer (top-down control). Warm spring temperatures may have resulted in a better match in the temporal overlap of larval fish predators and their crustacean prey (Napp et al., 2000; Smart et al., 2012).

Spatial overlap of predator and prey must also be considered. In cold years, access to the middle shelf for adult and juvenile pollock and cod is blocked by the cold pool (Swartzman et al., 1994; Ciannelli and Bailey, 2005; Kotwicki et al., 2005). Thus, the annual consumption of large crustacean zooplankton over the middle shelf by these predators may be substantially reduced. Conversely, during warm years, when temporal and spatial overlap between pollock and crustacean prey was higher, the predators also experienced increased metabolic demands due to the higher temperatures. This would have resulted in higher consumption rates of large crustacean zooplankton, than in cold years. Examination of these different mechanisms is needed.

Absence of strong temperature-dependent variation in small crustacean zooplankton in these data was observed by Coyle et al. (2011). Zooplankton production models (e.g., Hirst and Lampitt, 1998) predict a strong temperature growth response from small-bodied taxa, such as *Pseudocalanus* and *Acartia*. Previous comparisons of data from individual warm and cold years indicated higher concentrations of small crustacean zooplankton during warm years than during cold years (Coyle and Pinchuk, 2002). Our lack of pattern in summer concentrations could be a result of the small number of samples available (<10), or may be another indication that top-down population control is an important modifying mechanism in the eastern Bering Sea.

The recent increase in chaetognaths is interesting. The most recent review of chaetognaths in the region (Baier and Terazaki, 2005) did not have access to data from prolonged warm and cold periods. Based on the data available to them, they concluded that chaetognath concentration in May was positively correlated with the abundance of small copepods, but not to water temperature or ice extent. The more recent pattern may result from the sequence of cold years we are now experiencing, as opposed to the high interannual variability in temperature during their studies.

4.3. Higher trophic levels

The low recruitment success of pollock year classes in the warm period (2001–2005) was surprising, since pollock prefer temperatures above 2 °C (Stabeno et al., 2012; Wyllie-Echevarria and Wooster, 1998), and age-0 survival is maximal during summers with mean water temperatures of 7.5 to 8.5 °C (Mueter et al., 2011). Thus, a warmer shelf would provide them with a larger area of suitable habitat. In addition, the original Oscillating Control Hypothesis (OCH) predicted that higher abundance of zooplankton during spring would support greater survival of pollock and, hence, a stronger year class (Hunt et al., 2002). Adult pollock are cannibals of juvenile pollock, but the variation in total abundance was not aligned with year-class abundance and so cannot account for the year-to-year variability in year-class abundance. Recent revisions to the OCH (Hunt et al., 2011), a statistical relationship between pollock recruitment and temperature (Mueter et al., 2011), and new studies on the energy content of age-0 fish (Heintz and Vollenweider, 2010) provide an explanation. The most likely cause of low survival rates of young-of-the-year (YOY) pollock during these warm years was the lack of large crustacean zooplankton during the summer. YOY pollock must acquire sufficient energy stores by the end of the summer to survive their first winter (Sogard and Olla, 2000), and low abundances of large crustacean zooplankton with their energy-rich lipid stores were coincident with observations of YOY pollock with very low energy reserves (Heintz and Vollenweider, 2010; Moss et al., 2009). The measured energy content of YOY pollock in 2004 and 2005 was low compared to that in the cooler years of 2006 and 2007 (Moss et al., 2009). In fact, the measured energy content of fish caught during the warm period at the end of summer was comparable to that of fish caught at the end of winter from the Gulf of Alaska. Thus, the poor pollock-recruitment during recent warm years (Ianelli et al., 2010) may have resulted from low concentrations of large crustacean zooplankton and higher temperature-dependent metabolic rates. This likely had an adverse affect on other planktivorous fish, seabirds, and baleen whales that forage over the middle shelf.

