Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis

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Walleye pollock (*Theragra chalcogramma*) is an important component of the eastern Bering Sea ecosystem and subject to major fisheries. The Oscillating Control Hypothesis (OCH) predicted that recruitment of pollock year classes should be greatest in years with early ice retreat and late blooms in warm water, because more energy would flow into the pelagic (vs. benthic) community. The OCH further predicted that, with pollock population growth, there should be a shift from bottom-up to top-down regulation. New data support the predictions that in those years with early ice retreat, more primary production accrues to the pelagic compartment and that large numbers of age-0 pollock survive to summer. However, in these years, production of large crustacean zooplankton is reduced, depriving age-0 pollock of lipid-rich prey in summer and autumn. Consequently, age-0 pollock energy reserves (depot lipids) are low and predation on them is increased as fish switch to age-0 pollock from zooplankton. The result is weak recruitment of age-1 recruits the following year. A revised OCH indicates bottom-up constraints on pollock recruitment in very warm periods. Prolonged warm periods with decreased ice cover will likely cause diminished pollock recruitment and catches relative to recent values.

Keywords: Bering Sea, climate change, crustacean zooplankton, Oscillating Control Hypothesis, sea ice cover, *Theragra chalcogramma*, walleye pollock, year-class strength.

Introduction

The Oscillating Control Hypothesis (OCH) was developed as a conceptual model of how walleye pollock (*Theragra chalcogramma*) recruitment in the southeastern Bering Sea might be affected by climate variability (Hunt *et al.*, 2002a, 2008). The OCH was based on several assumptions about the relationships between temperature, zooplankton, and the growth and survival of young pollock. It was an extension of the ideas of Walsh and McRoy (1986) working in the Bering Sea and of Bailey (2000), who had determined that the control of walleye pollock recruitment in the Gulf of Alaska had shifted from bottom-up control of early larval survival to top-down control of juvenile stages. The OCH extended Bailey's work by attempting to develop explicit mechanistic hypotheses that would link pollock recruitment to the effects of climate in the southeastern Bering Sea. This paper reviews the assumptions and predictions of the OCH (Hunt *et al.*, 2002a) and updates the OCH to account for new information available since 2002. The result is a new version of the OCH, which still predicts variation in the dominant mechanism for control of pollock recruitment and now hypothesizes that the dominant mechanism affecting pollock recruitment in stanzas of very warm years will be bottom-up impacts on the survival of age-0 pollock in their first autumn and winter.

The eastern Bering Sea supports major fisheries, the largest of which is for walleye pollock, a gadid that is or has been the subject of fisheries throughout the northern Pacific Ocean from Puget Sound, WA, to the east coast of Japan and the Sea of Okhotsk (Hunt and Drinkwater, 2005). In the eastern Bering Sea, pollock biomass expanded rapidly in the 10 years after the 1976/1977 "regime shift" (Hare and Mantua, 2000), buoyed by the extraordinarily strong 1978 year class (Ianelli *et al.*, 2010). Because

pollock biomass had been low in the preceding years and there was an expectation of increased production of small neritic copepods in warm years, it was hypothesized that the strong 1978 year class was the result of a shift from cold to warm conditions, with an accompanying increase in copepods to support the survival of young age-0 pollock (Hunt et al., 2002a). Given the prevalence of cannibalism among pollock in the eastern Bering Sea, it was also anticipated that, in the absence of fisheries, pollock recruitment might become top-down limited as the population increased. Since 2000, the eastern Bering Sea has experienced some of the warmest years on record with early sea ice retreat (2001–2005), as well as a stanza of extraordinarily cold years (2007–2010) in which sea ice remained late into spring, thereby providing an opportunity to test the predictions of the OCH.

Over the past 10 years, a wealth of data has become available for the eastern Bering Sea, both from continued long-term monitoring of fish stocks and ocean conditions by the US National Oceanic and Atmospheric Administration (NOAA) and because of several large-scale, comprehensive research programmes. These include the Bering Sea and Aleutian Islands Salmon International Survey (BASIS; 2002–present), which also covered parts of the western Bering Sea, the Pribilof Domain Project (2004), the NOAA North Pacific Climate Regimes and Ecosystem Productivity programme (NPCREP; 2007–present), the Bering Sea Ecosystem Study (BEST; 2007–2011), and the Bering Sea Integrated Ecosystem Research Program (BSIERP; 2008–2012). These programmes, conducted in the context of striking environmental variability, have provided and continue to provide an unprecedented opportunity to assess how the Bering Sea ecosystem responds to extended periods of cold and warm conditions. This paper provides a brief overview of the newly available data and examines the assumptions and predictions of the OCH in light of these new data.

The eastern Bering Sea is dominated by a 500-km-wide shallow (70 m average) shelf that stretches northwest from the Alaska Peninsula to the coast of the Russian Federation (Figure 1). The shelf in summer is characterized by a number of domains that are defined by their hydrography (Stabeno et al., 2001). The middle domain extends from approximately the 50-m isobath to the 100-m isobath and, though well mixed in winter, is strongly stratified in summer. This stratification is dominated by temperature (Stabeno et al., 2010) and affects the amount of mixing that can occur between the nutrient-rich bottom layer and the nutrient-depleted upper mixed layer, thereby influencing the amount of post-spring bloom primary production (Coyle et al., 2008; Sambrotto et al., 2008).

The middle domain is important as a nursery area for fish, including age-0 pollock (Mueter et al., 2011). One of the main spawning areas for pollock is along the shelf edge just northwest of Unimak Pass (Bacheler et al., 2010). Many of the eggs and larvae from this spawning ground drift northeastwards, along the Inner Front that is the boundary between the middle domain and the coastal (inner) domain on the north side of the Alaska Peninsula (Kachel et al., 2002; Bacheler et al., 2010). The Inner Front facilitates a vertical flux of nutrients that supports new production at and offshore of the front during summer (Stockwell et al., 2001; Sambrotto et al., 2008). Copepods and euphausiids graze this production and become prey for juvenile fish, including
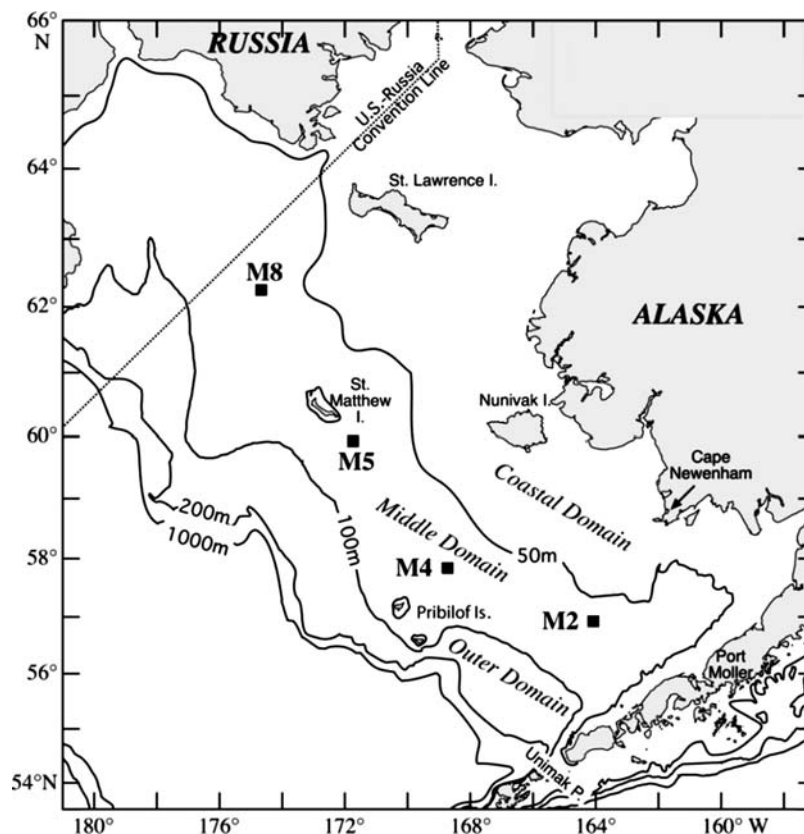

Figure 1. Map of the eastern Bering Sea shelf displaying the location of the inner, middle, and outer shelf domains and the positions of NOAA biophysical moorings (M2). Modified from Hunt et al. (2010).

salmon and pollock, as well as for seabirds (Coyle and Pinchuk, 2002; Hunt *et al.*, 2002b; Jahncke *et al.*, 2005). Similar nursery areas are present in the middle domain at and offshore of the structural fronts that encircle the Pribilof Islands (Brodeur *et al.*, 2002; Duffy-Anderson *et al.*, 2005; Swartzman *et al.*, 2005).

