Variation in annual production of copepods, euphausiids, and juvenile walleye pollock in the southeastern Bering Sea

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19 **Abstract**

20 We synthesize recent research on variation in annual production of copepods (*Calanus* spp.),
21 euphausiids (*Thysanoessa* spp.), and juvenile walleye pollock (*Gadus chalcogrammus*) in the
22 southeastern Bering Sea. We reach five conclusions: 1) the timing of the spring bloom is more
23 important than the amount of annual primary production for the transfer of primary to secondary
24 production (i.e., timing matters); 2) summer and fall, not just spring, matter: organisms must
25 maximize energy intake devoted to somatic growth and storage of lipids and minimize energy
26 expenditures during each season; 3) stored lipids are important for the overwinter survival of
27 both zooplankton and age-0 walleye pollock; 4) variation in ice extent and timing of ice retreat
28 affect the spatial distributions of phytoplankton, zooplankton, and age-0 walleye pollock; when
29 these spatial distributions match in late-ice-retreat years, the annual production of copepods,
30 euphausiids, and juvenile walleye pollock often increases (i.e., location matters); 5) if years with
31 late ice retreat, which favor copepod, euphausiid, and juvenile walleye pollock production, occur
32 in succession, top-down control increases. These conclusions help to explain annual variation in
33 production of copepods, euphausiids and juvenile walleye pollock. Copepods and euphausiids
34 often are more abundant in cold years with late ice retreat than in warm years with early ice
35 retreat due to bloom timing and the availability of ice algae during years with late ice retreat. As
36 a consequence, age-0 walleye pollock consume lipid-enriched prey in cold years, better
37 preparing them for their first winter and their overwinter survival is greater. In addition, there is a
38 spatial match of primary production, zooplankton, and age-0 walleye pollock in cold years and a
39 mismatch in warm years.

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41 Key words: climate, sea ice, productivity, zooplankton, walleye pollock, Bering Sea, match-
42 mismatch

43 **1. Introduction**

44 For over 100 years, an intellectual challenge for biological and fisheries oceanographers has been

to understand order-of-magnitude variation in annual production of zooplankton and fish (e.g., Cushing, 1982; Hjort, 1914). Annual production depends on: (1) the size of the mature population, (2) environmental variation leading to order-of-magnitude variation in abundance, and (3) the magnitude of top-down control (e.g., Bailey, 2000; Bakun, 1985; Hunt and McKinnell, 2006; Hunt et al., 2002; Hunt et al., 2011). Research in the North Pacific Ocean often has focused on spring (e.g., Dagg et al., 1984; Kendall and Duker, 1998) and the conditions that produce a strong spring phytoplankton bloom, and thus good feeding conditions for zooplankton and juvenile fish. The critical size that juvenile fish must reach to survive their first winter (critical size hypothesis, e.g., Beamish and Mahnken, 2001; Farley et al., 2009; Sogard and Olla, 2000) also has been repeatedly examined. Larger size confers reduced susceptibility to successful capture by gape-limited predators and enlarged energy reserves (Heintz and Vollenweider, 2010; Sogard, 1997). To understand variation in annual production of zooplankton and juvenile fish, a multi-factor hypothesis and integrated research approach is necessary (Hare, 2014).

In this paper, we synthesize recent integrated research on the annual production of copepods (*Calanus* spp.), euphausiids (*Thysanoessa* spp.), and juvenile walleye pollock (*Gadus chalcogrammus*) in the southeastern Bering Sea in relation to net primary production, and emphasize a bioenergetics perspective. In a strongly seasonal system, the nutritional energy available to zooplankton and juvenile fish strongly varies among seasons and among years. Further, the capacity of zooplankton and juvenile fish to store energy and bridge seasonal gaps in energy production may be limited depending on their life history stage and strategy. These organisms must obtain and maintain sufficient lipid stores each season; a full energy store only in spring is not enough (e.g., Sogard and Olla, 2000; Hurst, 2007). In addition, there may be a relationship between population size and recruitment that magnifies the impact of back-to-back years of poor or good recruitment.

The Bering Sea Project was a large, integrated ecosystem research program focused on the eastern Bering Sea shelf and the role of seasonal sea-ice cover (Fig. 1) (Wiese et al., 2012). Sea

ice consistently covers the northern Bering Sea each winter (Stabeno et al., 2012a), while ice extent and retreat timing vary annually in the southeastern Bering Sea (Stabeno et al., 2012b). The interaction of annual ice extent and the broad (500 km), nearly flat shelf makes the eastern Bering Sea spatially rich, with three cross-shelf domains (inner, middle, outer) (Coachman, 1986) and a distinct northern Bering Sea domain (Eisner et al., 2014; Grebmeier et al., 2006; Sigler et al., 2011; Stabeno et al., 2012a). The Bering Sea Project field years (2007-2010) occurred during a period of several cold years in succession when ice retreat was late in the southeastern Bering Sea (2006 - 2012), and followed a period of several warm years in succession when ice was absent or retreat occurred early (2001-2005) (Stabeno et al., 2012b) (Fig. 2). The abundances of copepods, euphausiids, and age-0 walleye pollock were low during the early-ice-retreat years and increased during the late-ice-retreat years (Fig. 2) (Coyle et al., 2011; Eisner et al., 2014; Hunt et al., 2011; Ohashi et al., 2013).

Icy winters and late ice retreats occur when winds from the north are frequent and Arctic in origin. The direction and force of the winds are influenced by the location of the Aleutian Low Pressure System, i.e., variations in storm tracks (Rodionov et al., 2007). Following late ice retreats, a subsurface 'cold pool' of water ($< 2^{\circ}\text{C}$) occupies much of the middle domain of the southeastern Bering Sea for the entire summer. The resulting pelagic ocean habitats structure forage fish distributions (Hollowed et al., 2012; Parker-Stetter et al., 2013), and influence zooplankton communities; for example, the recent cooling led to an increased presence of the large arctic amphipod (*Themisto libellula*) in the middle domain of the southeastern Bering Sea (Pinchuk et al., 2013).

