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# Climate change and the control of energy flow in the southeastern Bering Sea

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## Abstract

We examine how coupling between physical and biological processes influences the production and transfer of energy to upper trophic-level species in the southeastern Bering Sea. We review time series that illustrate changes in the marine climate of the southeastern Bering Sea since the mid-1970s, particularly variability in the persistence of sea ice and the timing of its retreat. Time series (1995 – 2001) from a biophysical mooring in the middle domain of the southeastern shelf support the hypothesis that retreat of the winter sea ice before mid-March (or the failure of ice to be advected into a region) results in an open water bloom in May or June in relatively warm water ( $\geq 3^{\circ}\text{C}$ ). Conversely, when ice retreat is delayed until mid-March or later, an ice-associated bloom occurs in cold ( $\leq 0^{\circ}\text{C}$ ) water in early spring. These variations are important because the growth and production of zooplankton and the growth and survival of larval and juvenile fish are sensitive to water temperature. The Oscillating Control Hypothesis (OCH) recently proposed by Hunt et al. (2002), predicts that control of the abundance of forage fish, and in the case of walleye pollock (*Theragra chalcogramma*), recruitment of large piscivorous fish, will switch from bottom-up limitation in extended periods with late ice retreat to top-down in warmer periods when ice retreat occurs before mid-March. In support of this hypothesis, we review recent data from the southeastern Bering Sea that show 2- to 13-fold changes in copepod abundance with changes in spring water temperatures of 3 to 5°C. We also provide indirect evidence that the abundance of adult pollock on the eastern Bering Sea shelf negatively affects the abundance forage fishes (including juvenile pollock) available to top predators. Although there is evidence that pollock year-class strength is positively related to temperature, we lack the time series of pollock populations in extended periods (8 – 10 years) of cold-water blooms necessary to test the OCH. © 2002 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

In recent years, correlations between climate patterns and responses of marine ecosystems have been the focus of considerable attention. In the North Atlantic, North Pacific and Southern Oceans, decadal-scale climate changes impact stocks of phytoplankton, zooplankton and fish (e.g. papers in Beamish, 1995; Murphy, Clarke, Symon & Priddle, 1995; White & Peterson, 1996; Reid, Edwards, Hunt & Warner, 1998; Hare & Mantua, 2000; McFarlane, King & Beamish, 2000; Pershing et al., 2001). In the North Atlantic, climate plays a significant role in the population dynamics of the economically important northern cod (*Gadus morhua*) (e.g. Ottersen & Stenseth, 2001; Drinkwater, in press). These various fluctuations in the marine environment in far-flung corners of the world oceans are related through atmospheric teleconnections (e.g. Overland, Bond & Mileta, 2001).

The Bering Sea, as a marginal ice zone, should be particularly sensitive to climate change, because small changes in wind velocities can make large differences in the extent, timing and duration of wintertime sea ice. Although such far-reaching signals as El Niño/Southern Oscillation (ENSO) on occasion may affect the climate of the Bering Sea (e.g. Overland, Bond & Mileta, 2001), the climate of the southeastern Bering Sea is most strongly influenced by the Pacific North American pattern (PNA) (with which the Pacific Decadal Oscillation [PDO] is correlated), and by the Arctic Oscillation (AO) (Overland, Adams & Bond, 1999). Recent work has shown that ecosystem responses to decadal-scale changes in these and other indices of North Pacific Ocean and Bering Sea climate have been pervasive and of great economic importance (Francis et al., 1998; Hare & Mantua, 2000; McFarlane et al., 2000; Hollowed et al., 2001).

Climate change can affect both the base of a marine food web and its productivity, as well as the distribution and abundance of upper trophic-level consumers (Reid, Edwards, Hunt & Warner, 1998; Hare & Mantua, 2000; Hunt et al., 2002). Thus, there is the potential for climate change to cause shifts in the distribution and abundance of predators that, in turn, control the abundance of lower trophic level organisms such as small fish or zooplankton (top-down control). Alternatively, changes in primary or secondary production may affect the abundance of higher trophic level organisms that can be supported (bottom-up control). The relative importance of top-down and bottom-up control of the structure and function of ecosystems has been a central problem in ecology since Hairston, Smith and Slobodkin (1960) hypothesized that herbivores respond to changes in basal productivity when the food chain is composed of two (no predators) or four levels (top predators suppress the herbivore's predator), but not when the food chain is three levels (the predator limits the herbivore) (Hairston et al., 1960; Slobodkin, Smith & Hairston, 1967). Although more recent work shows this to be an oversimplification (e.g., Arditi & Michalski, 1996; Vanni, 1996; Vanni & de Ruiter, 1996), the implications of food web theory are important for fisheries management, as the removal of top predators may allow intermediate-level predators to increase with the relaxation of both competition and intra-guild predation (Polis, Myers & Holt, 1989; Polis & Holt, 1992; Winemiller & Polis, 1996; Crowder, Reagan & Freckman, 1996; Parsons, 1996). Of particular concern is the possibility that the combined effects of climate change and fisheries removals may shift marine ecosystems into alternative stable states, which may have a lower yield of species valuable to people (Parsons, 1996; Scheffer, Carpenter, Foley, Folks & Walker, 2001).

Recently, Hunt et al. (2002) proposed the Oscillating Control Hypothesis (OCH) to explain climate-related variation in ecosystem control in the middle domain of the southeastern Bering Sea. According to this hypothesis, during periods when the spring bloom occurs in cold water, recruitment to populations of large predatory fish, such as walleye pollock (*Theragra chalcogramma*), should be limited by bottom-up processes because zooplankton prey will be in short supply for larval and juvenile fishes. However, during periods when the bloom coincides with warm water temperatures, the control of pollock populations would become top-down. This is because copepod growth and production will be high, as will be the survival of larval and juvenile fishes, including those of large piscivorous fish. As these fish mature, the incidence of cannibalism and predation on small fish will increase, eventually limiting the recruitment of pollock.