The southeastern middle domain also is subject to high interannual variability in climate-driven sea ice cover and water temperature (Stabeno *et al.*, 2001; Hunt *et al.*, 2010). To understand climate impact on the southeastern Bering Sea ecosystem, it is useful to distinguish the impacts of sea ice cover from those of temperature, *per se*, though the two are clearly linked. The amount of ice melt and its location in late winter and spring determines the bottom temperatures over the shelf when the melt water is mixed to the bottom by winter storms. Water column temperature is affected by the amount of ice that melts, regardless of the time of melting, as well as the amount of solar radiation reaching the ocean surface during the year, in particular during summer. In the early 1970s and in 2006–2009, most years experienced very cold water temperatures. An exception was 2006, which was intermediate in temperature, because of the heat remaining in the water column from the previous warm years. A series of years with light ice and warm summers will result in increasing integrated water temperatures, because heat from the preceding warm years remains in the water column; series of years with heavy ice cover and cloudy summers will result in decreasing temperatures over time. Therefore, it might be useful to distinguish among cold years (early 1970s, 1999, and 2007–2009), warm years (most of the 1980s and 1990s), and exceptionally warm years (2001–2005).

The timing of retreat of the sea ice affects both the near-surface stratification by the release of freshwater at the surface and the availability of light for supporting photosynthesis. Based on its effect on the timing of the spring bloom, late ice retreat is considered to happen when ice lingers after the end of March (Stabeno *et al.*, 2001; Hunt *et al.*, 2002a). In this paper, we focus on how climate variability, particularly because it affects sea ice cover, affects the pelagic foodweb of this region and the resulting interannual variability in walleye pollock year-class strength. We focus on the timing of ice retreat, because it apparently has the major impact on the timing of the spring bloom and the water temperatures in which it occurs (Hunt *et al.*, 2002a).

Methods
Biophysical measurements at Mooring 2
The biophysical mooring, M2 (Figure 1), has been maintained since 1995. During summer, a surface mooring was deployed there, whereas in winter, a subsurface mooring was deployed because of the periodic presence of sea ice. The mooring was instrumented to measure temperature, salinity, nutrients, and chlorophyll fluorescence. In most cases, temperature was measured every 3–4 m in the upper 35 m and every 5–8 m below that. In winter, the uppermost instruments were at ~11 m. Refer to Stabeno *et al.* (2001, 2007) for details of mooring design and instrumentation.

Age-0 pollock, relative abundance, and diets
BASIS surface-trawl stations were sampled from 2003 to 2009 along the eastern Bering Sea shelf from 159 to 168°W and from the Alaska Peninsula to 60°N, with station spacing of ca.

30 nautical miles. Although initially designed for sampling juvenile salmon, age-0 pollock were also caught in the surface trawls, following the methods described in Farley *et al.* (2005) and Moss *et al.* (2009). The net used was a 198-m-long midwater rope trawl with hexagonal mesh wings, a 12-mm mesh liner in the codend, and a mouth opening of 55 m wide by 20 m deep. The trawl was towed for 30 min at 6.5–9.3 km h^{-1}, during daylight at or near the surface (ca. top 20–22 m). Age-0 pollock were counted and diet analysis (estimation of stomach contents) was conducted immediately on fresh samples. At each station, stomachs of ~20 randomly selected fish were pooled for each size class and stomach contents were identified to the lowest possible taxonomic level and weighed by prey group (Moss *et al.*, 2009). Diets from all fish <150 mm were combined to estimate proportional contributions (based on wet weights of prey groups) by year. The number of pooled samples in a year varied between 14 and 70; the number of fish stomachs varied between 122 and 1141.

The interannual comparison of both the number and the size of age-0 pollock caught in these trawls and their diets is based on the assumption that there were no systematic differences in the depth distribution of the age-0 pollock or net selectivity between stanzas of very warm and very cold years. If present, either of these factors could cause a systematic error in our comparisons. For example, if the smaller fish that predominated in cold years were not caught as efficiently as the larger fish in warm years, this could have created a bias in favour of the prediction that there would be fewer age-0 pollock in late summer after a cold spring. Acoustic surveys have been initiated in conjunction with the surface trawl survey and over the next few years, they should help resolve this issue of possible sampling bias. These data should be treated with some caution when interpreted as indicators of abundance and condition of age-0 pollock, but we believe that they are the best available source of information and sufficiently representative to include here.

Energy content of age-0 pollock
Estimates of the age-0 pollock energy content were made each year for pollock collected during BASIS surveys. Only hauls from south of 60°N are included in the current analysis. A random sample of fish from each haul was sampled for energy content via bomb calorimetry. The number of fish processed from each haul was proportional to the haul's contribution to the total catch during the survey and included fish from surface tows and midwater tows in 2008 and 2009. Within the southern middle shelf domain, no significant differences were detected in the energy content from surface- and midwater-caught fish; therefore, samples were combined. Based on the results from 2008 and 2009, we assumed that data from surface-caught fish in earlier years could be compared with those from later years.

Before 2007, 25–116 fish in a given year were processed and since then, sample sizes have been ~51 fish. Before 2006, fish were processed as described in Moss *et al.* (2009) and dried at 55°C for 24–36 h. After 2006, the method was altered by drying the samples at 135°C for ~3–4 h with a Leco 601 Thermogravimetric analyser. The dried homogenate was combusted in a Parr 1425 semi-micro-bomb calorimeter. Total energy per individual age-0 pollock was found as the product of the average energy density (kJ g^{-1} wet mass) and the average wet mass of age-0 pollock sampled in a given year.

Abundance of copepods by species in midsummer

Copepod abundance in midsummer was sampled using double-oblique tows of paired bongo nets (20 cm frame, 150 μm mesh and 60 cm frame, 333 μm mesh) taken to within 5 m of the seabed (Napp et al., 2002). Samples from 1998 to 2008 were taken aboard the T/V "Oshoro Maru" and were preserved in buffered 5% formalin–seawater solution and sent to the Polish Plankton Sorting and Identification Centre for identification and enumeration. For comparison with earlier years, concentrations of selected species were obtained from Smith et al. (1982). Means and standard errors were calculated using transformed data (Napp et al., 2002).