Primary production in the southeastern Bering Sea is not remarkably high, but because the shelf is wide (500 km), overall ecosystem production is high. Production estimates for the different domains of the southeastern Bering Sea shelf cover similar ranges of $126\text{-}142\text{ g C m}^{-2}\text{ y}^{-1}$ (Brown et al., 2011), $110\text{-}150$ (Rho and Whitledge, 2007), $75\text{-}225$ (Springer et al., 1996), and $162\text{-}166$ (Walsh and McRoy, 1986), and are similar to the global mean value of $140\text{ g C m}^{-2}\text{ y}^{-1}$ (Brown et al., 2011). Millions of seabirds and marine mammals rear their young there (National Research

Council, 1996), and large, industrial fisheries in the southeastern Bering Sea produce about 40% of U.S. catches (Voorhees and Lowther, 2012). Large copepods, euphausiids, and juvenile walleye pollock are major forage species in this region (Buckley et al., this issue; National Research Council, 1996; Springer, 1992), and adult walleye pollock are the target of the largest single-species fishery in the U.S. (Bailey, 2013; Voorhees and Lowther, 2012).

Some predictions for the southeastern Bering Sea based on the original hypotheses of the Bering Sea Project were that: 1) warming would increase production of forage species such as large crustacean zooplankton (copepods and euphausiids) and juvenile walleye pollock (Hunt et al., 2002); 2) warming would increase available habitat for subarctic species such as walleye pollock and Pacific cod (*Gadus macrocephalus*) (Mueter and Litzow, 2008); 3) back-to-back warm years of high zooplankton production would shift control of pelagic production from bottom-up to top-down (Hunt et al., 2002); and 4) warming would affect the spatial distributions of predators and prey and thus predator-prey relationships (BEST, 2004; Wiese et al., 2012).

In this paper, we connect the major findings of the Bering Sea Project for climate, sea ice, phytoplankton, zooplankton, and juvenile walleye pollock. Our intent is to tie pieces together, drawing from published papers from the Bering Sea Project. We also introduce a few new results and ideas. Our work builds on previous syntheses by Hunt et al. (2002, 2011) and Coyle et al. (2011). Hunt et al. (2002, 2011) focused on bloom timing, zooplankton, and juvenile walleye pollock, and Coyle et al. (2011) focused on zooplankton and juvenile walleye pollock. In our paper we emphasize a bioenergetics perspective, and: 1) add more recent results on bloom timing, zooplankton and juvenile walleye pollock; and 2) add new sections on the sufficiency of primary production to support secondary production and the spatial overlap of phytoplankton, zooplankton, and juvenile walleye pollock. First, we examine the links between primary and secondary production and factors affecting their interannual variation. Second, we consider these findings from a bioenergetics perspective. Third, we examine how the location of phytoplankton, zooplankton, and juvenile walleye pollock affect trophic webs. Fourth, we place the results of the Bering Sea Project with field years in 2007-2010 into a historical context to gain a longer view

of operative mechanisms. Lastly, we provide some insights into what may happen in the future.

2. Primary and Secondary Production

2.1. Seasonal pattern of primary production

In the southeastern Bering Sea, annual net primary production (NPP, equal to gross primary production minus phytoplankton respiration) is determined by several factors including ice algal production, a spring bloom driven by seasonal stratification, and a fall bloom driven by the breakdown of that stratification (Alexander and Niebauer, 1981; Niebauer et al., 1995; Rho and Whitledge, 2007; Springer et al., 1996). In addition, during summer, a series of smaller blooms associated with wind events mix nutrients from below the pycnocline (Sambrotto et al., 1986, 2008; Stabeno et al., 2010). Each winter, strong winds and the breakdown of frontal structure result in cross-shelf flow so that nutrient-rich slope waters are transported onto the shelf and refresh the nutrient inventories (Danielson et al., 2012a, b; Stabeno et al., this issue), which, in turn, support ice algal production and the spring bloom. Primary production in ice-covered areas can occur in two modes, both of which precede the traditional spring bloom. The first mode is production at the base of the ice (Poulin et al., 2011), and the second mode is an ice-associated bloom near the ice edge, as the ice melts and retreats (e.g., Niebauer et al., 1995). Both forms of primary production can represent an important source of early-season food for copepods and euphausiids (Baier and Napp, 2003; Durbin and Casas, 2013; Pleuthner et al., this issue). The ice-edge associated bloom, arising from a salinity-stabilized water column, gives rise to the traditional spring phytoplankton bloom fueled by increased light availability and high nutrient concentrations. Nutrients in the upper mixed layer are depleted eventually, leading to termination of the bloom. In years when ice is absent or retreats very early in spring (before March 25th, Hunt et al., 2002), the spring bloom is delayed until the end of the winter storms when solar heating creates a buoyant upper mixed layer (Brown and Arrigo, 2013; Hunt et al., 2002; Sigler et al., 2014; Stabeno and Hunt, 2002).

In winter and spring, the daily rates of primary production are controlled by temperature and light that limit growth rates (Lomas et al., 2012), while in summer low nutrient concentrations

limit growth rates (Lomas et al., 2012) and high microzooplankton grazing rates may limit biomass accumulation (Stoecker et al., 2014). In fall, when the increased frequency and intensity of storms and the overall cooling of the water column reduces stratification and deepens the mixed layer, nutrients found beneath the pycnocline mix to the surface to fuel the fall phytoplankton bloom (Eisner et al., this issue). The fall bloom is usually weaker than the spring bloom (Brown et al., 2011; Rho and Whitledge, 2007; Sigler et al., 2014), as it is driven by nutrients that were isolated and therefore left over from the major spring bloom, and from those arising from recycling on the shelf during the growing season, rather than replenishment from basin waters (Mordy et al., 2012).

2.2. Comparison of cold years with late ice retreat versus warm years with early ice retreat

Whether a year is classified as ‘cold’ or ‘warm’ is most influenced by ice extent and the timing of ice retreat. A common classification is based on the depth-averaged temperature anomaly in the middle domain of the southeastern Bering Sea (mooring M2, see Fig. 1); years with sea ice on the shelf in March and April tended to have below-average temperatures, and years without ice had either average or above average temperatures throughout the year (Stabeno et al., 2012b). The phenology of annual primary production differs between early- and late-ice-retreat years (Fig. 3). Primary production peaks in late May when ice is absent or retreats early; when ice retreats late, primary production timing is related to ice retreat timing, with the spring bloom moving northward from late April to early June as the eastern Bering Sea becomes ice free (Brown and Arrigo, 2013; Hunt et al., 2002, 2011; Sigler et al., 2014). In cold years, the spring bloom is shorter in duration and reaches a greater daily volumetric maximum (primary production per unit volume) (Lomas et al., 2012) than in warm years, when the spring bloom is more prolonged and the maximum chlorophyll concentration is lower (Rho and Whitledge, 2007). In cold years, a larger fraction of annual production occurs during the spring bloom than in warm years (Lomas et al., 2012; Rho and Whitledge, 2007).