In contrast, arrowtooth flounder recruitment did not respond to warm and cold in the same way as pollock and cod recruitment. Unlike pollock, arrowtooth flounder settle to a benthic existence within a few months of hatching in June or July. Upon settling, they feed primarily on benthic crustaceans (mostly mysids and amphipods) and become piscivorous (Janet Duffy-Anderson, NOAA, pers. comm.). The effect of zooplankton availability on arrowtooth flounder as pelagic larvae is probably mitigated during the latter half of the summer when the juveniles adopt a different diet. Like arrowtooth flounder, cod adopt a demersal existence and feed on mysids and amphipods, but the primary prey of cod, however, remains calanoid copepods. So, unlike arrowtooth flounder, cod retain a planktonic component of their diet even after settlement (Abookire et al., 2007). This may explain why cod are more similar to pollock in their response to planktonic prey oscillations than arrowtooth flounder.

The lower encounter rates for fin whales during the summer of 2002 compared to 1999 could be related to the paucity of large crustacean zooplankton in the middle shelf domain during warm years. Stafford et al. (2010) showed how the calling rates for fin and right whales increased following peaks in euphausiid and copepod biomass at M2 in 2006–07, further suggesting that whale occurrence was related to prey availability. While these observations are intriguing, additional local-scale measurements of prey and predator abundance and movements are needed to provide a realistic functional response model for baleen whales (e.g., Piatt and Methven, 1992) for inclusion in ecosystem-based assessments.

4.4. *Scales of temporal variability and its impact on fish*

Historically, there have been other years (e.g., 1978, 1989, and 1998) that can be categorized as warm, during which pollock and cod populations did not decline as precipitously as they did in 2001–2005. The primary difference between the recent warm period and earlier ones was in duration. From 2001–2006, there were six years in which there was no significant ice around M2. The Bering Sea has historically had high year-to-year variability, and the frequent oscillation between warm and cold apparently sustained high biomasses of commercial and protected resources. A change in the temporal variability in the system, i.e., prolonged periods of warm or cold, may subject important components of the ecosystem to stresses not experienced during years of high year-to-year variability.

During the warm period, water temperatures over the southeastern Bering Sea shelf peaked in 2005. Despite cold atmospheric conditions in 2006, it was a transition year (average water temperatures). Cold atmospheric conditions had to first remove the accumulated heat in the water column from the previous five years. The subsequent cold period persisted for at least four years (2007–2010) with more moderate, but still cool, conditions in the winter/spring of 2011. Inevitably, a transition to warm conditions will occur, but the form of the transition is, as yet, unknown.

That changes in temporal variability can impact an ecosystem is evident from recent events in the southeastern Bering Sea, however, the mechanisms are not clear. On the biological side, favorable (unfavorable) conditions during a period of low year-to-year variability may tend to build large (small) population sizes. These abundance swings will be large compared to what occurs in periods of high year-to-year variability. Favorable conditions during a period of low year-to-year variability may also shift the system from bottom-up control at the beginning of the period to top–down control by multi-age fish species through cannibalism and predation (Hunt et al., 2002, 2008, 2011). Walleye pollock, Pacific cod and arrowtooth flounder may live ten or more years (so adults are multi-age), so that strong year classes have the potential to exert strong negative influence on subsequent year classes.

5. Conclusion

There is a strong history of ecosystem-based management of living marine resources on the eastern Bering shelf (Livingston et al., 2011). The present work helps to further refine a working paradigm, the Oscillating Control Hypothesis (Hunt et al., 2002, 2008, 2011) used in regional management. It also generates a new series of questions regarding control of production at higher trophic levels (e.g., depletion of prey resources through top-down control). Further exploration of the BEST–BSIERP data sets has the potential to resolve many of these issues.

What does the future hold for the Bering Sea? Several important questions remain unanswered. For example, is this new pattern of decreased interannual variability here to stay? Will the duration of the periods of warm and cold remain at 5–6 years, or will the southeastern Bering Sea return to strong interannual variability as suggested by Overland et al. (2012)? Was the ecosystem response to the warm period 2001–2005 a foreshadowing of the predicted warming as an effect of anthropogenic climate change (IPCC, 2007)? Careful examination of these questions and the ecosystem function during the warm period is important for the effective management of commercial and protected resources in this highly productive ecosystem.

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