Abundance of copepods and amphipods in late summer/autumn

Small zooplankton was sampled with a 0.1-m^2 Juday net having 168 μm mesh (Volkov, 1984; Volkov et al., 2007). The net was towed vertically from the bottom to the surface at $\sim$1 m s^{-1}. The samples were separated into three size fractions using two sieves of 0.5 and 1.2 mm mesh. If large zooplankton was present (euphausiids, medusae, and hyperiids), the samples were initially sieved through 3–4 mm mesh to facilitate processing. The small size fractions were counted using a Bogorov chamber; the large fraction was counted entirely and abundance estimates were corrected for net avoidance (Volkov, 1996; Volkov et al., 2007). Large zooplankton was collected with a 60-cm bongo net having 505 μm mesh. Double-oblique tows were done from the surface to near the bottom, and the volume filtered was measured with General Oceanics flowmeters. Samples were preserved in 5% formalin–seawater; collections before 2005 were sorted at the Morski Instytut Rybacki Plankton and Identification Centre (Szczecin, Poland) to the lowest taxonomic level and developmental stage possible. Wet weights were not measured. Collections from 2005 to 2009 were processed at the University of Alaska as outlined in Coyle et al. (2008); wet weights on all taxa and stages were taken. Zooplankton was collected primarily during the day. Zooplankton data were power-transformed (raised to 0.15) for statistical analyses.

Acoustic surveys of euphausiids

Scientists from the NOAA Fisheries–Alaska Fisheries Science Center conduct acoustic surveys of age-1 and older midwater walleye pollock on the middle and outer Bering Sea shelf during summer (Honkalehto et al., 2009). Since 2004, these surveys have collected acoustic data at five frequencies (18, 38, 70, 120, and 200 kHz), allowing objective classification of acoustic backscatter from pollock and some other common acoustic targets, including euphausiids (De Robertis et al., 2010). An acoustic index of euphausiid biomass consisting of acoustic backscatter at 120 kHz, with a frequency response consistent with euphausiids, is currently under development (P. Ressler, NOAA, Alaska Fisheries Science Center, unpublished data). Assuming that euphausiids are the dominant acoustic target in layers of this euphausiid backscatter and that euphausiid size and species composition have remained relatively consistent over successive surveys, these backscatter data may be interpreted as a proxy for euphausiid biomass in the survey area.

Periodically, the composition of layers of euphausiid backscatter was sampled with a large plankton–ichthyoplankton trawl (a Methot trawl with a 5-m^2 mouth opening, 2 $\times$ 3 mm oval mesh in the body and 1 mm mesh in the hard codend; Methot, 1986). Samples from these tows were preserved in buffered 5% formalin–seawater solution and sent to the Polish Plankton Sorting and Identification Centre for identification and enumeration. The composition of these catches has averaged >90% euphausiids, both by volume and by number, consisting principally of the species *Thysanoessa raschii* and *T. inermis* with an average length of $\sim$18 mm.

Comparison of recruitment trends

To compare recruitment trends between pelagic- and benthic-feeding juvenile fish, estimated time-series of recruitment for walleye pollock and four flatfish species (arrowtooth flounder, *Atheresthes stomias*; flathead sole, *Hippoglossoides elassodon*; yellowfin sole, *Limanda aspera*; and rock sole, *Lepidopsetta* spp.) were obtained from the North Pacific Fisheries Management Council's 2009 stock assessments (NPFMC, 2009). Recruitment anomalies for the flatfish group were computed by log-transforming and normalizing (removing mean and dividing by standard deviation) each of the individual recruitment series and summing annual deviations across the four. Pearson's product–moment correlations between the two series were then computed and tested for significance after adjusting the time-series for possible autocorrelation using the method of Pyper and Peterman (1998).

Results and discussion

In the southeast Bering Sea at M2 (Figure 1), the timing of sea ice retreat and the last winter storm influence the timing of the spring bloom (Figure 2; Stabeno et al., 2001; Hunt et al., 2002a). If the sea ice retreats before the last of the winter storms, strong wind mixing delays the start of the bloom until insolation warms the upper water column sufficiently to prevent mixing. Under these circumstances, the bloom happens late in spring, in relatively warm water (2–5°C). In contrast, if the sea ice remains until after the last of the severe winter storms, then a very thin (1–2 m) layer of freshwater from ice melt stabilizes the upper layer sufficiently to permit an ice-associated bloom in cold (ca. −1.7°C) water. Because the sea ice can remain in the southeastern Bering Sea until May or even June, the calendar date of an ice-associated bloom could be later than that of an open-water bloom. Although 2006 was a year with late ice retreat over most of the southern shelf (Figure 3), at M2 the ice had retreated early and the bloom there was late (Figure 2). Ice-associated blooms can occur in what might be classified as "warm years" based on summer sea surface temperature (SST; e.g. 1997).

Satellite imagery might detect blooms that are not recorded by the mooring sensors and hence more work should be done to understand the relationships seen at M2 and those seen by satellite. For example, satellite ocean colour chlorophyll *a* data indicate that there was an early (March) ice-associated bloom in 2003, which is not evident in Figure 2 (see Hunt et al., 2010).