Although summer primary production is generally low, pulses of intense production are linked to wind mixing that bring nutrient-rich bottom water and viable phytoplankton cells into the

euphotic zone (Mordy et al., 2012; Sambrotto et al., 1986, 2008). These pulsed events make substantial contributions to total summer production, but are insufficient to boost total annual production (Liu et al., this issue). Primary production in summer does not appear to differ significantly between cold and warm years (Liu et al., this issue), nor does the frequency of wind mixing events (Eisner et al., this issue). Fall bloom timing is similar for cold and warm years, typically occurring in late September (Sigler et al., 2014). In fall, chlorophyll concentrations are greater in warm years and a greater percentage of the phytoplankton biomass is comprised of large phytoplankton cells (Eisner et al., this issue), indicating that rates of primary production in fall likely are higher in warm years than cold years, or that grazing on these cells is lower.

2.3. Primary production likely does not limit secondary production

There are a number of fates for NPP, including export to the benthos, cross- or along-shelf advection, and grazing by secondary producers (e.g., Baumann et al., 2013). Using information on the fate of primary production, we can constrain the fraction of NPP that is available to support secondary production (i.e., production of heterotrophic biomass), which is termed net community production (NCP) (Williams et al., 2004). NCP can be estimated by the seasonal drawdown of nutrients and/or carbon dioxide during net production of new organic matter (e.g., Cross et al., 2014; Mathis et al., 2010; Mordy et al., 2012). Year-to-year variability (~20%) in initial nutrient content and nutrient recharge each winter does not differ greatly between cold and warm years (Stabeno et al., this issue).

In cold years, when the spring bloom is ice-associated, it appears that NCP is greater (Mathis et al., 2010; Stabeno et al., this issue), and a larger fraction is exported to the benthos (50%; Moran et al., 2012; Baumann et al., 2013). In contrast in warm years, when the spring bloom occurs in ice-free waters, NCP is sometimes lower (Codispoti et al., 1986), and a smaller fraction reaches the benthos (~20%) (M. Lomas, pers. comm.). In the cold years of 2008 and 2009, NCP in the middle and outer domains averaged 25 ± 10 to 54 ± 32 mmol C m⁻² d⁻¹ ($\pm$ SD) (1 mmol C = 12 mg C), depending on the domain and year (Mathis et al., 2010; Cross et al., 2012). In cold years, euphausiid production is ~4 mmol C m⁻² d⁻¹ (as determined from models; Gibson and Spitz,

2011; Hunt et al., this issue) or 8-20% of NCP. This estimate is based on assumptions of trophic transfer efficiency and estimated euphausiid biomass from a nutrient-phytoplankton-zooplankton model (Gibson and Spitz, 2011), which can be reconciled with other estimates of euphausiid biomass by accounting for net avoidance (net-based estimates) and target strength (acoustic-based estimates) (Hunt et al., this issue). A similar NCP-consumption value has been estimated for copepods based upon direct comparison of other fates; it has been estimated that the fraction of NCP consumed by copepods in spring is ~15-20% when chlorophyll is $<2\mu\text{g L}^{-1}$ and ~1% when chlorophyll is $>10\mu\text{g L}^{-1}$ (Campbell et al., this issue), but the value of 1% is based on only a few measurements. In addition, the fraction of NPP consumed by microzooplankton in spring is 40 - 50% (Sherr et al., 2013). If ~50% of NCP is exported to the benthos or off the shelf in cold years (Baumann et al., 2013), sufficient NCP ($13\text{-}27\text{ mmol C m}^{-2}\text{ d}^{-1}$, using the 2008 and 2009 estimates) could still remain for copepod and euphausiid grazers. This carbon accounting approach suggests the availability of organic carbon is not likely to limit secondary production in cold years (Liu et al., this issue). Campbell et al. (this issue) also found that only about 50% of the primary production is grazed during spring during cold years and the majority of it was consumed by microzooplankton.

In the warm years of 1980 and 1981 (Coachman, 1986 (Fig. 37)), NCP in the middle domain was $14\text{-}23\text{ mmol C m}^{-2}\text{ d}^{-1}$ in 1980 and $100\text{-}200\text{ mmol C m}^{-2}\text{ d}^{-1}$ in 1981 (Codispoti et al., 1986), bracketing the cold years of 2008 and 2009 which had an NCP of $25\text{-}54\text{ mmol C m}^{-2}\text{ d}^{-1}$ (Mathis et al., 2010; Cross et al., 2012). Assuming that 20% of NCP sinks to the benthos, and using the lower 1980 range, that leaves a minimum of $11\text{-}18\text{ mmol C m}^{-2}\text{ d}^{-1}$ that could accumulate in the biomass of all heterotrophs, including large crustacean zooplankton in these warm years, compared to $13\text{-}27\text{ mmol C m}^{-2}\text{ d}^{-1}$ in cold years when 50% of NCP is estimated to be exported to the benthos. Late summer small crustacean zooplankton biomass did not vary as a function of regime in recent cold and warm periods ($p > 0.05$), whereas late summer large crustacean zooplankton biomass was much higher in cold than in warm years ($p < 0.05$) (Eisner et al., 2014). As respiration is already accounted for in the NCP estimate, this lower biomass of large crustacean zooplankton in warm years likely translates into lower copepod and euphausiid

demand for food, although food quantity and quality will impact production. These analyses imply that in both cold and warm years, there is likely to be sufficient net organic carbon production to support secondary production. A full evaluation of this conclusion awaits estimates of copepod and euphausiid production in warm years and a better constraint on upper trophic level production. Instead of quantity of NCP, the timing of availability of under-ice algae and of the spring bloom may be more important influences on secondary production, as we will discuss in section 2.4.

One question is whether differences in summer/fall production between cold and warm years can compensate for better conditions for large crustacean zooplankton during spring in cold years. Mechanisms that might promote greater primary production in summers of warm years versus cold years appear to be lacking (see section 2.2). Although chlorophyll concentrations are higher in the fall of warm years, this may be because grazing pressure is lighter due to a reduced biomass of large zooplankton. While the euphausiid *Thysanoessa raschii* may continue breeding in summer (40% of individuals caught 8 -13 August 1989 were carrying spermatophores (Hunt et al., 1996)), given the life histories of most of the large zooplankton and their need to store lipids, it seems unlikely that they would be able to increase population size in response to increased levels of phytoplankton in late September and early October.