The objective of this paper is to provide further evidence in support of the OCH. To this end, we briefly review some of the previously published evidence for changes in the marine climate of the southeastern Bering Sea shelf, and for ecosystem-wide changes in the ecology of organisms responding to the shifts in climate forcing that occurred in 1976/77 and 1989. We then examine the environmental variability of the 1990s, and what we were able to learn about ecological processes that occurred in earlier periods by examining some of the impacts of the extreme conditions encountered in the 1990s. We present new evidence for the OCH, including the importance of depth-averaged temperatures for zooplankton and pollock, and the relationship between the biomass of adult pollock on the shelf and the productivity of Pribilof Island-nesting black-legged kittiwakes (*Rissa tridactyla*), a piscivorous seabird that forages for juvenile walleye pollock and other small fishes.

## 2. The eastern Bering Sea region

The shelf of the southeastern Bering Sea is wide (> 500 km wide) and shallow (Fig. 1). Shelf waters are differentiated into three regions, or domains (coastal, middle and outer), by hydrographic features associated with characteristic bathymetric ranges (Coachman, 1986; Stabeno, Bond, Kachel, Salo & Schumacher, 2001). The coastal domain (depth < 50 m) typically is weakly stratified or well-mixed as a result

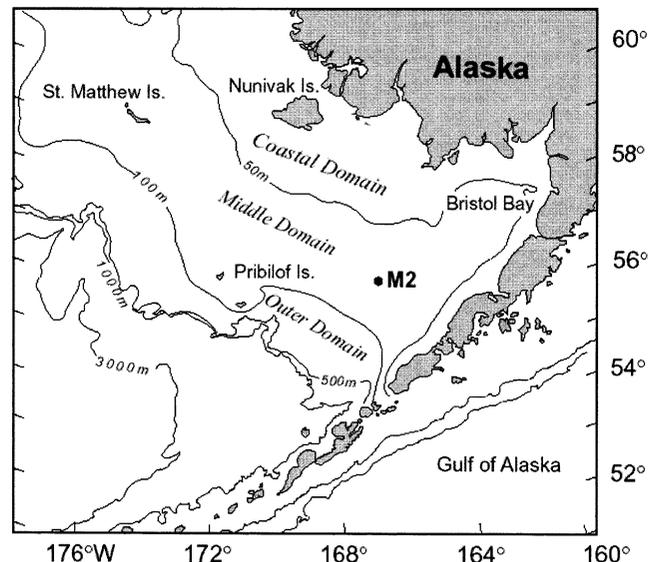


Fig. 1. Southeastern Bering Sea, Alaska, with 50, 100, 200 and 1000-m isobaths. M2 marks the location of the NOAA biophysical mooring from which data on the timing of ice retreat and the spring bloom were obtained.

of the balance between tidal and wind stirring. In the middle domain (depth 50 to 100 m), mixing energy is insufficient to stir the entire water column in the presence of a positive buoyancy flux during summer. As a result, in summer, there is a strongly stratified two-layered water column with a wind-mixed surface layer (15 to 40 m), and a tidally-mixed lower layer (below ~ 40 m). During summer, changes in density are dominated by temperature rather than salinity. The outer shelf domain (depth 100 to 200 m) has a wind-mixed surface layer and a tidally mixed bottom layer separated by an intermediate layer.

Transition or frontal zones (middle transition and shelf break front) separate the middle shelf regions from those of the outer shelf, and also the outer shelf from the slope waters (Coachman, 1986; Schumacher & Stabeno, 1998; Stabeno, Schumacher & Ohtani, 1999). A structural front, on average ~ 30 km wide, separates the middle and coastal domains (Schumacher, Kinder, Pashinski & Charnell, 1979; Kachel et al., 2002). This feature, which is evident along the entire southeastern shelf, limits the horizontal flux of salt, nutrients and heat between the middle and coastal domains (Coachman, 1986; Kachel et al., 2002). A similar feature occurs around the Pribilof Islands, where it enhances feeding opportunities for higher trophic level organisms (Kinder, Hunt, Schneider & Schumacher, 1983; Decker & Hunt, 1996; Hunt, Coyle, Hoffman, Decker & Flint, 1996a; Brodeur, Wilson & Ciannelli, 2000).

Sea ice is an important component of the marine environment in the southeastern Bering Sea, and shows great interannual variability in its extent and duration over the southeastern shelf (Hunt et al., 2002). The sea ice that reaches the southeastern Bering Sea is annual ice that forms in the lee of islands and coasts of the Bering Sea. This ice is pushed south by the prevailing winds in winter, melts along its southern edge as it encounters warm water (Pease, 1980; Niebauer et al., 1990). The amount of ice-melt and its distribution affects water column temperatures over the shelf for the remainder of the year (Stabeno, Bond, Kachel, Salo & Schumacher, 2001).

### 3. Physical evidence for climate change in the eastern Bering Sea

During the past three decades, there have been two so-called regime shifts, one in 1976/77 that was associated with changes in both the PDO and the AO, and in 1989 there was a less dramatic shift that was associated primarily with changes in the AO (Fig. 2). Marine climate responses to the regime shifts were most obvious subsequent to the 1976/77 change. In comparison to the previous decade, there was a

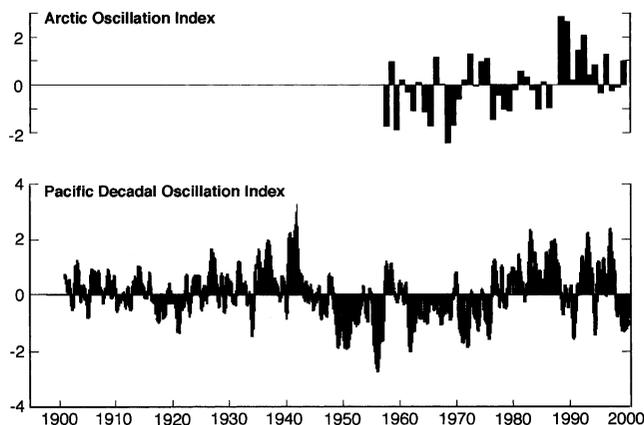


Fig. 2. Time series of the Arctic Oscillation (AO) and the Pacific Decadal Oscillation (PDO), after Overland, Adams and Bond (1999).

marked reduction in duration, concentration and extent of winter sea ice (Fig. 3) (see also Hunt et al., 2002). In addition, there was a lengthening of the period of light summer winds from about three months to five months, and an overall decrease in the wind speed subsequent to the 1976/77 regime shift (Hunt et al., 2002). These changes constitute a shift to an earlier spring transition in the Bering Sea that was related to changes in the Arctic Oscillation (Stabeno & Overland, 2001).