Based on the assumption that blooms in warm water are more efficiently grazed by zooplankton than those in cold water (Walsh and McRoy, 1986; Huntley and Lopez, 1992) and that larval pollock growth and survival are higher in warmer waters (Bailey et al., 1996), Hunt et al. (2002a) predicted that survival and growth of age-0 pollock should be greater in years with early sea ice retreat and open-water blooms in warm (2°C) water. Evidence from surface trawls conducted over a wide area of the middle shelf of the eastern Bering Sea from 2003 to 2009 revealed high catch per unit effort (cpue) of age-0 pollock in years with
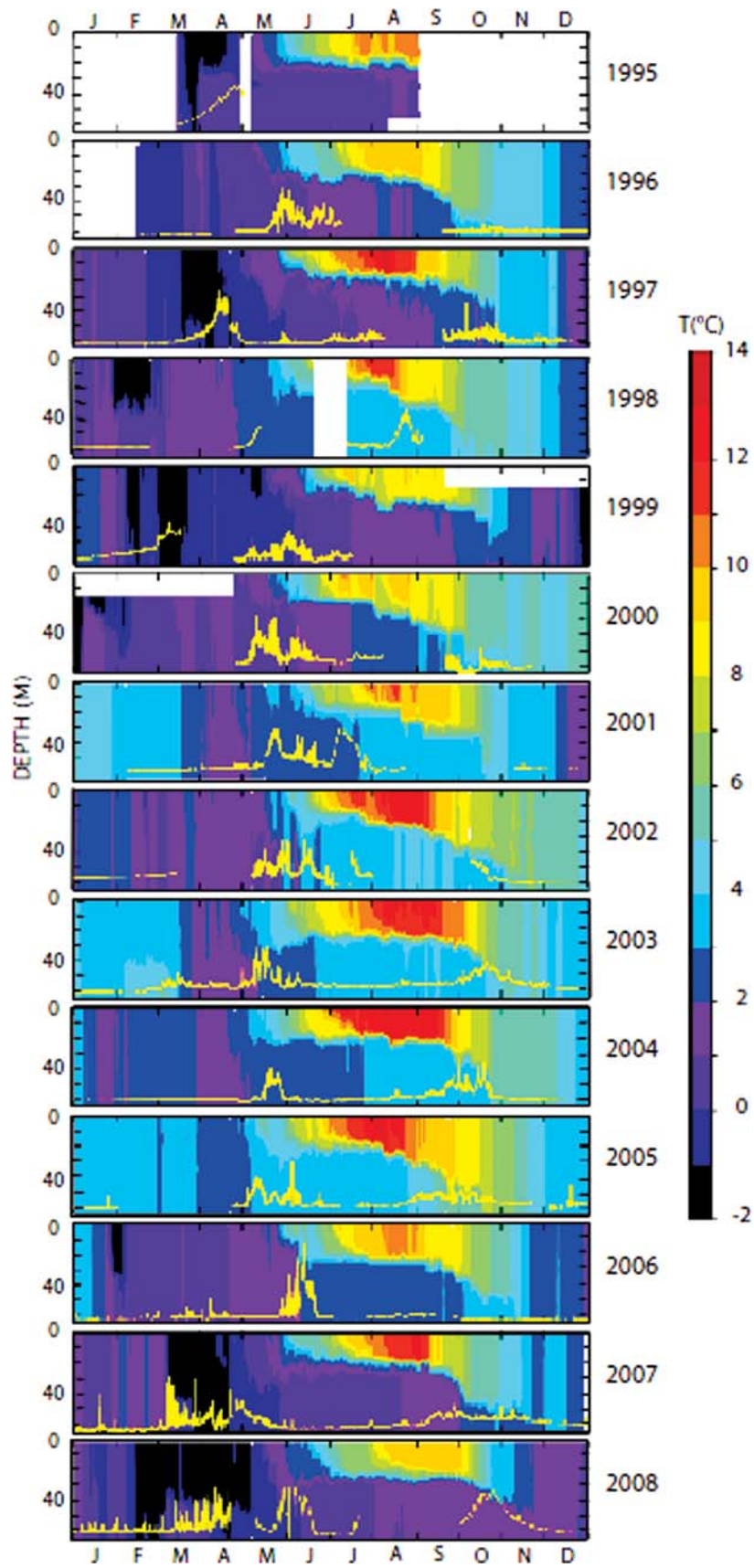
Figure 2. Mooring 2 time-series of temperature profiles and fluorescence. Yellow lines coming up from the bottoms of the panels indicate fluorescence scaled to the maximum in each year. Modified from Hunt *et al.*, 2002a.
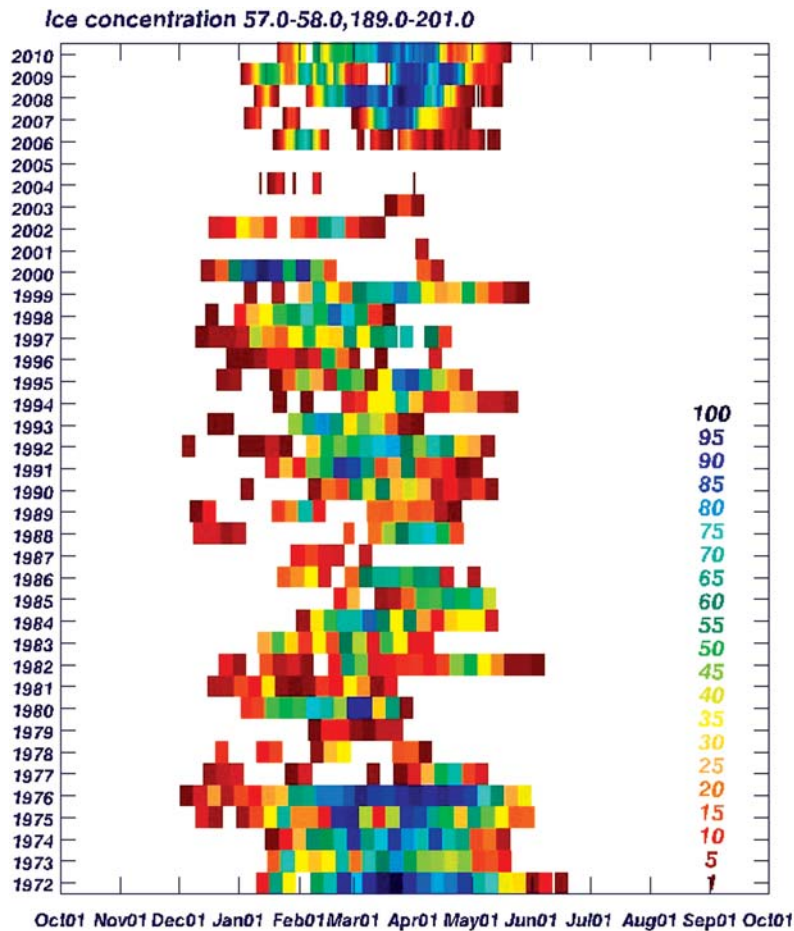
Figure 3. Mean ice concentration over all the pixels in a "box" from 57 to 58°N and 189 to 201°E (i.e. 171–159°W). The scale is percentage ice cover (concentration). The figure was created with data from the National Ice Center (1972–2002) and AMSR-E (the Advanced Microwave Scanning Radiometer Earth Observing System sensor on the MODIS satellites) from 2003 to the present. NIC data were read from their CD and Arctic and Antarctic Sea Ice Data and downloaded from their website. Files for AMSR-E were downloaded from the EOS data pool at NSIDC. The plot does not apply correction factors to either dataset. NIC data are weekly and AMSR data are daily files. Reproduced from Hunt *et al.,* 2010.
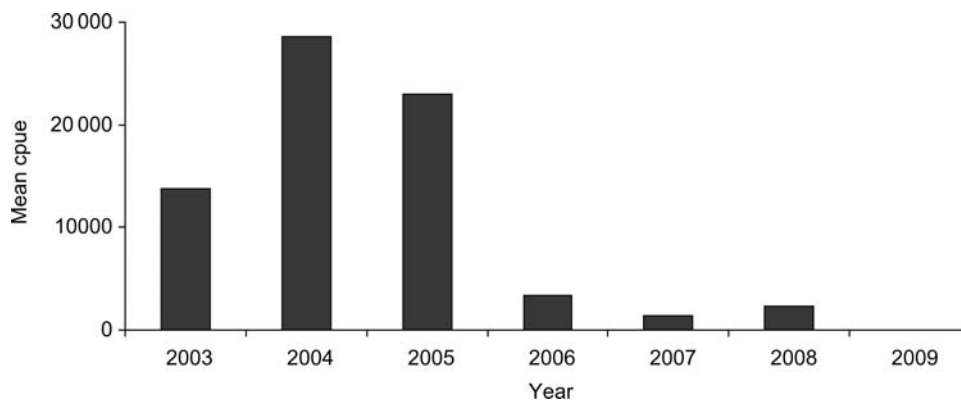

Figure 4. Mean abundance per haul (cpue) for age-0 pollock in the southeast Bering Sea from BASIS late summer/autumn (mid-August–September) surface trawls (top 20–22 m) for 2003–2009.

early ice retreat (2003–2005; Figure 4); a finding consistent with the prediction of the OCH that young age-0 pollock should have high survival under warm conditions in spring. The small numbers of age-0 pollock caught in the years with late ice retreat (2006–2009) could reflect lesser survival of young age-0 pollock, as predicted by the OCH, or they might result from the fish having descended in the water column below the area swept by the surface trawl.

There is also limited evidence that the lengths of age-0 pollock in the upper mixed layer were greater in the years of early ice retreat (2004 and 2005) than they were in "cold" years when ice lingered late in the southeastern Bering sea (1999, 2006, and 2007; Coyle *et al.*, 2008; R. Heintz, NOAA, Alaska Fisheries Science Center, unpublished data), indicating faster growth in warm springs, as predicted by the OCH. However, age-0 pollock lengths were not smaller in 2008 or 2009 (L. Eisner, unpublished data); therefore, the results of this prediction remain equivocal and need further investigation.

Additional support for the predicted relationship between the timing of sea ice retreat and the production of strong pollock year classes comes from an examination of recruitment anomalies of walleye pollock, which largely depend on pelagic prey during the larval and juvenile stages, vs. flatfish, which depend on benthic prey after settling to the bottom during their first summer (Figure 5). It was reasoned that if copepods were more efficient at grazing an open-water bloom in warm water than an ice-associated bloom in cold water, there should be an inverse relationship between the transfer of primary production to the pelagic and benthic foodwebs (Hunt *et al.*, 2002a). The results presented in Figure 5, an extension of the work of Mueter *et al.* (2006), support this prediction. Recruitment anomalies of fish species whose juveniles forage in the water column are out of phase with the recruitment anomalies of fish whose juveniles forage in the benthos ($r = -0.52$, $p = 0.005$), implying that in years when energy is captured in the pelagic compartment, less energy is available in the benthic compartment and *vice versa*. This interpretation assumes that recruitment strength is affected by food availability at the juvenile stage, because larval flatfish share the pelagic environment with pollock until settlement.