2.4 Importance of spring bloom timing

After the year 2000, several warm years (2001-2005) occurred in succession when ice was absent or retreated early; these warm years were followed by several cold years (2006 -2012) when ice retreated late (Stabeno et al., 2012b). Abundance of large crustacean zooplankton was low during the early-ice-retreat years (2001-2005, Fig. 2) and increased during the late-ice-retreat years (2007-2010) (Coyle et al., 2011; Eisner et al., 2014; Hunt et al., 2011). So, if not food limited (section 2.3), why did large crustacean zooplankton abundance increase during late-ice-retreat years, but not in years with early ice retreat? The evidence points to spring bloom timing as an answer based on evidence from fieldwork (Baier and Napp, 2003) and modeling (Banas et al., 2014) (Fig. 3), as well as to a decrease in walleye pollock biomass, which will be

discussed in section 5.

Metamorphosis of the copepod *Calanus* spp. to the copepodite stage occurs over a relatively short period, coincident with the spring bloom, and is enhanced in cold years; the magnitude of copepodite (C1-C5) abundance was greatest in cold years (Baier and Napp, 2003). Banas et al. (2014) coupled a model of phytoplankton and microzooplankton to the BESTMAS model of temperature, currents, and ice (Zhang et al., 2010) to examine whether variations in primary production during spring could explain the association of abundant *Calanus* spp. copepods with cold years. They found that, in general, production of both phytoplankton and microzooplankton is weakly positively correlated with temperature, and that the exceptions to this pattern are matters of bloom timing, not bloom magnitude. The implication of this model result is that direct effects of temperature on rates of photosynthesis or respiration do not appear to be major drivers of interannual or interdecadal variation in primary production, compared with the direct and indirect effects of ice cover on bloom timing.

A likely mechanism underlying the importance of spring bloom timing is food availability to zooplankton (Fig. 3). When ice retreats late, spring bloom timing is related to ice retreat timing ($p < 0.001$) (Sigler et al., 2014) and the spring bloom occurs near the ice edge (Lomas et al., 2012). Ice algae are present in cold years; phytoplankton and ice algae are the dominant food sources for copepods and euphausiids, especially during blooms (Lessard et al., 2012; Campbell et al., this issue). It was previously hypothesized that ice algae is an important food source for copepodites prior to the main spring bloom (Baier and Napp, 2003) based on previous reports of ice algal feeding by *Calanus* in another high latitude system (Runge and Ingram, 1991; Tourangeau and Runge, 1991). More recently, *Calanus glacialis*, a close relative of *C. marshallae*, was found to initiate feeding and reproduction under extensive ice in the northern Bering Sea during late winter despite very low mean water column chlorophyll *a* concentrations (Durbin and Casas, 2013). Although it takes phytoplankton bloom conditions (i.e., Chla >3 $\mu\text{g/L}$ or ca. 150 $\mu\text{g C/L}$) to saturate the grazing response of common copepods (e.g., *Pseudocalanus* spp., *Neocalanus* spp., and *Calanus* spp.) and the euphausiid *Thysanoessa* spp. during spring

(Campbell et al., this issue), copepod grazing responds to the presence of ice algae. During shipboard grazing experiments, ingestion rates were highest when copepods (Campbell et al., this issue) and euphausiids (Campbell et al., this issue; E. Lessard, U. Washington, pers. comm.) were fed mixtures of ice algae and water column phytoplankton. When ice retreats late, the availability of ice algae and the timing of the ice-associated bloom match the timing of egg production and the metamorphosis of *Calanus* spp. from nauplii to copepodites (Baier and Napp, 2003), as well as lipid accumulation and reproduction for *Thysanoessa* spp. (Falk-Petersen et al., 2000; Smith, 1991) (Fig. 3). Thus, the early, large, high-quality pulse of organic matter from ice algae and ice-edge phytoplankton blooms appears important in determining the population dynamics of large crustacean zooplankton in the southeastern Bering Sea. A contributing factor may be reduced predation; walleye pollock consume copepods and euphausiids (Buckley et al., this issue), but avoid the cold pool (Hollowed et al., 2012) and are not found under the ice (De Robertis and Cokelet, 2012). When the ice extent is far south, there is a large area in which the copepods and euphausiids are likely to experience reduced predation; in a warm year, the size of the refuge is much reduced and is farther north.

3. Bioenergetics Perspective

3.1 Background

To reach maturity and reproduce, organisms (zooplankton or fish) must negotiate multiple life history stages (Megrey et al., 1996). As development progresses, an organism's capacity to buffer against environmental variation increases through increased energy storage (e.g., Siddon et al., 2013a). The buffering allows survival through marginal conditions; consequently the interaction of energy storage, life history stage, and environmental conditions creates multiple pathways by which an individual can survive. In these strategies, the organism balances growth (to avoid size-dependent predation) and energy storage (to buffer against poor environmental conditions). Growth, development, and energy storage are mutually exclusive sinks for energy acquired by organisms. We emphasize a bioenergetics perspective in this section, which we begin by introducing some background information for copepods, euphausiids, and juvenile walleye pollock.

Recruitment of *Calanus* spp. on the southeastern Bering Sea shelf involves many different processes. Here we simplify *Calanus* spp. life history into four major steps from winter/late spring through the following winter: spawning, metamorphosis, accumulation of lipids, and overwintering. The timing of spawning by *Calanus* spp. in the southeastern Bering Sea is protracted, lasting from February to May (Baier and Napp, 2003), and the longer that conditions are suitable, the more total eggs each female will produce (E. Durbin, U. Rhode Island, pers. comm.). In ice-covered Arctic regions, *C. glacialis* utilizes the ice algal bloom to fuel spawning in spring, while growth and development of the new generation is primarily supported by the phytoplankton bloom (Daase et al., 2013). Besides the availability of ice algae, matching reproduction with the ice-associated phytoplankton bloom likely benefits egg production in cold years (Baier and Napp, 2003). Metamorphosis from the nauplius stage to the copepodite stage is enhanced by a late ice retreat and early spring bloom production (Baier and Napp, 2003). *Calanus* spp. start accumulating lipids after the third copepodite stage, and thus begin allocating energy to both lipid storage and growth. Summer growth and accumulation of lipids are dependent on summer primary production and microzooplankton production (Sambrotto et al., 1986; Sherr et al., 2013; Stoecker et al., 2014). Respiration is a function of temperature (Saumweber and Durbin, 2006), so that energy use is higher when temperature is higher, which may deplete stored lipids. *Calanus* spp. overwinter as stage 5 copepodites and reach the adult stage in late winter-early spring (Baier and Napp, 2003). Farther north, *Calanus* spp. may overwinter at a sub-adult stage and develop to adults during their second winter (C. Ashjian, Woods Hole Oceanographic Institution, pers. comm.).