Using the Global Ice and SST data sets to estimate a time series for sea surface temperatures (SST) in the middle domain at 56°N, 165°W, Hunt et al. (2002) found that there was a period in the early- to mid-1970s with unusually cold spring and summer SSTs, which was followed by a period from the mid-1970s to the mid-1980s with unusually warm spring and summer SSTs. In addition to these decadal-scale shifts in SST associated with the 1976/77 regime shift, between 1960 and 1999 there was also a persistent warming trend that has resulted in an increase of about 1°C in July SSTs (Bond & Adams, 2002). The April SST data also show a marked decrease in SST in the late 1960s to mid-1970s, but unlike the SST trace for June and July, there is no suggestion of a trend toward warming of the April SST post-1978. Because the water column is well mixed during winter and this condition usually persists into April, one can infer that bottom temperatures were markedly colder in the period between 1969 and 1978 than they were either before or after that period. This is supported by observations over the southern middle shelf, where the heat content during the early 1970s was substantially less than that observed in the 1980s and 1990s (Stabeno et al., 2001). A reduction in SST at the Pribilof Islands provided evidence of the 1989 regime shift in the southeastern Bering Sea (Hare & Mantua, 2000).

#### 4. Where do the late 1990s fit in?

Recent research (Stabeno & Overland, 2001) has pointed to two changes in the physical environment over the southeastern Bering Sea shelf in the period 1989–1998. Monthly average atmospheric temperatures during April at 850 millibars were 3°C warmer than those observed during 1980–1988. In conjunction with this increase, there was a change in the rapidity of sea ice retreat. While ice persisted longer over the southeastern shelf, over the northeastern shelf it retreated more rapidly, resulting in less ice during spring. These changes in April are indicative of earlier springs over the eastern shelf, which have had important repercussions on the ecosystem, but are thought to be related to variability in the AO, as opposed to the PDO (Stabeno & Overland, 2001).

During 1996–1999, the eastern Bering Sea presented extremes of conditions and great interannual vari-

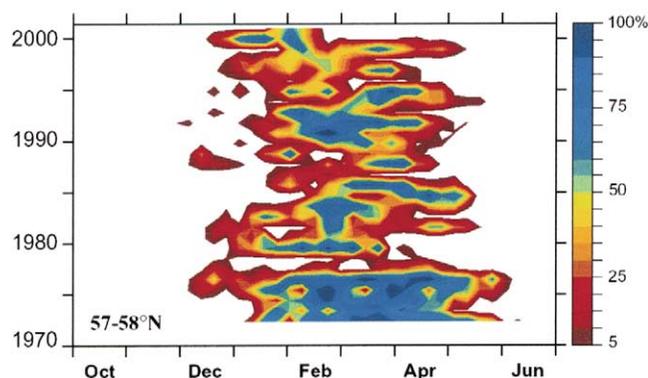


Fig. 3. Concentration (% cover) of sea-ice over the southeastern Bering Sea shelf between latitudes 57°N and 58°N. Modified from Hunt et al. (2002).

ation. Between 1996 and 1998, the eastern Bering Sea experienced longer and calmer summers with a warmer upper mixed layer than before. In contrast, 1999 was similar to the 1972/1976 period, with cold temperatures, late departure of ice, and stormy weather. The warmest SST recorded since the 1960s occurred in 1997, whereas one of the coldest years on record was 1999 (Stabeno, Bond, Kachel, Salo & Schumacher, 2001). Although SSTs in 1997 were among the warmest on record (Stabeno, Bond, Kachel, Salo & Schumacher, 2001) the depth-averaged temperature, which is a measure of the heat present in the water column, that year was not unusual (Fig. 4). In contrast, during May and June 1998, depth-averaged temperatures were the warmest in the 1990s. This was in part because of the persistence of heat stored in the water column from the previous fall that had not been completely removed by winter cooling (Stabeno, Bond, Kachel, Salo & Schumacher, 2001).

Depth-averaged temperatures over the shelf are more closely related to the previous winter's temperatures and ice cover than they are to the SST. Over the middle shelf, the surface mixed layer caps the bottom layer and the sharp thermocline at the base of the surface mixed layer insulates the bottom layer from surface heating. Thus, winter conditions are likely to be more important to organisms that live at depth in the water column and are sensitive to environmental temperatures than are spring and summer SSTs, which may have little effect on the temperatures to which the organisms are exposed. Depth-average temperatures during most of the 1990s were cooler than those during the warm late 1970s and early 1980s, and warmer than the cold conditions of the early 1970s (lower set of blue Xs in Fig. 4). However, depth-averaged temperatures in 1999 were close to the coldest recorded from previous decades. Interestingly enough, both 2000 and 2001 had depth-averaged temperatures at the beginning of May similar to those observed in 1998.

There were also marked differences in biological processes in the 1990s compared to those that had been observed in earlier years. The biomass of large predatory fish over the eastern shelf surged post 1978, whereas during the 1980s the biomass of forage fish declined, particularly over the southern portion of the eastern shelf (Hunt et al., 2002). The late 1970s and 1980s were a period during which the populations of upper trophic level organisms changed dramatically in abundance and, where studied, in diet (e.g., Sinclair, Loughlin & Percy, 1994; Decker, Hunt & Byrd, 1995; Hunt, Decker & Kitaysky, 1996b). In the late-1990s, the biomass of large predatory fish appeared to decline. The biomass of baleen whales on the shelf increased between the mid-1970s and the late-1980s (Baretta & Hunt, 1994). Populations of piscivorous marine birds and pinnipeds declined, particularly in the vicinity of the Pribilof Islands (Hunt et al.,

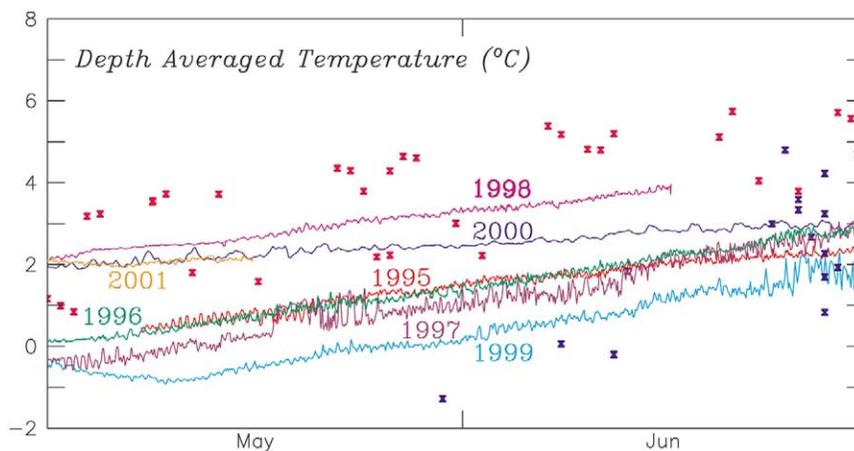


Fig. 4. The depth-averaged temperatures from the mooring at M2 (56.8°N, 164°W) are shown as colored lines. The blue Xs represent the data from the hydrographic surveys between 1966 and 1976, the red Xs from surveys between 1977 and 1994, all collected within 25 km of the mooring.