However, the production of age-1 pollock recruits from the recent exceptionally warm period (2001–2005) was much weaker than that from the subsequent cold period (Figure 6), an observation not consistent with the OCH. Although the 2001 year class was near the long-term average, the 2002–2005 year classes were all well below average, whereas the 2006, 2008, and 2009 year classes were above average (Ianelli *et al.*, 2010). This observation in conjunction with the apparent large numbers of age-0 pollock in summers of the warm years suggests that recent pollock year-class strength in the eastern Bering Sea has been largely determined by factors affecting age-0 pollock in autumn and winter of their first year, not in spring and early summer as assumed in the OCH (Hunt *et al.*, 2002a).

Two avenues of investigation have suggested potential reasons for the failure of recruitment of age-0 pollock in the warm years. First, examination of the stomach contents of large age-0 pollock reveals that in the very warm years with little sea ice (2003–2005), there was more cannibalism than in the colder years of 2006–2009, when sea ice was present in the southeastern Bering Sea into May or even June (Figure 7). Similarly, juvenile salmon diets included a much larger proportion of age-0 pollock during the very warm years (Moss *et al.*, 2009; Coyle *et al.*, 2011), suggesting increased predation on these young pollock by other fish as well. Second, the total energy content of individual age-0 pollock in late summer was significantly lower in 2003–2005 and 2007, all years with apparently low survival of age-0
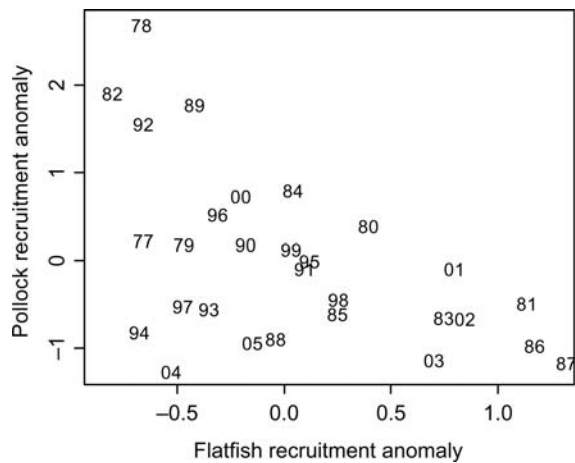

Figure 5. Scatterplot of pollock recruitment anomalies against standardized recruitment anomalies of flatfish. Numbers denote year of hatching.
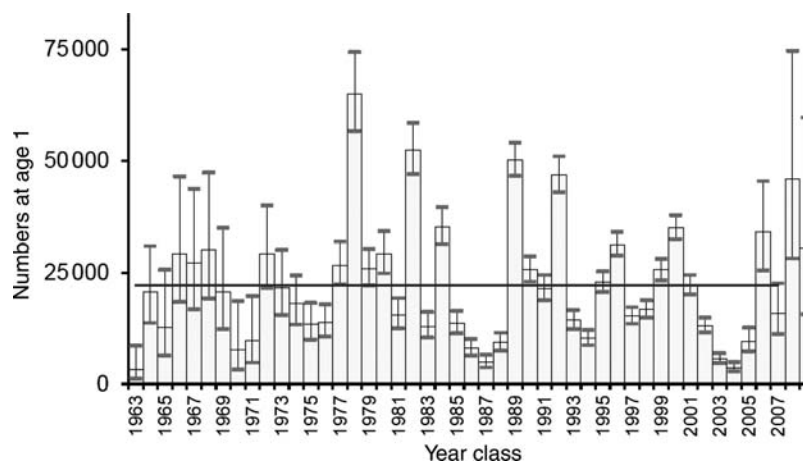

Figure 6. Time-series of assessment model output of age-1 recruits from the 2010 assessment document. Recent years depend primarily on survey results, whereas earlier years are adjusted to reflect numbers that must have been present to support the observed biomass of adults of a given year class (from Ianelli *et al.,* 2010).
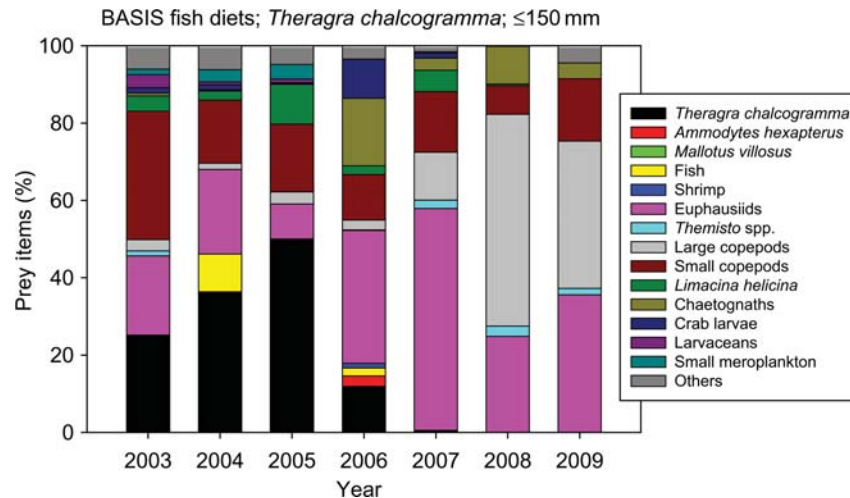
Figure 7. Diets of small (<150 mm) pollock, obtained during the BASIS surveys in August–September 2001–2009. Modified from Coyle et al., 2011.

pollock and was high in 2006, 2008 and 2009, years with apparently strong age-0 survival (Figure 8).

One possibility that could explain both the low lipid content of age-0 pollock and increased predation during the years with early ice retreat would be the loss of large species of crustacean zooplankton from the southeastern middle shelf during the 2001–2005 period, in particular those species that store large amounts of lipids before overwintering. Several lines of evidence suggest that these large zooplankton species were scarce from 2001 to 2005 and that they increased thereafter when spring ice cover increased. Samples of zooplankton taken in July, initially as part of the T/V "Oshoro Maru" sampling programme, demonstrate that the medium-sized copepod, *Calanus marshallae*, was virtually absent from both the middle and outer domains from 2001 to 2005, then increased from 2006 to 2008 (Figure 9a). Similarly, acoustic surveys of the outer and middle domains by the Alaska Fisheries Science Center suggested a low biomass of euphausiids in 2004, with marked increases in biomass over the period 2006–2009 (Figure 9b). Likewise, late summer (August–September) surveys of the middle domain using both Juday nets and bongo nets revealed low abundances of both *C. marshallae* and the cold-water amphipod, *Themisto libellula*, between 2003 and 2005, followed by significant increases annually from 2006 to 2008 (Figure 10). Together, these data reveal that there was a scarcity of these three species of medium to large crustacean zooplankton during the light sea ice years of 2001–2005 and that subsequent to 2005, when sea ice cover during spring was heavy, populations of these zooplankton species increased. What is particularly noteworthy is the prolonged period needed to reconstitute the stocks of this zooplankton once depleted over a period of years. The absence of large zooplankton species during years with early sea ice retreat would be expected to result in the loss of this energy-rich prey from the diets of the age-0 pollock, with a concomitant loss of condition and lipid reserves for overwintering in the age-0 fish.