The dominant middle (*T. raschii*) and outer (*T. inermis*) domain euphausiids of the southeastern Bering Sea transition through multiple life stages including eggs, nauplius, metanauplius, feeding calytopsis and furcilia larvae, juveniles (first year of life), and then adults (longevity likely 2-3 years) (Pinchuk and Hopcroft, 2010a, b; Harvey et al., 2012). These euphausiid species are primarily herbivorous, but also may feed on detritus in the nepheloid layer, and are known to feed directly on ice algae growing on the undersurface of sea ice (Campbell et al., this volume;

Lessard et al., 2010). It is likely that microzooplankton are an important food for euphausiids in the summer when phytoplankton are fewer (E. Lessard, University of Washington, pers. comm.). In 1980 and 1981 in the southeastern Bering Sea, *T. inermis* began spawning in early April whereas *T. raschii* began spawning in mid or late May (Smith, 1991). *T. inermis* stores more lipids than *T. raschii* (Harvey et al., 2012), building up lipid stores for reproduction the following winter and spring (capital breeder). In contrast, *T. raschii* support reproduction directly through feeding (income breeder) (Falk-Petersen et al., 2000). Thus, as for *Calanus* spp., the availability of ice algae and the ice-associated phytoplankton bloom in the southeastern Bering Sea likely promote egg production for *Thysanoessa* spp. in cold years (Fig. 3) (see also Hunt et al., this issue).

Yolk-sac larval walleye pollock have a supply of yolk that is used to develop a digestive apparatus and sight for finding prey (Porter and Theilacker, 1999). Very little growth takes place during this organogenesis period. Once feeding initiates (Dagg et al., 1984), fish begin growing, but little energy is stored (Siddon et al., 2013a). During these early and late larval stages for walleye pollock, variability in the energy content of individuals is low (R. Heintz, pers. obs.). Once metamorphosis to the juvenile stage is complete, age-0 walleye pollock are larger, have completed organogenesis, and are capable of storing energy. This storage capacity is important in late summer because winter represents a season of impoverished food supply. By late summer, age-0 pollock survival is associated with the ability to reach a larger size while maximizing energy storage (Heintz et al., 2013). Because of the allometric relationship between fish length and storage capacity, larger walleye pollock have a disproportionately greater capacity to store energy and survive winter (Heintz and Vollenweider, 2010). Larger fish also have greater potential to escape from predators. Thus age-0 walleye pollock face dual, conflicting demands: store energy to avoid starvation versus allocate energy to somatic growth to enable greater storage capacity and to reduce predation.

3.2 Summer and fall, not just spring, matter

An organism's survival is dependent on its ability to obtain and maintain sufficient energy stores

to meet life history requirements, but it is often overlooked that bottlenecks for marine zooplankton and fish may occur in seasons other than spring. Historically, recruitment process research on early life survival in the North Pacific Ocean has focused on spring (Kendall et al., 1996; Kendall and Duker, 1998; Napp et al., 2000). This time period was viewed as a critical period when, nearing yolk sac depletion, first feeding walleye pollock larvae must successfully locate, capture, and consume appropriately sized prey under the prevailing physical conditions to survive (Dagg et al., 1984; Porter et al., 2005). While spring is a logical season to focus research, recruitment bottlenecks are non-stationary and can shift to other life history stages (e.g., Bailey, 2000; Hunt et al., 2002).

Research in the southeastern Bering Sea has broadened to consider other seasons and other critical periods have been identified. This research has shown a clear relationship (2003-2011) between late summer energy content of age-0 walleye pollock and eventual survival to age-1 (Heintz et al., 2013). Prior to their first winter, age-0 walleye pollock must have sufficient energy stores to survive that long period with low food availability (Sogard and Olla, 1996; Vollenweider et al., 2010; Heintz et al., 2013). In warm years with early ice retreat, the spring bloom is later and age-0 walleye pollock are more abundant (Moss et al., 2009; Hunt et al., 2011), yet by late summer their energy stores are low and cannibalism is prevalent. Diets of early age-0 walleye pollock (30-50 mm total length (TL)) include small adult copepods (e.g., *Pseudocalanus* spp.), euphausiids, amphipods, and chaetognaths, then shift after approximately 50 mm TL to larger prey including euphausiids and large copepods (*Calanus* spp.) (Brodeur et al., 1998; Duffy-Anderson et al., this volume; Strasburger et al., 2014). The open water bloom in warm years results in a zooplankton community dominated by small crustacean zooplankton, which are sufficient to support high numbers of age-0 walleye pollock larvae and early life stages, but are insufficient to enable larger (>50 mm TL) age-0 walleye pollock to store adequate lipids for the winter.

While a warm spring with good larval survival results in abundant age-0 walleye pollock, differences in the summer foraging environment appear to affect their eventual survival.

Medium-sized copepods like *Calanus* spp. are abundant in cold years with late ice retreat, but not in warm years with early ice retreat (Coyle et al., 2011; Hunt et al., 2011; Stabeno et al., 2012b). As a consequence, age-0 walleye pollock consume diets richer in lipids during the summers of cold years; the percent lipid content of age-0 walleye pollock diets averages 10% in cold years and only 4% in warm years (Heintz et al., 2013). The richer diet in cold years better prepares age-0 walleye pollock for their first winter and enhances their survival (Heintz et al., 2013). In contrast, the open water bloom in warm years with early ice retreat results in a zooplankton community dominated by small crustacean zooplankton (e.g., *Acartia* spp., *Pseudocalanus* spp.), which are deficient in the lipids necessary to support accumulation of fat by older, larger age-0 walleye pollock (>50 mm) (Coyle et al., 2008, 2011; Eisner et al., 2014). Those *Calanus* spp. that are found in warm years also have much lower lipid levels than those sampled during cold years (Heintz et al., 2013). This accounts for abundant, but lean age-0 walleye pollock in late summer in warm years and their low overwinter survival (Coyle et al., 2008, 2011; Eisner et al., this issue; Heintz et al., 2013). Overall, recent year classes of walleye pollock have been weak during early-ice-retreat years and often strong during late-ice-retreat years (Coyle et al., 2011; Hunt et al., 2011) (Fig. 2).