2002). In the late 1990s, coccolithophore blooms dominated the eastern shelf phytoplankton in July and August (Sukhanova & Flint, 1998; Vance et al., 1998; Napp & Hunt, 2001; Stockwell et al., 2001). There appear to have been more copepods (during 1997 and 1998) and jellyfish in the late 1990s, but there is no evidence for significant changes in euphausiid abundances (Coyle & Pinchuk, 2002b; Brodeur, Sugisaki & Hunt, 2002). To understand these changes, the mechanisms by which climate affects the fate of biological production need to be investigated.

## 5. Biological responses to changes in the marine climate

The timing of the spring bloom and the water temperatures in which it occurs have considerable impact on the fate of the bloom (Walsh & McRoy, 1986). Studies of springtime primary production in the mid-1970s emphasized the importance of ice-associated blooms that occurred in cold water ( $-1^{\circ}\text{C}$ ) (e.g. Alexander & Niebauer, 1981; Niebauer, Alexander & Henrichs, 1990), whereas those working in the late 1970s and early 1980s emphasized the importance of open water blooms that occurred in comparably warm water ( $2^{\circ} - 5^{\circ}\text{C}$ ) (e.g. Sambroto et al., 1986; Walsh & McRoy, 1986). The variability in the timing of ice retreat during the 1990s provided an opportunity to reconcile these different views of springtime production regimes.

Since 1995, a biophysical mooring has been maintained almost continuously at M2 in the middle domain of the southeastern Bering Sea shelf ( $56.8^{\circ}\text{N}$ ,  $164^{\circ}\text{W}$ ; Fig. 1). Measurements of temperature, salinity, currents, and fluorescence or chlorophyll were collected year around, while atmospheric data were collected during the summer months (Stabeno, Bond, Kachel, Salo & Schumacher, 2001). Data from this mooring, together with other moorings that were maintained more sporadically, have revealed a clear pattern relating sea-ice and the spring phytoplankton bloom (Fig. 5). Ice is formed in polynyas on the leeward side of islands and the Alaskan coast and is blown southward over the shelf. The leading edge of the ice melts and cools the water to  $\sim -1.7^{\circ}\text{C}$ . These cold temperatures are evident in the records as the black areas in the temperature fields. When the ice retreats, there is a rapid increase in water temperature of  $1-1.5^{\circ}\text{C}$ . The yellow lines are fluorescence (volts) at approximately 11 m below the surface. Whenever there was ice over the mooring after mid-March, fluorescence was enhanced at the site.

The burst of early, ice-associated production persists until the nutrients are drawn down. This sequence of events occurred in 1995, 1997 and 1999. In the remaining four years, either sea-ice was not advected over mooring site (1996 and 2001), or it retreated before mid-March, 1998, 2000. In those years, a bloom occurred in late May or even June. This is the classic spring bloom that occurs when winds weaken and solar energy increases sufficiently to stratify the water column (Eslinger & Iverson, 2001; Stabeno, Bond, Kachel, Salo & Schumacher, 2001). An examination of primary production and ice charts from earlier years, supports these patterns of production relative to the timing of ice retreat (Table 1). It is of interest that Arrigo, Weiss and Smith (1998) found a similar inverse relationship between the timing of sea ice melt and the timing of the spring bloom in the southern Ross Sea, Antarctica, which they hypothesized was linked to seasonal changes in the mixing depth.

The timing of the bloom is important because it is related to the temperature of the water over the southeastern shelf. When sea ice persists late into March or April and the bloom is associated with the melting ice, when water column temperatures range between  $-1.7^{\circ}\text{C}$  and  $1^{\circ}\text{C}$ . In contrast, when the ice has retreated prior to mid-March and the bloom occurs in open water in May or June, water temperatures in the upper mixed layer typically range from  $2.2^{\circ}\text{C}$  to  $5.1^{\circ}\text{C}$  or higher. These differences in temperature are important because of the effect of temperature on the metabolism of organisms. Within the range of viability, higher temperatures result in increased metabolic rates that cause increases in growth rates, reduction in time to maturity, and increased production rates of zooplankton (McLaren, 1963; Toda, Arima, Takahashi & Ichimura, 1987; Ikeda, 1990; Iguchi & Ikeda, 1995). Thus, Vidal (1980) and Dagg, Clarke,