The absence of large zooplankton species from the middle shelf could further result in increased predation on age-0 pollock because of prey switching (Cooney et al., 2001). The same large zooplankton species that are important prey for age-0 pollock are also a major dietary component of salmon and of juvenile
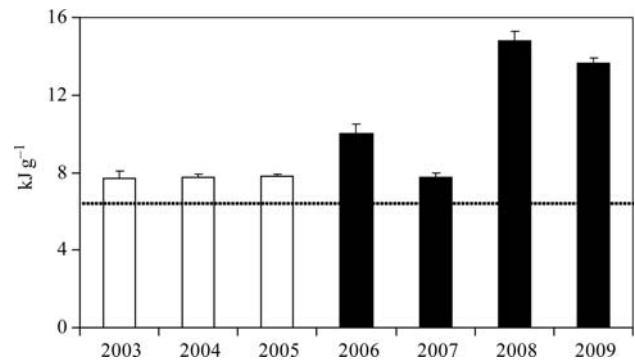

Figure 8. Estimated average ($\pm$ 95% confidence interval based on the estimate of energy density among individual fish) energy content (kJ g^{-1}) of age-0 pollock collected on BASIS surveys during August–September. Open bars indicate pollock from warm years; solid bars depict cold years. The horizontal line displays the average energy content of age-1 pollock sampled in southeastern Alaska during March 2002.

and adult pollock in the eastern Bering Sea (Aydin et al., 2007; Moss et al., 2009). Predators might switch from consuming primarily large zooplankton to consuming primarily age-0 pollock during low sea ice years when large zooplankton is scarce. Although this hypothesis is supported by the available diet data from age-0 pollock and juvenile salmon (Figure 7; Moss et al., 2009; Coyle et al., 2011), the hypothesized role of prey switching in adult pollock and other predators has yet to be examined.

Although we cannot predict when individual strong year classes of pollock will occur, there is evidence that both predation (including cannibalism) and warm summer SSTs have significantly influenced recruitment strength since at least 1977 (Mueter et al., 2011). In combination, these indices explain 44% ($p = 0.001$) of the variance in pollock recruitment. Summer SSTs are correlated with temperatures in spring and with the timing of ice melt (Mueter et al., 2011) and might not only provide a proxy for summer stratification and the resulting decrease in nutrient supplies to support summer production, but also provide a proxy for spring conditions that affect the recruitment of large crustacean zooplankton.
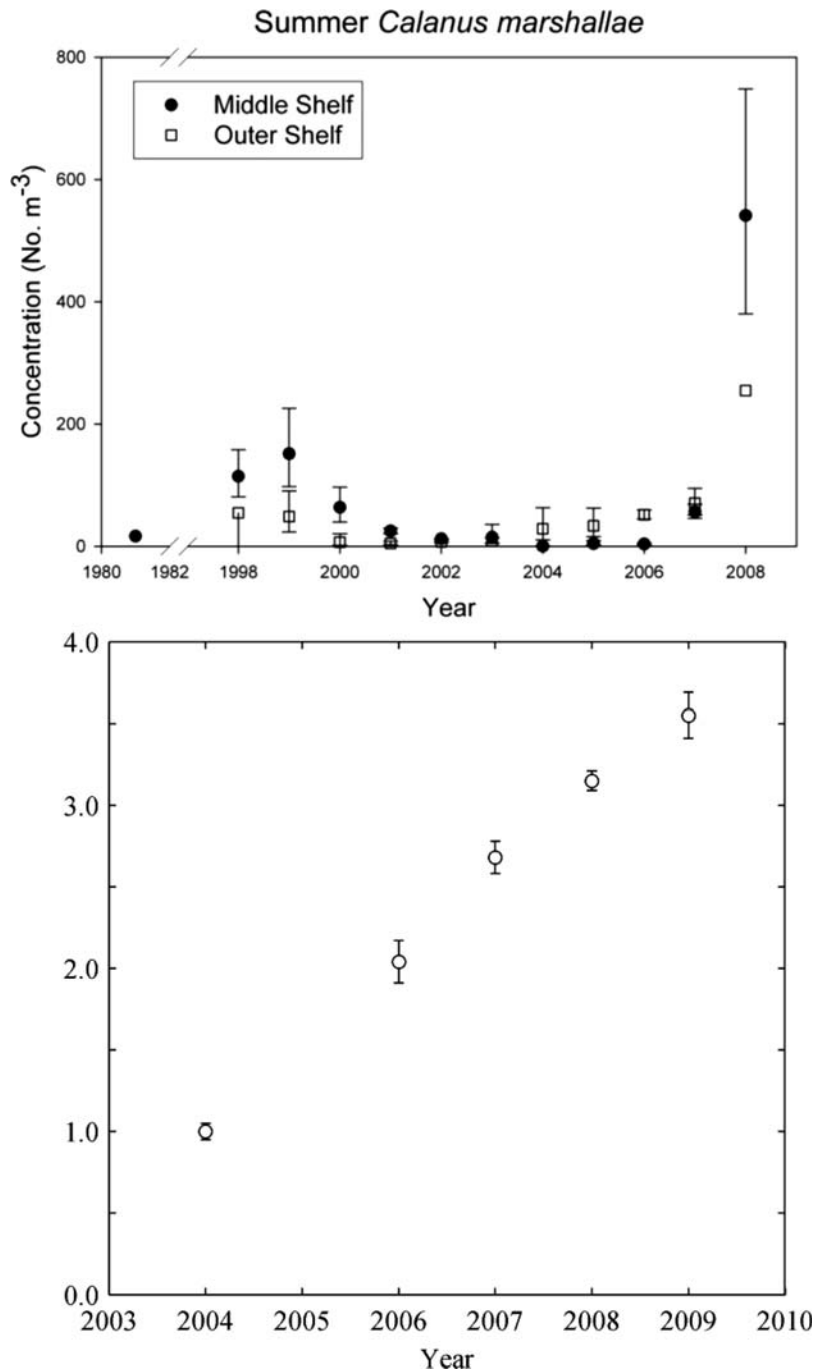
Figure 9. (a) Summer concentrations of *C. marshallae*. Mean and standard error of all *C. marshallae* copepodites collected over the middle and outer shelf domains during midsummer. Data from 1981 are from PROBES and data from 1998 to 2008 were collected with the T/V "Oshoro Maru" (from Hunt *et al.*, (2008). (b) Euphausiid backscatter from the NOAA-AFSC acoustic survey of midwater pollock on the middle and outer Bering Sea in 2004 and 2006–2009. Each value is the sum of euphausiid s_A (m²nautical mile^{-2}; MacLennan *et al.*, 2002) over the entire water column in 0.5-nautical mile horizontal intervals along all survey transects, normalized to the sum observed in 2004 to illustrate the temporal trend since that year. Error bars indicate a geostatistical estimate of sampling error about this sum (Petitgas, 1993).

Reassessment of the OCH

There are two parts to the OCH and its application to the recruitment of walleye pollock in the eastern Bering Sea: the relationship between the timing of sea ice retreat in spring and its effect on the abundance and types of crustacean zooplankton available to developing pollock and the potential for alternation of top-down and bottom-up controls of pollock recruitment (Hunt *et al.*, 2002a). The new evidence, some of which is highlighted in this paper, requires that both aspects of the OCH must be revised. These revisions are discussed below.