While strong year classes of walleye pollock often occur during cold years with late ice retreat, weak year classes can also occur. For example, walleye pollock recruitment has frequently been above average since the recent late ice retreat period began in 2006 (Ianelli et al., 2014). However, the 2007 year class was below average. Two mechanisms may be responsible for this small year class. First, the hatching of pollock eggs is negatively affected by the presence of sea ice and associated cold water, which significantly delays the hatching of pollock eggs and may result in higher egg mortality (Blood, 2002). Additionally, an explanation for the reduced year class size was offered by Eisner et al. (this issue) based on summer conditions in 2007. If summer storms are weak and few, surface nutrients are not replenished following the spring bloom, summer blooms are few and small, there may be reduced availability of large, lipid-rich crustacean zooplankton, and age-0 walleye pollock may be smaller. In 2007, the number of June-August wind events were few, surface silicate concentrations were lower and the ratio of

nitrogen to silicate was higher (>1) in some regions, and age-0 walleye pollock were smaller in size (Eisner et al., this issue). Silicate is required by diatoms, but usually is not limiting in the Bering Sea. In addition, the assimilation number (ratio of primary production to chlorophyll *a*, which is an indication of phytoplankton biomass) was low, due in part to changes in the phytoplankton community. Lastly, observed phytoplankton cells were smaller. The implication is that summer feeding conditions for age-0 walleye pollock were poor in 2007, presumably as a secondary consequence of surface nutrient concentrations limiting growth of large phytoplankton and reducing efficiency of energy transfer to higher trophic levels during summer.

While recent research has demonstrated that summer and fall conditions, in addition to spring conditions, determine age-0 walleye pollock survival, little work has examined how conditions the following spring affect age-1 walleye pollock survival. For example, Mueter et al. (2011) examined relationships among walleye pollock survival and environmental variables and found significant relationships with spring and summer conditions, but did not test for effects of conditions the following spring. An exception is Quinn and Niebauer (1995) who found a positive relationship between the survival of pollock to age-2 and temperature during and after their first winter. More recently, Martinson et al. (2012) found that a cool late summer followed by a warm spring is associated with stronger walleye pollock year classes. This result indicates that conditions through at least the first year influence walleye pollock year-class strength, with adequate provisioning for winter followed by good growth the following spring promoting survival. Laboratory studies with maximum rations have shown that warmer conditions enhance age-1 walleye pollock food consumption and growth rates (Kooka et al., 2007; Smith et al., 1986). Still unknown, though, is what prey are available to support enhanced growth for age-1 walleye pollock during a warm spring; one possible prey is age-2 and age-3 euphausiids that survive winter.

3.3 Stored lipids are important for overwinter survival

One of the major results of the Bering Sea Project was the recognition of the important role of lipid accumulation by age-0 walleye pollock in preparation for their first winter (Heintz et al.,

2013; Siddon et al., 2013a). For age-0 walleye pollock, high energy content prior to their first winter enhances survival (Heintz et al., 2013). Age-0 walleye pollock allocate energy to somatic growth and organogenesis during spring, presumably to escape size-dependent predation, then shift to energy storage during late summer and fall in preparation for winter (Heintz and Vollenweider, 2010; Siddon et al., 2013a). The critical period for lipid storage occurs between the completion of metamorphosis to the juvenile stage in August and the onset of winter (Siddon et al., 2013a). Small age-0 walleye pollock continue to forage throughout winter because lipid storage is insufficient to last the winter, whereas large age-0 walleye pollock catabolize their lipid stores, limiting winter foraging and exposure to predators (Heintz and Vollenweider, 2010).

Once provisioned for winter, overwinter survival depends on winter conditions. This result applies not only to age-0 walleye pollock, but also to species they prey upon, especially those that use stored energy to produce their first crop of eggs such as *Calanus* spp. and *T. inermis*. Daily calculated respiration rates for *Calanus* spp. are 47% higher for average winter bottom temperatures of warm (2 °C) versus cold (-1.8 °C) years in the southeastern Bering Sea (Sigler et al., 2014). In warm years lacking cold bottom water over the southern middle domain, respiration rates increase and lipid stores may be exhausted as early as November 1, based on a physiological model of *Calanus* spp. growth, development, and respiration (Coyle et al., 2014). Thus, sea ice may influence *Calanus* spp. survival by generating a cold bottom layer which provides a thermal refuge for individuals that undergo diapause, increasing the likelihood of survival through the following spring (Coyle et al., 2011, 2014). *Calanus* spp. that survive a warm winter also face an unfavorable foraging environment (Coyle et al., 2011; Sigler et al., 2014) following warm winters because ice algae is limited or absent and the spring bloom occurs later (Brown and Arrigo, 2013; Hunt et al., 2002, 2011; Sigler et al., 2014). Inadequate provisioning during the previous summer and fall can exacerbate these differences between cold and warm years. Warmer bottom water in the absence of ice cover during the growing season results in smaller *Calanus* spp. that store smaller amounts of lipid (Coyle et al., 2011). The lipid content of *Calanus* spp. was 27% lower in a warm year (2004, 10.6% lipid, SD = 5.3) compared to a cold year (2009, 14.5% lipid, SD = 3.5) (Heintz et al., 2013).

4. Location matters

The spatial match-mismatch of age-0 walleye pollock and their most energy-dense prey further explains recent recruitment variability of walleye pollock (Siddon et al., 2013b). This match-mismatch ultimately is due to annual variations in the spatial distribution and timing of primary production, which is controlled by annual variations in ice extent (Brown and Arrigo, 2013; Hunt et al., 2002, 2011; Sigler et al., 2014). Similar match-mismatch evidence on ice timing and extent, primary production, and zooplankton has been advanced for other ice-influenced ecosystems (Soreide et al., 2010; Wassmann and Reigstad, 2011). We hypothesize that when the ice-associated bloom matches in time and space with reproducing and growing *C. marshallae* and *T. raschii*, the recruitment of these large zooplankton is strong (Baier and Napp, 2003; Hunt et al., this volume) and their lipid concentration is higher (Heintz et al., 2013; Siddon et al., 2013b). Thus, if the ice edge is far enough south, and lasts long enough into the spring, there more likely will be a strong recruitment of these large zooplankters in a region where they can be consumed in summer by growing age-0 pollock. However, if maximum ice extent, the ice-associated bloom, ice algae production, and the ensuing zooplankton are located north of the summer range of age-0 walleye pollock, this mismatch will diminish age-0 walleye pollock survival (Fig. 4).