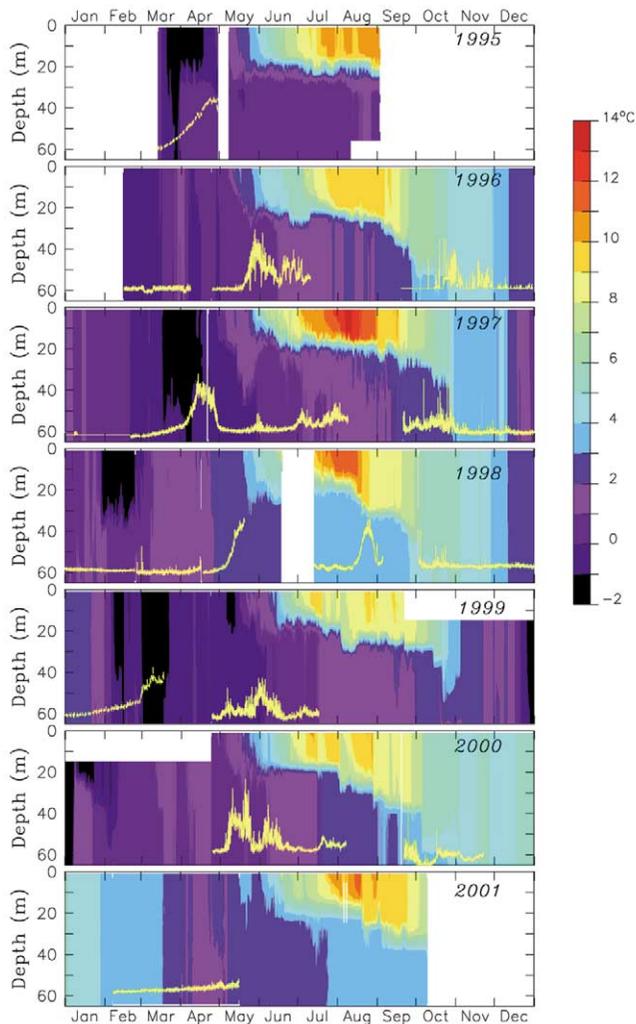


Fig. 5. Time series of sea water temperature and fluorescence (yellow trace) from Mooring 2 in the southeastern Bering Sea for 1995 through 2001. Note that periods when water temperatures were  $-1$  to  $-2^{\circ}\text{C}$ , melting ice was present. In 1997, ice retreat occurred in April, and the spring bloom occurred early and in association with the ice. In 1998, ice was gone by the end of February, and the bloom occurred in open water in May. Modified from Stabeno, Bond, Kachel, Salo and Schumacher (2001).

Table 1  
Relationship between the timing of ice retreat and the type of spring bloom

	Bloom Occurs at the Ice Edge	Bloom in Open Water
Ice Gone by mid-March	0	7
Ice remains after late March	6	0

Nishiyama and Smith (1984) have argued that in the cold waters of the Bering Sea, temperature is a more important determinant of copepod production than prey abundance. On this basis Walsh and McRoy (1986) hypothesized that if the spring bloom occurred when water temperatures were warm, zooplankton production would be accelerated, and a greater proportion of the primary production would go to support a pelagic versus a benthic food web. In contrast, in cold years, phytoplankton would fall to the benthos as a sub-surface chlorophyll layer.

More recently, Huntley and Lopez (1992) showed that temperature alone explains more than 90% of the variance in copepod growth rates, and that most often in nature, food was not limiting growth. They found that copepod production could be predicted from temperature by the following relationship:  $P = B \cdot 0.0445 e^{0.111T}$ , where P is production  $d^{-1}$ , B is the initial biomass of copepods, and T is the water temperature in which the copepods are growing. Based on this relationship, daily biomass production by copepods would be 0.05 times B at 1°C, 0.07 B at 4°C and 0.11 B at 8°C, assuming that food was not limiting. At M2, integrated water column temperatures in May were 2 – 3°C warmer in 1998, 2000 and 2001, years with early ice retreat, than they were in 1995, 1997 and 1999, years with late ice retreat, when temperatures ranged from –1 and 0°C (Fig. 4). Temperatures in 1996 were cool (~ 1°C) compared to other years with an early ice retreat. These differences in temperature could result in a 2-fold or greater difference in rates of copepod production. If we consider the period from 1967 to 2001 (Fig. 4), depth-averaged temperatures in late May ranged from < -1°C to > 5°C, which could have resulted in more than a two-fold interannual variation in copepod production. It is reasonable to assume that food does not limit copepod production during the bloom, but it is less clear whether food is sufficient in the eastern Bering Sea to support maximal copepod production either before or after the bloom. Slow-growing copepods may suffer higher mortality rates at early developmental stages, either because of a failure to molt, or because a longer duration at a small instar exposes them to greater vulnerability to predation (Huntley & Lopez, 1992).

Two sets of data from the middle domain of the southeastern Bering Sea shelf support the contention that water temperatures during spring have a significant effect on zooplankton production and the biomass of copepods that will be available to planktivores in a given year. Smith and Vidal (1986) compared the growth rates of *Calanus marshallae* in 1980 and 1981, a ‘cold’ year and a ‘warm’ year, respectively and found that *C. marshallae* produced two generations in the warmer year, but only one generation in the cooler year. They also compared the abundance of copepods available in the two years (Table 2). During

Table 2

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

Variable	Year 1980	1981
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*
Temperature during Bloom – top 20 m	2.22	5.06*
<i>Acartia</i> spp. All copepodids	18.9	8.5
<i>Acartia</i> spp. Adult males and females	9.4	2.8*
<i>Pseudocalanus</i> spp. All	83.1	308.5*
<i>Calanus marshallae</i> All copepodids	31.7	30.6*
<i>Calanus marshallae</i> Adult females	0.1	0.8*
<i>Metridia pacifica</i> all copepodids	1.6	20.3*
<i>Oithona</i> spp.	269.6	233.4

May, which was when the bloom was active in 1980 and 1981, several taxa were more abundant in the warm year by factors from 3X to 13X, although one taxon decreased in abundance (Smith & Vidal, 1986).

More recently, Coyle and Pinchuk (2002b) reported, depending upon taxon, decreases in copepod abundance between the warm years of 1997 and 1998 and the cold year of 1999 of 2X to 13X (Table 3). They found that temperatures of the bottom layer and the integrated water column in June were predictive of copepod biomass, but that upper mixed layer temperatures were not. Data from M2 show that surface temperatures in late spring and summer are not closely related to depth-averaged temperatures. For instance, 1997 had very warm SSTs in June and July, but depth-averaged temperatures were cooler than normal. In contrast, SST during June and July 1998 were cooler than 1997, but the depth-averaged temperatures were among the warmest in the last decade (Stabeno, Bond, Kachel, Salo & Schumacher, 2001).

The studies of Smith and Vidal and Coyle and Pinchuk are not directly comparable, as the Coyle and Pinchuk data were obtained in June, after the bloom, whereas those of Smith and Vidal (1986) were obtained in May, during the bloom. Additionally, the gear used by Coyle and Pinchuk differed from that used by Smith and Vidal, and there is insufficient data to permit controlling for potential differences in the rates of predation by planktivores. Nevertheless, we now have evidence of significant shifts in the abundance of copepods, both when going from a cold year to a warm year and when going from warm years to a cold year. These shifts were greater than would have been predicted by the relationship between temperature and production modeled by Huntley and Lopez (1992), implying that the differences seen in the abundance of copepods between the warm and cool years must involve temperature-related differences in other factors, such as mortality. These data support the hypothesis that, in years when sea ice lingers late into the spring and the spring bloom occurs in cold water in association with the melting ice, there will be fewer copepods available to fish and other planktivores than in years when the ice retreats early and the bloom occurs in late spring in warm water.