The initial assumption of the OCH, based on Stabeno *et al.* (2001) and mooring data to 2000, was that the timing of ice
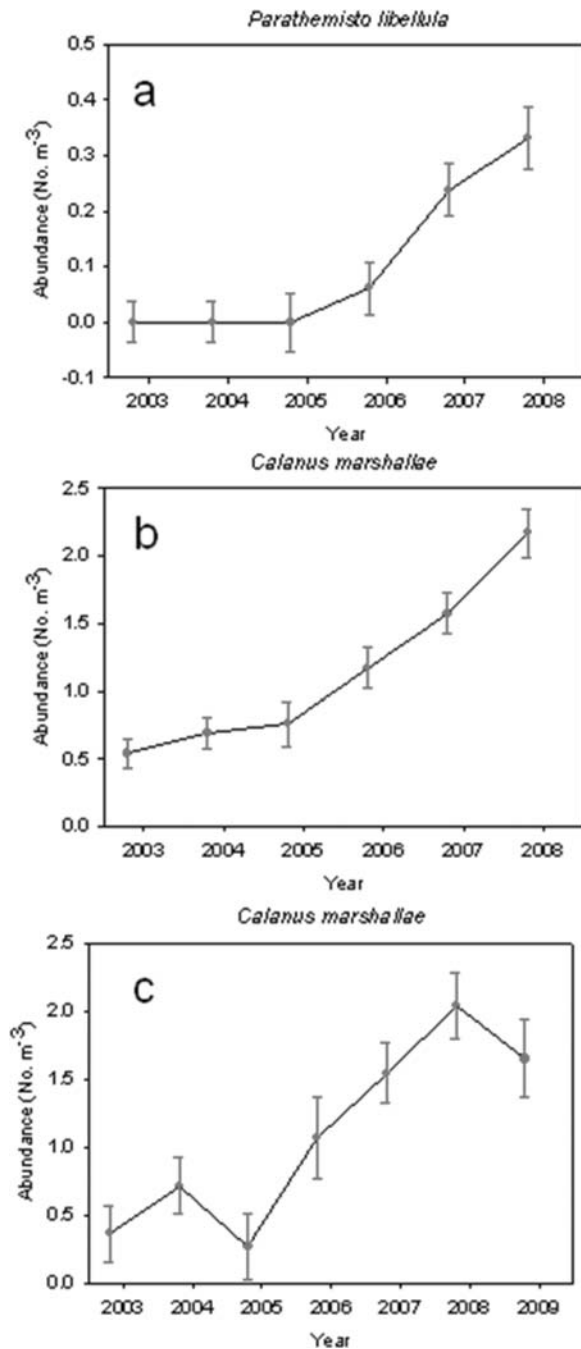
Figure 10. Mean abundance (power transformed) of C. marshallae and Themisto spp.; August – September 2003 – 2009. (a and b) bongo net samples; (c) Juday net samples.

retreat at M2 influenced the timing of the spring bloom there, as determined from the mooring's fluorescence signal. Subsequent observations from M2 confirm that in almost all years to 2009, a late ice retreat yields an ice-associated bloom in cold (ca. $-1.7°C$) water and an early ice retreat yields a late bloom in open water that is relatively warm ($2-5°C$).

The OCH was also built on the assumption that neritic crustacean zooplankton, specifically copepods, would grow more rapidly and crop more of the primary production when the bloom occurred in warm water than when it occurred in cold water. The new data currently available reveal that this assumption

was incorrect. The biomass or abundance of the small neritic species (Acartia spp., Pseudocalanus spp.) was apparently no greater in years with blooms in warm water than in years with blooms in cold water (Hunt et al., 2010). More importantly, a variety of sampling efforts reveals that there were many fewer of the medium-sized, lipid-rich shelf copepod C. marshallae in the years with blooms in warm water (Figures 9–11). These results support the findings of Baier and Napp (2003) that C. marshallae requires an early bloom in cold water to recruit successfully from nauplii to copepodites in the southeastern Bering Sea.

Despite these new findings, two of the predictions of the OCH apparently are supported by the new data and analyses. First, in years with blooms in warm water, more spring primary production goes into the pelagic component of the shelf ecosystem (Mueter et al., 2006; Figure 5). Second, the available data support the OCH prediction that in years with blooms in warm water, more age-0 pollock survive to summer. Apparently, feeding conditions during spring and early summer of the warm years supported rapid growth and survival of these small pollock. If their subsequent survival had continued to be good or average, the large numbers of age-0 pollock would have resulted in strong year classes in years with early ice retreat and a late bloom in warm water; the predictions of the OCH would have been supported and it could have anticipated that periods of warm conditions with early ice retreat would have yielded growing populations of pollock (and other predators) that would have resulted eventually in the top-down regulation of pollock recruitment. This has not been the case.

An important new finding is that, despite the presence of substantial numbers of age-0 pollock following late spring blooms in warm water, there were no strong year classes between 2001 and 2005. This implies that autumn and overwinter survival of age-0 pollock was exceptionally poor following years with early ice retreat and warm springs and summers.

Two factors could explain high post-summer mortality of age-0 pollock in these very warm years (Figure 12). Both are related to the lack of the medium-sized copepod, C. marshallae, and the euphausiids, T. raschii and T. inermis, in summers during the exceptionally warm period between 2001 and 2005. These copepods and euphausiids combined constitute up to 70% of the diets of both juvenile and adult pollock (Aydin et al., 2007). Additionally, they are important constituents of the diets of juvenile salmon entering the Bering Sea (Moss et al., 2009). Both C. marshallae and T. raschii are lipid-rich, because they store lipids in preparation for overwintering. When they are scarce, pollock and juvenile salmon in the southeastern Bering Sea shift their diets to include more age-0 pollock (Moss et al., 2009), much as was the case in Prince William Sound where adult pollock in the absence of large lipid-rich copepods of the genus Neocalanus increased their consumption of juvenile salmon and Pacific herring (Clupea pallasii; Cooney et al., 2001). Therefore, in the southeastern Bering Sea, the lack of C. marshallae and T. raschii in exceptionally warm years with early ice retreat is hypothesized to result in increased predation on age-0 pollock by larger pollock, salmon, and possibly other large fish (Figure 12). Interestingly, during the extended exceptionally warm period of 2001–2005, large jellyfish also declined in abundance over the shelf (Hunt et al., 2010), though by 2009, their abundance was once again high (M. B. Decker, pers. comm.), suggesting a widespread effect of this exceptionally warm period on the marine ecosystem of the shelf.
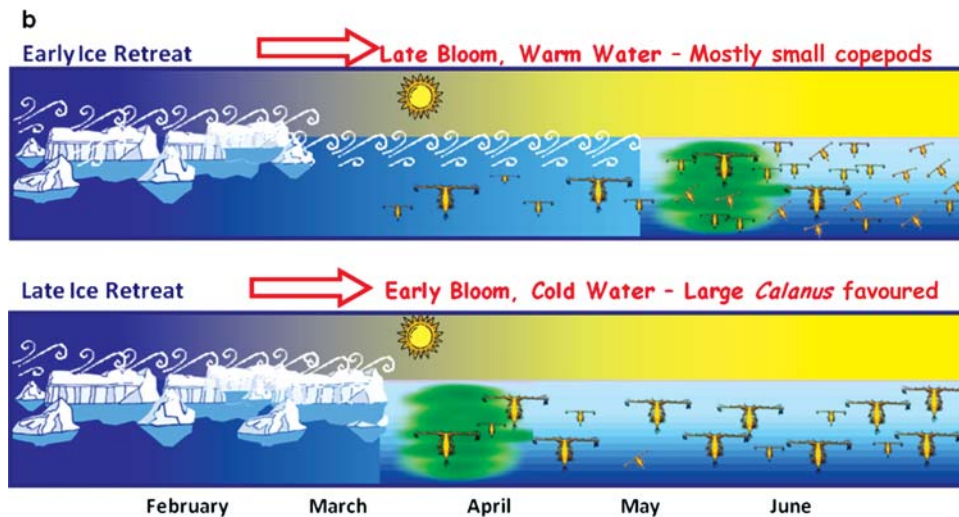
Figure 11. Cartoon illustrating the revised relationships among the timing of ice retreat, the bloom, and the production of copepods of different size classes. When there is an early ice retreat, the bloom occurs late in relatively warm water. These conditions favour small neritic copepods over mid- to large-sized *C. marshallae*. When the ice retreats late, the bloom occurs early, in association with the ice, and *C. marshallae* constitutes a major portion of the copepod biomass produced. Modified from Hunt *et al.* (2002a).
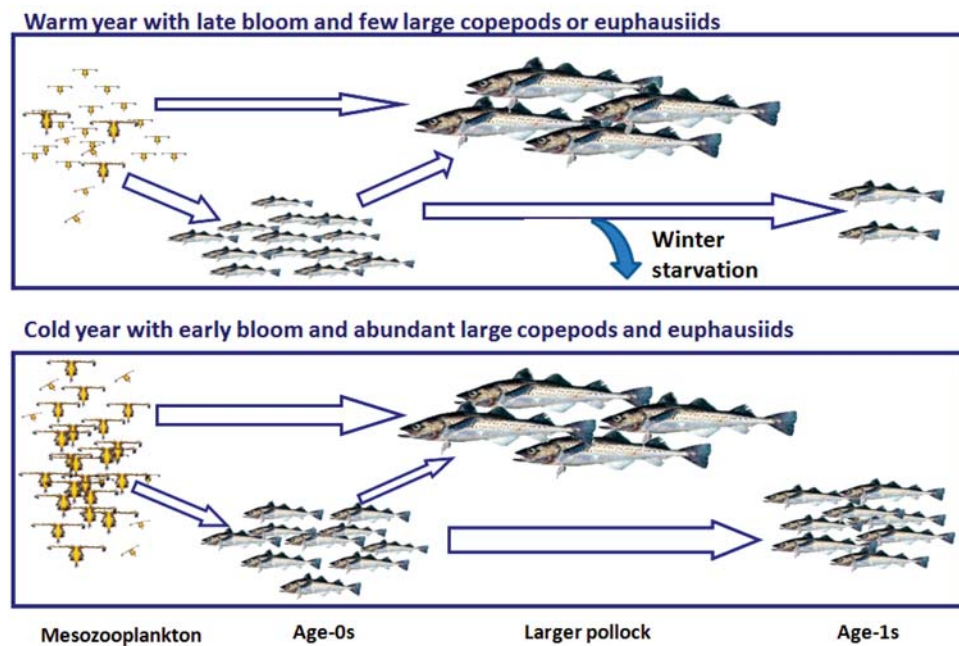