There is considerable evidence in support of this hypothesis. The timing and location of the ice-associated bloom is related to the timing of ice retreat in the eastern Bering Sea (Hunt et al., 2002, 2011; Sigler et al., 2014), i.e., the ice-associated bloom and ice retreat are tied together. During 1995-2011, ice always extended south to about 60 °N and sometimes as far south as about 56 °N (Stabeno et al., 2012a; Sigler et al., 2014). When ice extends farther south and lingers into late March or early April, there is stronger recruitment of *C. marshallae* and *T. raschii* in the middle domain of the southeastern Bering Sea than when the ice retreats early (Baier and Napp, 2003; Hunt et al., this volume). Recent work by Eisner et al. (2014) shows that a zooplankton species assemblage characterized by *Calanus* spp., Cnidaria and *Parasagitta*

elegans, mostly occurred north of 60 °N during the warm years of 2004-2005, whereas during the cold years of 2006-2009, this assemblage extended further south to 56 °N (Eisner et al., 2014, Fig. 3). Since the centers of distributions of the early life stages (egg, larvae, and age-0 juvenile) of walleye pollock lie south of about 57 °N (Duffy-Anderson et al., this issue), when the synchronization of primary production and zooplankton occurs far enough south, their location will match the summer distribution of age-0 walleye pollock, which will benefit (i.e., their energy density will be higher). If on the other hand, primary production and zooplankton occur too far north, then there will be a mismatch with age-0 walleye pollock, which will suffer. This pattern provides a ‘location matters’ explanation for interannual variation in *Calanus* spp. production in addition to the ‘timing matters’ explanation (section 2.4).

The previous arguments focused on middle domain taxa and less on outer domain taxa that have not been as closely analyzed. We must broaden our view and test whether or not the operative mechanisms described previously for middle domain zooplankton species and juvenile walleye pollock also hold true for the outer domain where age-0 pollock also may be found (e.g., Parker-Stetter et al., 2013). Here we briefly describe some results for the outer domain, which deserves more study. The large crustacean zooplankton taxa *Calanus* spp. and *T. raschii* primarily occupy the middle domain, whereas *Neocalanus* spp. and *T. inermis* and *T. longipes* are farther offshore (Cooney and Coyle, 1982; Smith and Vidal, 1986). Summer measurements of the biomass of these large crustacean zooplankton were not significantly different between the middle domain and the outer domain ($p > 0.05$; Napp et al., 2002). The middle and outer domains differ in ways that may affect primary and secondary production. In cold years when sea ice extends to the outer domain, melting ice provides dissolved iron necessary for the assimilation of available nitrate and thus can influence the characteristics of the spring algal bloom (Aguilar-Islas et al., 2008). Along-shelf advection is strong near the shelf break whereas advection generally is low for the middle domain (Ladd, 2014; Stabeno et al., 2010). On-shelf advection can transport large oceanic copepods, primarily *Neocalanus* spp., from the basin all the way into the middle domain (Gibson et al., 2013). This on-shelf advection may also transport *T. inermis* and *T. longipes* to the outer domain. Although advective characteristics differ for the middle domain and outer

domain, extensive sea ice in cold years and on-shelf advection also connect these two areas. In cold years, sea ice can cover both the middle domain and the outer domain. In some areas, on-shelf advection crosses the outer domain and the middle domain. Because of this connectivity, we hypothesize that similar operative mechanisms act upon both the middle domain and the outer domain, which warrants further examination. More testing of our hypothesis is needed, in particular a comparison of the annual spatial overlap of ice extent, ice-associated bloom, zooplankton, and age-0 pollock.

5. Shifting top-down control

Whether cold years, which favor copepod, euphausiid, and walleye pollock production, occur singularly or in succession affects the variability of mature walleye pollock biomass and walleye pollock harvests, as well as when top-down control increases (Hunt et al., 2002, 2011, this issue; Ressler et al., 2012, 2014). Top-down control may occur through walleye pollock cannibalism of juvenile walleye pollock (Hunt et al., 2002, 2011) and walleye pollock predation of copepods and euphausiids (Ressler et al., 2012, 2014; Hunt et al., this issue). The production of copepods, euphausiids, and juvenile walleye pollock decreased during years when ice was absent or retreat occurred early (2001-2005) and increased during the years when ice retreat was late (2006 - 2012), as explained in previous sections. The successive unfavorable years led to a ~50% drop in mature walleye pollock biomass in the fishery. In turn, the successive favorable years (and temporary reduction in catch quotas) led to a recovery to near pre-decline levels (Ianelli et al., 2014). The successive unfavorable years had a critical, negative impact on the fishery because they led fishery managers to impose the lowest catch quotas since at least the late 1970s.

As walleye pollock biomass fell, top-down control of euphausiids and copepods likely decreased; when environmental conditions improved in 2006, decreased top-down control likely continued for a year or two and facilitated the increase of euphausiids and copepods until walleye pollock biomass was rebuilt. Eventually the successive favorable years may have caused

an increase in top-down control of euphausiids (Ressler et al., 2012; Hunt et al., this issue) and copepods through predation by walleye pollock. Fishing removes ~15% of walleye pollock mature biomass each year (Ianelli et al., 2014), and is the ultimate top-down control, influencing not only walleye pollock population dynamics, but also the impact of pollock on the rest of the ecosystem.

Overland et al. (2012) placed the two recent time periods (successive unfavorable warm years and then successive favorable cold years) into a 95-year context. Their analysis is based on the air-temperature record at St. Paul Island in the Pribilof Islands. The St. Paul weather record is a good indicator of air temperature for the entire Bering Sea (Rodionov et al., 2005); ice cover and retreat timing both are correlated with air temperature (Brown and Arrigo, 2013). Thus, the longer air temperature record provides insight into historical ice cover and retreat timing. Overland et al. (2012) found that the recent multi-year period observed during the Bering Sea Project is not unique in the last 95 years and that previous multi-year cold (and warm) periods have occurred. These warm and cold multi-year events were associated with a shift in the location of the Aleutian Low Pressure System during February-April (Overland et al., 2012). The Aleutian Low is centered over the Bering Sea during warm years, west of its position over the Gulf of Alaska during cold years (Overland et al., 2012). This cold-year pattern combines with high pressure over the northwestern Bering Sea to advect cold Arctic air over the southeastern Bering Sea during winter (Rodionov et al., 2007) and produces below average temperatures (Overland et al., 2012), more extensive ice cover, and later ice retreat. While warm ocean temperatures in the fall and winter can delay the arrival of sea ice, cold northerly winds are the primary controller of sea-ice extent in the southeastern Bering Sea (Reynolds et al., 1985; Staben0 et al., 2007).