Several authors have investigated the coupling between secondary production and planktivores, including walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. Springer (1992) estimated that pollock should consume virtually all of the secondary production of the middle and outer domains. More recent modeling efforts by Trites et al. (1999) and Aydin et al. (in press) suggest that in both the 1980s and the 1990s over 90% of copepod production has been required to support planktivores (73% to large zooplankton, 11% to juvenile pollock, 8% to adult pollock, 15% other, 7% unaccounted for). These copepod-consumers include not only pollock, but also larger zooplankton such as euphausiids and gelatinous zooplankton. In the vicinity of the Pribilof Islands, Swartzman et al. (in press) have observed an inverse relationship between the biomass of age-1 pollock and the biomass of zooplankton remaining at the end of summer. Interestingly, Coyle and Pinchuk (2002a) found no significant differences in copepod abun-

Table 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 and inner shelf in June 1997, 1998 and 1999. \* = difference significant at  $p < 0.05$ . Data from Coyle and Pinchuk (2002b) and Hunt et al. (2002)

Variable	Year		
	1997	1998	1999
Onset of Bloom	Mid-April	Early May	Late March
Depth averaged Water Temperature during June (°C)	5.53	3.79	0.45*
<i>Acartia</i> spp.	961	711	64*
<i>Pseudocalanus</i> spp.	1168	893	240*
<i>Calanus marshallae</i>	34	72	3.7*
<b>Calanoid nauplii</b>	616	626	322*
<i>Oithona similis</i>	99	219*	28

dances in the summers (late July – early September) of 1997, 1998 and 1999 despite the striking differences seen between June 1999 and the two warmer years (1998 and 1999). They concluded that in each year copepod abundances were reduced to similar levels by a combination of predation and declining primary production. An interpretation of this observation is that this common level of abundance represented a ‘threshold’ below which predators had little further effect on reducing copepod abundance, and that this ‘threshold’ was not affected by the initial abundance of copepods in the ecosystem. It is reasonable to hypothesize that in years with a cold spring and low production of copepods, planktivore growth and survival may be limited by their ability to obtain sufficient prey.

## 6. The oscillating control hypothesis

To link changes in climate, pollock recruitment and the availability of forage fish to marine birds and mammals in the middle domain of the southeastern Bering Sea, Hunt et al. (2002) developed the ‘Oscillating Control Hypothesis’ (OCH) to relate decadal-scale changes in climate to alternation between bottom-up and top-down control of large piscivorous fish recruitment in the southeastern Bering Sea (Fig. 6). This hypothesis predicts that, when there is a prolonged series of years with delayed ice retreat and spring phytoplankton blooms that occur in cold water, the production of large piscivorous fish, such as pollock, should be limited from the bottom-up by a lack of zooplankton, in particular calanoid copepods, to support larval and juvenile fish. In contrast, in periods of late blooms in warm water, there will be greater supplies of zooplankton that initially will result in higher rates of recruitment. However, as these large year-classes mature and become predators of small fish, control of recruitment will become top-down.

Four elements are essential to this hypothesis:

1. The timing of sea ice retreat in spring determines whether there will be either an early, ice-associated bloom in cold water, or a late-spring, open water bloom in warm water.
2. Copepods, a critical prey of larval and juvenile pollock, are sensitive to the temperature of the water in which they are developing. Therefore copepod production and the number of cohorts produced in years when the spring bloom occurs in warm water would be substantially greater than in years when the spring bloom occurs in cold water.
3. There is close coupling between the production of crustacean zooplankton and demand for this resource by planktivores. Consequentially, in cold years, a reduced production of copepods could limit the survival of either larval or juvenile pollock.
4. When adult pollock and other large piscivores are abundant, they have the potential to control recruitment of juvenile pollock because of cannibalism.

Evidence supportive of elements 1, 2 and 3 has been presented above and appears adequate as a starting point for building the hypothesis. Water temperatures are lower when the bloom occurs early in the spring, in association with the ice, as compared to when it occurs in open water in May or June (Fig. 5) (Hunt et al., 2002). Likewise not only do physiological (e.g., McLaren, 1963) and empirical studies (Huntley & Lopez, 1992) show that the growth and reproduction of copepods are sensitive to temperature, but in the middle domain of the southeastern Bering Sea, there is direct evidence that springtime sea temperatures are more important than prey abundance in limiting the growth of small-bodied copepods (e.g., Vidal, 1980; Dagg, Clarke, Nishiyama & Smith, 1984). The data of Smith and Vidal (1986) (Table 2) and those of Coyle and Pinchuk (2002b) (Table 3) show that the result is a positive relationship between integrated water temperature and the abundance of copepods available to support juvenile fishes. Models suggest that planktivores can be food limited, as do data on the impact of salmon on the plankton of the subarctic North Pacific (Shiomoto, Tadokoro & Ishida, 1997) and the central Bering Sea (Sugimoto and Tadokoro, 1997).