Figure 12. Cartoon illustrating the differences in trophic pathways depending on the availability of mid- to large-copepod, *C. marshallae* and the euphausiid, *T. raschii*, on the southeastern Bering Sea shelf. When large *C. marshallae* and *T. raschii* are not available, predation and cannibalism of age-0 pollock by larger pollock and other fish increases, as does overwinter mortality of age-0 pollock because of insufficient energy stores. When *C. marshallae* and *T. raschii* are abundant, cannibalism and predation on age-0 pollock are decreased and the age-0 pollock might have more abundant energy stores, resulting in stronger recruitment of age-1 pollock.

The lack of *C. marshallae* and *T. raschii* in late summer deprives the age-0 pollock of a lipid-rich prey source at a time of the year when they should be accruing lipid stores to carry them through their first winter (Sogard and Olla, 2000; Figure 12). The new evidence on the energy content of age-0 pollock in summers of warm years suggests that they are near or below the amount of lipids needed to survive winter (Figure 8). In addition to their higher energy content, lipid-rich zooplankton could contain essential

fatty acids needed by certain groups of fish (Litzow *et al.*, 2006). If true, in the absence of these nutrients, age-0 pollock in the southeastern Bering Sea might be under additional stress.

There are at least two non-exclusive hypotheses why *C. marshallae* and *T. raschii* do not thrive in warm years, one involving the timing and conditions under which the spring bloom occurs and the other focusing on summer stratification and post-bloom production. The first, based on the work of Baier and Napp

(2003), suggests that at least *C. marshallae* requires an early bloom, usually associated with the melting of the sea ice, to provide food essential to the recruitment of copepodites from the nauplii. In addition, Coyle et al. (2011) suggest that delay in the spring bloom, particularly in years where winter ice melt has been insufficient to cool the bottom waters, will stress the lipid reserves of *C. marshallae* and could adversely affect their survival and reproduction. *Calanus marshallae* depends on its lipid reserves to pass winter in diapause and warm temperatures would accelerate the exhaustion of these reserves through temperature-elevated metabolic rates. Similarly, *T. raschii* relies on its stored lipids to overwinter (Falk-Petersen et al., 2000). In the Barents Sea, the abundance of *T. raschii* has been found to decrease in warm periods, then subsequently increase in cold periods (Drobysheva, 1994), much as has now been demonstrated for this species in the Bering Sea. Recently, *T. raschii* has been observed foraging on under-ice algae in the Bering Sea and feeding rates were enhanced in the laboratory when they were allowed to feed on large algal cells from the under-ice surface (Lessard et al., 2010).

A second hypothesis is that strong stratification in summer depresses post-bloom new production; therefore, the large crustacean zooplankters, lacking appropriate food resources, leave the water column when the surface layer warms (Coyle et al., 2008). Coyle et al. (2011) also hypothesize that elevated water temperatures will interfere with the ability of both *C. marshallae* and *T. raschii* to amass sufficient lipid stores for overwintering. These hypotheses are discussed in Hunt et al. (2008) and Coyle et al. (2011).

It must be emphasized that there is likely an interaction of different time-scales for the processes described in this paper. The length of the period of exceptionally warm years with early ice retreat was likely a factor in its impact. The ocean accumulates heat slowly and it cools slowly; several consecutive years with similar conditions might be necessary for a maximal impact of climate on integrated water column temperatures. Likewise, though most copepods have generation times of a year or less, some copepods and euphausiids have lifespans that exceed a year, thereby allowing them to regenerate a population quickly after a single unfavourable year. With several unfavourable years in a row, it might then require multiple years to regenerate the population. Similarly, pollock have a lifespan of 15 or more years, thereby allowing them to weather several years unfavourable to reproduction. The removal of adults by fishing decreases the ability of the population to regenerate after a series of years with poor recruitment.

Concluding remarks

The new data presented in this paper reveal that in years with exceptionally early ice retreat there are likely to be weak year classes of walleye pollock. Of the years with the ten earliest ice retreats, five were also among the 10 years with the weakest year classes. However, there was not a reciprocal relationship for years with late ice retreat; only two of those years were in the top 10 years for year-class strength. Therefore, contrary to previous expectations, walleye pollock in the eastern Bering Sea might not benefit from high water temperatures. Mueter et al. (2011) recently found a dome-shaped relationship between temperature and year-class strength in walleye pollock from the 1970s to the present. This result suggests that either extremely high or extremely low sea temperatures might not be favourable for the production of strong year classes. It is noteworthy that many of the years in the 1970s and 1980s with strong year classes of pollock (Figure 6) were also years when sea ice was present into April (Figure 3), which would have been expected to sustain the production of the large lipid-rich crustacean zooplankton. Conversely, though we can say that the availability of large crustacean zooplankton is critical for the production of a strong pollock year class, it is not sufficient. Year-class strength in 1987 was weak, yet euphausiids were apparently abundant over the middle shelf that year, because they were a major component of seabird diets then (Hunt et al., 1996, Jahncke et al., 2008). The ability to define what is needed for a strong pollock year class remains elusive. However, if the Bering Sea continues to experience prolonged periods of unusually warm conditions, such as those observed in 2001–2005, a predominance of weak year classes is likely. The expectation is that pollock stocks would be unable to sustain the fishing pressure that they could during periods of frequent strong year classes.

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