6. What does the future hold for the eastern Bering Sea?

The eastern Bering Sea is not a steady state system. The Bering Sea is different now from what

Walsh and McRoy (1986) studied or even what the system was like during the early 2000's. We anticipate a ~2°C increase in surface air temperatures for the Bering Sea region from global warming over the next 50 years (Wang et al., 2012). However, ice cover will continue to occur in winter, at least in the northern Bering Sea (Sigler et al., 2011; Stabeno et al., 2012a). The effects of warming will be greatest in the southeastern Bering Sea, which will experience warm years more frequently than at present (Mueter et al., 2011; Hermann et al., 2013). Statistical models predict a decline in walleye pollock stocks as a result (Ianelli et al., 2011, Mueter et al., 2011).

We characterized the dynamics of the southeastern Bering Sea based on a few (4) warm years and a few (5) cold years with extensive and long-lasting sea ice. While we benefited from the integrated nature of the Bering Sea Program, which provided detailed information on many ecosystem features, we recognize that more cold and warm years must be observed to increase sample sizes for statistical testing of the identified ecological mechanisms. Further, these additional observations must continue to be sufficiently detailed to document whether or not the important physical and biological relationships described in this paper continue to be true. While the time series of integrated research is relatively short, a much longer time series (~40 years) has been used to quantify the statistical relationship between sea surface temperature and walleye pollock production, and these support the overall finding that walleye pollock production is reduced with warmer temperatures (Ianelli et al., 2011, Mueter et al., 2011).

The Bering Sea Project proposed to test the hypothesis that “as heat content increases, the area suitable for spawning and foraging by subarctic species [e.g., walleye pollock] will expand northward and subarctic species will occupy areas formerly occupied by Arctic species [e.g., snow crab]”. This hypothesis is akin to temperature envelope models (*sensu* Cheung et al., 2009) and was overly simplistic in its approach. It assumed that all spatial variation in temperature occurs latitudinally, that timing and amount of primary production are unaffected by temperature, and that emergent biological interactions among species (predation, parasitism) are unimportant. We demonstrated that the eastern Bering Sea does not fit the assumptions of simple temperature envelope models. First and foremost, climate projection models predict that the

northern Bering Sea will continue to have extensive winter and spring sea ice, although ice thickness may decrease (Stabeno et al., 2012a), and that the summer cold pool over the northeastern middle domain will continue to be a barrier to many species such as walleye pollock. Species affected by the cold pool can exist farther north if they inhabit the outer domain, rather than the middle domain where the cold pool occurs (Hollowed et al., 2012; Kotwicki and Lauth, 2013). Our paper also found that survival and recruitment of walleye pollock and their zooplankton prey are regulated by complex ecological relationships, which include temperature. Timing and location effects are in large part responsible for match-mismatch and variation in annual production in primary production, zooplankton, and juvenile walleye pollock in the southeastern Bering Sea.

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Figure legends

Fig. 1. Study area showing principal oceanographic moorings (in order from south to north, M2, M4, M5, M8). The three cross-shelf domains usually are defined by water depth (inner: 0-50 m; middle: 50-100 m; outer: 100-180 m) (Coachman, 1986) and the northern Bering Sea domain by latitude (60 °N) (Grebmeier et al., 2006; Sigler et al., 2011; Stabeno et al., 2012a).

Fig. 2. Ice retreat day for the southernmost oceanographic mooring (M2) (if ice was absent that year, then ice retreat day is zero) (Sigler et al., 2014) and abundances of large crustacean zooplankton (mostly copepods) (number m⁻³) (Eisner et al., 2014), euphausiids (mmt wet weight) (Ressler et al., 2014), and age-1 walleye pollock (billions of walleye pollock at age-1; in this case, year 0 is birth year) (Ianelli et al., 2014).

Fig. 3. A conceptual model comparing a warm year with early ice retreat or ice absent to a cold year with late ice retreat (modified from Hunt et al., 2011). Ice algae blooms occur during ice cover and ice retreat and begin as early as mid-February (R. Gradinger, Norwegian Institute of Marine Research, pers. comm.). *Calanus* spp. egg production begins well before the bloom and continues for a few months whereas metamorphosis from nauplii to copepodite is coincident with the spring bloom (Baier and Napp, 2003). *Thysanoessa inermis* uses stored energy to spawn near the start of the spring bloom whereas *Thysanoessa raschii* acquires more energy before spawning at the culmination of the spring bloom (Falk-Petersen et al., 2000; Smith, 1991). Fall blooms occur during September and October (Sigler et al., 2014). Zooplankton respiration is higher in warmer temperatures and lower in cooler temperatures (Coyle et al., 2011; Sigler et al., 2014). In late summer, age-0 walleye pollock often are energy-rich in cold years and energy-poor in warm years; walleye pollock recruitment is positively correlated with late summer energy content (Heintz et al., 2013).

Fig. 4. A conceptual model of the spatial and temporal patterns of the spring bloom for late and early-ice-retreat years. In areas and years that ice is absent or retreats early (before mid-March), there is no ice-associated bloom because the water remains mixed by winter storms and sunlight is insufficient to initiate an ice-associated bloom. Instead an open-water bloom occurs; this pattern applies only in the southeastern Bering Sea (Sigler et al., 2014). In areas and years that ice retreats after mid-March, an ice-associated bloom occurs and moves northward as the ice retreats; this pattern applies throughout the eastern Bering Sea (Sigler et al., 2014). The symbols represent ice extent (blue), the ice-associated bloom (bright green) and open-water bloom (olive green). The locations of age-0 walleye pollock and their zooplankton prey match in late summer in cold but not warm years (Eisner et al., 2014, Fig. 3; Duffy-Anderson et al., this issue, Fig. 3).

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Early April

Late May

Late August

Early ice retreat year

Late ice retreat year