# Oscillating Control Hypothesis

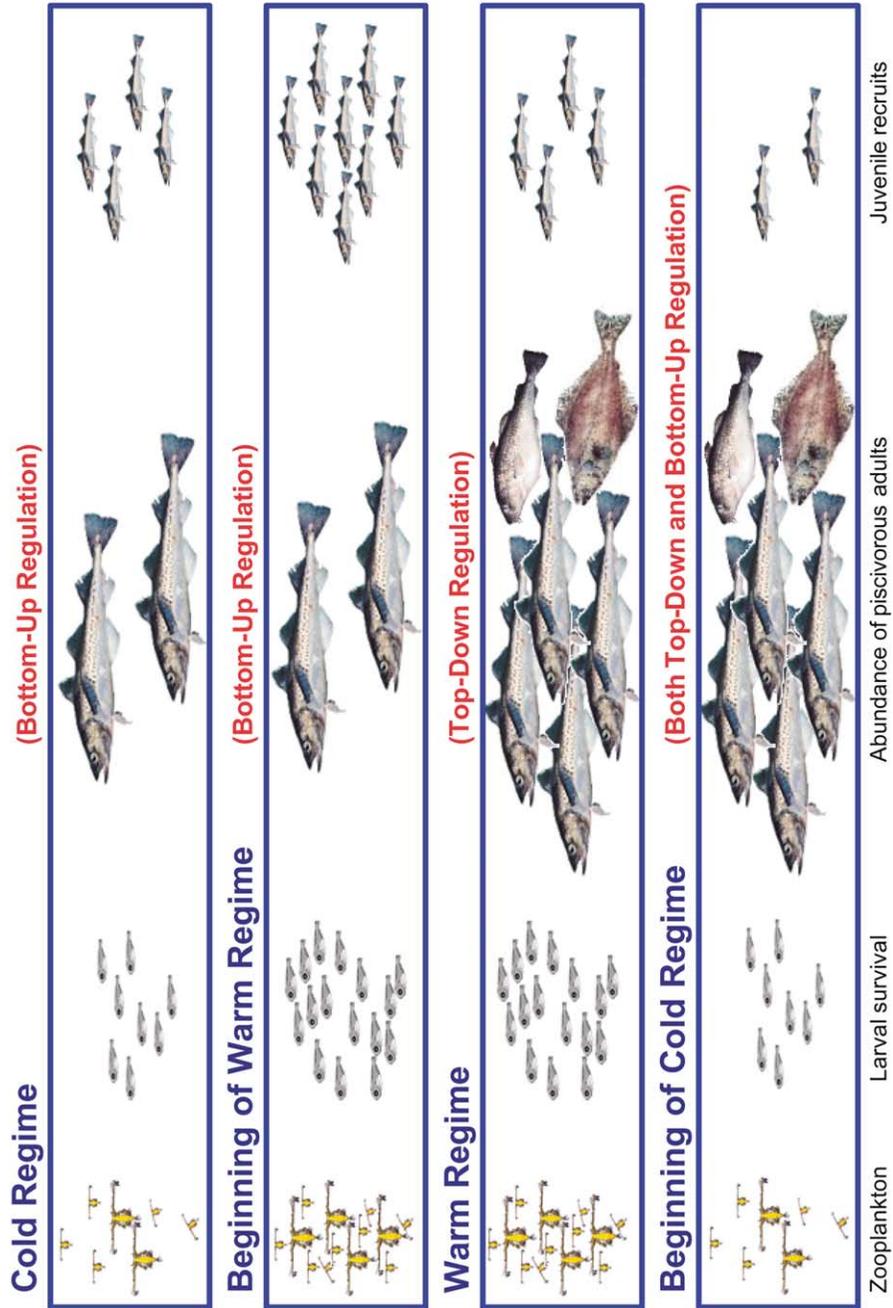


Fig. 6. Cartoon depicting the function of the Oscillating Control Hypothesis (OCH). See text for description. From Hunt et al. (ms).

Data indicating that adult pollock are capable of exerting top-down control of their own recruitment support element 4. Cannibalism of older fish on smaller fish is well documented (Dwyer, Bailey & Livingston, 1987; Livingston, 1989; Livingston & Lang, 1996; Wespestad & Quinn, 1996). Quinn and Niebauer (1995) showed that the relationship between the spawning biomass of pollock and recruitment fits a Ricker curve and suggested that the most likely density-dependent mechanism for explaining this relationship is cannibalism. Wespestad, Fritz, Ingraham and Megrey (2000) provide evidence that in recent years strong year-classes of pollock in the southeastern Bering Sea have been associated with wind forcing that resulted in the advection of eggs and larval pollock onto the shelf in areas where they would be isolated from cannibalism. Models of pollock recruitment in the Gulf of Alaska show that large piscivorous fish are capable of exerting top-down control of pollock recruitment (Bailey, 2000), and it seems likely that adult pollock in the Bering Sea are also capable of top-down control when their biomass is sufficient. It is relevant that there is a significant negative relationship between the biomass of age-3+ pollock on the eastern Bering Sea shelf and the production of young by piscivorous black-legged kittiwakes nesting on the Pribilof Islands (Fig. 7). The implication of this observation is that adult pollock are able to depress the abundance of small fishes consumed by kittiwakes sufficiently to impact the ability of kittiwakes to raise young (Livingston, Low & Marasco, 1999).

The OCH predicts that in cold years a lack of prey will limit the survival of age-0 and age-1 pollock. Evidence that pollock year-class strength is reduced in cold years was developed by Quinn and Niebauer (1995). They found that, after fitting a Ricker spawner-recruit curve to pollock recruitment at age two, the residuals of pollock recruitment were significantly correlated with air temperature at St Paul Island, Pribilof Islands, when lagged by a year ( $R = 0.462 \pm 0.204$  SE,  $p \leq 0.05$ ). In contrast, there was little or no effect of sea surface temperature on recruitment. Air temperature at St. Paul Island is influenced by winter sea ice cover and sea surface temperatures in the immediate vicinity of the island, where the water column is well mixed, the surface temperature reflects the integrated water column temperature. Thus air temperature at St. Paul Island may provide a better indication of the water column temperatures to which developing copepods would have been exposed than would SSTs of the middle domain obtained away from the island.

The OCH provides a mechanism that would explain the abrupt increase in the biomass of adult pollock over the eastern shelf following the 1976 regime shift. The warm years following the shift would have resulted in increased production of copepods and high survival of larval and juvenile pollock, as the biomass of adult pollock was still moderate. However, with the increase in the biomass of adult pollock as the 1978 and other strong year-classes matured, there would have been increased levels of cannibalism that would have reduced the survival of young pollock (Bailey, 2000; Hunt et al., 2002). This reduction in the abundance of young pollock appears to have been particularly severe in the southeastern Bering Sea, where stocks of Pacific cod (*Gadus macrocephalus*), arrowtooth flounder (*Atheresthes stomias*), and other piscivorous fishes increased, possibly in response to the warming sea temperatures (Hunt et al., 2002).

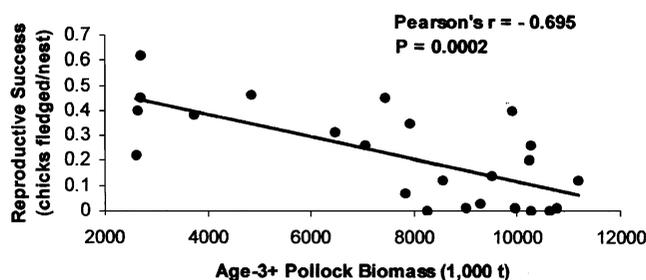


Fig. 7. Relationship between the biomass of age-3 and older walleye pollock over the eastern Bering Sea shelf and the production of young per nest by black-legged kittiwakes nesting in the Pribilof Islands. Pollock data from Ianelli, Fritz, Honkalehto, Williamson and Walters (2000) and kittiwake data from Dragoo, Byrd and Irons (2000). Modified from Livingston, Low and Marasco (1999).

These increases in predator abundance apparently caused a shift to top-down from bottom-up control of recruitment (Bailey, 2000; Hunt et al., 2002).

A decrease in the abundance of age-1 pollock and capelin (*Mallotus villosus*) in the vicinity of the Pribilof Islands coincided with the warmer temperatures and increases in the biomass of adult pollock there, and deprived the marine birds and pinnipeds there of two of their most important forage fishes. These decreases may have been caused both by predation by large pollock, and in the case of capelin, by warming of the water to temperatures above the preferred range (Hunt et al., 2002). In 1999, the water temperatures in the southeastern Bering Sea cooled, and capelin have been reported to have returned to areas of the Gulf of Alaska and the southeastern Bering Sea from which they have been largely absent since the late 1970s (Sue Moore, Pers. Comm.).

When top-down processes regulate pollock recruitment, the removal of cannibalistic adult fish should improve the survival of pre-recruits. Thus during warm regimes, fisheries removals of adult fish should be compensated by improved recruitment. In contrast, in cold regimes with bottom-up regulation, adult fish may not be as quickly replaced because larval and/or juvenile survival is food-limited. If, as appears to be the case, adult pollock are limiting the production of black-legged kittiwakes at the Pribilof Islands through competition for forage fish, then reduction of the biomass of adult pollock on the shelf could lead to improved reproductive success of kittiwakes. Since other top predators, such as murre (*Uria* spp.) and northern fur seals (*Callorhinus ursinus*) have considerable dietary overlap with kittiwakes, it is possible that reduction of adult pollock biomass might also be of advantage to them. However, reduction of pollock biomass alone would be unlikely to benefit these top predators in the long run if populations of other large piscivorous fish, such as Pacific cod and arrowtooth flounder were to increase in the absence of competition from pollock.

Despite the shift to cooler water temperatures in 1999, there is no evidence of a significant decline in the biomass of adult pollock in the southeastern Bering Sea as of 2001. Both 2000 and 2001 were warm years, and the 1996 year-class was a large one, which will take a number of years to be removed by natural mortality or fisheries. Thus, there has yet to be a sufficiently prolonged cold period to test the prediction of the OCH that pollock should become bottom-up limited during an extended period of cold. In the meanwhile, the data of Coyle and Pinchuk (2002b) show that, in the cold year of 1999, there was a major reduction in the abundance of copepods, and thus the potential for the development of bottom-up limitation. A decline in the size-at-age of age-1 or 2 pollock in years with low water temperatures would provide support for such bottom-up limitation. If pollock are presently subject to both bottom-up and top-down limitation of recruitment, they are potentially more vulnerable to over-fishing than they were when top-down processes were likely the primary control of recruitment.

Adult pollock diets include zooplankton in addition to small fish (Dwyer, Bailey & Livingston, 1987; Livingston & Lang, 1996). Variation in the abundance of zooplankton may affect the survival of forage fishes by causing adult pollock to alter the proportion of small fish in their diets (Cooney et al., 2001). For example, when the biomass of large copepods dropped below  $0.2 \text{ g m}^{-3}$  in Prince William Sound, northern Gulf of Alaska, adult pollock switched from a diet rich in copepods to one that included a greater proportion of nekton, including juvenile pink salmon (*Oncorhynchus gorbuscha*) (Willette et al., 2001). In the southeastern Bering Sea, pollock take both small fishes and zooplankton, including copepods (Dwyer, Bailey & Livingston, 1987; Livingston & Lang, 1996), and it is likely that prey switching similar to that recorded in Prince William Sound occurs. The effects of this switching would be additive to the effects of the OCH. During cold regimes when copepods are predicted to be in low abundance, adult pollock individually might be expected to increase their consumption of small fish, including juvenile pollock, although if the adult population was itself low, it might take a smaller proportion of the total supply of small fishes than would be the case when populations of these large fish were high. The impact of the switching behavior on the recruitment of pollock will depend on the spatial distribution of adult and juvenile

fish, as well as on the relative abundance of juvenile fish and zooplankton at the small spatial scales at which foraging takes place. Additional research on these aspects of pollock foraging ecology are required.

The OCH most closely applies to biophysical dynamics over the middle shelf of the southeastern Bering Sea. It is unlikely to apply to the coastal domain, as the inner front appears to block age-0 pollock from that region (Kachel et al., 2002; Hunt et al., 2002). It is also unclear whether the OCH applies in the outer domain, as most of the copepod biomass there consists of large oceanic species with annual life cycles and the ability to graze the bloom very early in the spring (Cooney & Coyle, 1982). In addition, sea ice occurs rarely over the outer shelf south of the Pribilof Islands. Relatively little is known about zooplankton dynamics and the biology of larval and juvenile fish over the shelf north of St Matthew Island. Ice remains there longer there than in the southeastern Bering Sea, and shows less interannual variation (Hunt et al., 2002). Thus, it might be expected that most phytoplankton production there would be associated with the melting of the sea ice and would occur in cold water as described by Alexander and Niebauer (1981) and Niebauer, Alexander & Henrichs, 1990, 1995). These conditions might be expected to result in slower growth and a lesser production of zooplankton, and thus a bottom-up limitation of fish recruitment compared to farther south on the shelf. New studies are needed to examine the ability of the northern parts of the shelf to support larval and juvenile fish, and how climate change may affect the relative importance of the northern and southern portions of this shelf to support fish populations. Investigation of production and its fate in the northern Bering Sea might provide a useful means of testing the prediction of the OCH that during a period of repeated cold springs with ice-associated blooms, the system should become controlled by bottom-up limitation of fish recruitment.

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