

Contribution to the Themed Section: *Marine zooplankton time series: essential tools to understand variability in productivity-determining processes in the oceans*

Climate warming and the loss of sea ice: the impact of sea-ice variability on the southeastern Bering Sea pelagic ecosystem

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Hunt, G. L. Jr., Yasumiishi, E. M., Eisner, L. B., Stabeno, P. J., and Decker, M. B. Climate warming and the loss of sea ice: the impact of sea-ice variability on the southeastern Bering Sea pelagic ecosystem. – ICES Journal of Marine Science, 79: 937–953.

Received 1 April 2020; revised 29 September 2020; accepted 3 October 2020; advance access publication 24 December 2020.

We investigated relationships among three metrics of sea-ice cover in eight regions of the eastern Bering Sea and the abundance of *Calanus* copepods, jellyfish medusae, and year-class strength of walleye pollock (*Gadus chalcogrammus*). In summer, *Calanus* spp. were more abundant over the middle shelf when sea ice lingered late into spring, and, to a lesser extent, when February sea-ice cover was heavy. Between 1982 and 1999, there were no significant ($p \leq 0.05$) relationships between the amount or timing of sea-ice cover and pollock recruitment. However, between 2000 and 2015, pollock year-class strength was positively correlated with sea ice in the outer and middle shelves, with 17 of 24 regressions significant. Pollock year-class strength was best predicted by days with sea-ice cover after February. Pollock recruitment was positively influenced by copepod numbers, particularly in the middle shelf, with r^2 values from 0.36 to 0.47. We hypothesize that the *Calanus* spp. present in the southeastern Bering Sea are primarily *Calanus glacialis* that have been advected south in association with sea ice. None of our sea-ice metrics explained the variance in jellyfish biomass. Jellyfish biomass in our study area in the pollock age-0 year was not correlated with pollock recruitment 3 years later.

Keywords: Bering Sea, *C. glacialis*, *Calanus*, climate variability and fish recruitment, copepods, *Gadus chalcogrammus*, jellyfish, pelagic ecology, sea ice, walleye Pollock

Introduction

Climate change affects the subarctic eastern Bering Sea through both reduction in sea-ice cover and increasing sea temperatures. These waters support the largest fishery (walleye pollock *Gadus chalcogrammus*; hereafter pollock) by weight in the United States (National Marine Fisheries Service, 2020). Successful, sustainable management of this fishery depends on annually-gathered data on not only the biomass, age composition, and weight-at-age of pollock but also the status of the eastern Bering Sea marine

ecosystem. This ecosystem-based approach to management employs data on physical conditions in the ocean, as well as measures of the abundance and distribution of essential predator and prey species (e.g. Ockendon *et al.*, 2014; Angel *et al.*, 2019; Guo *et al.*, 2019; Link *et al.*, 2020). Environmental information is now being used to assess the likelihood that the age-0 pollock of a given year-class will have strong survival rates to age-1, and the number that will enter the fishery at age-3 (e.g. Gann *et al.*, 2019; Siddon *et al.*, 2019; Yasumiishi, 2019; Eisner *et al.*, 2020).

The survival of pollock to age-1 in the eastern Bering Sea is affected by climate variability at a variety of spatial and temporal scales. Here, we focus on the impact of climate variability on prey availability during the late larval and juvenile stages of pollock (c.f., Heintz *et al.*, 2013; Strasburger *et al.*, 2014; Duffy-Anderson *et al.*, 2016; Kimmel *et al.*, 2018; Eisner *et al.*, 2020). Large, lipid-rich copepods, such as *Calanus glacialis/marshallae* (hereafter *Calanus* spp.) are among the most important prey of both adult and juvenile pollock (Moss *et al.*, 2009; Buckley *et al.*, 2016). Hunt *et al.* (2002, 2011) proposed the Oscillating Control Hypothesis that relates the timing of sea-ice retreat to the transfer of energy to *Calanus* spp. Initial investigations indicated that pollock year-classes were stronger in years with early sea-ice retreat (Hunt *et al.*, 2002), whereas the analyses presented in Hunt *et al.* (2011) indicated that years with late sea-ice retreat produced the larger year-classes. Here, we focus on how the timing of sea-ice retreat affects the recruitment of pollock, and how this relationship may have changed over time.

Sea-ice algae are an important food for *Calanus* spp. (Durbin and Casas, 2014; Wang *et al.*, 2015; Campbell *et al.*, 2016). The maximum extent of sea ice and the timing of its retreat in spring affect where and when sea-ice algae will be available (Hunt *et al.*, 2011; Sigler *et al.*, 2014, 2016). In the Bering Sea, if sea ice fails to extend to the southern middle shelf, or if it retreats early in spring (before mid- to late-March), there is a mismatch between the availability of sea-ice algae and the nutritional needs of *Calanus* spp. (Baier and Napp, 2003; Brown and Arrigo, 2013). Years with late sea-ice retreat are favourable for the production of abundant *Calanus* spp., whereas in years with little or no sea ice after mid-March, the abundance of *Calanus* spp. over the southeastern middle shelf is low (Baier and Napp, 2003; Coyle *et al.*, 2011; Hunt *et al.*, 2011; Eisner *et al.*, 2014); the abundance of *Calanus* spp. over the middle shelf may be reduced by as much as 95% in years with early sea-ice retreat as compared to those in which sea ice lingers into the spring (Renner *et al.*, 2016).

Age-0 pollock require lipid reserves to survive through their first winter (Sogard and Olla, 2000; Moss *et al.*, 2009). The lipid content of age-0 pollock in the southeastern Bering Sea varies as a function of the abundance of large, lipid-rich crustacean zooplankton there, in particular *Calanus* spp. and the euphausiid *Thysanoessa raschii* (Moss *et al.*, 2009; Andrews *et al.*, 2019; Eisner *et al.*, 2020). In cold years (late sea-ice retreat), *Calanus* spp. and *T. raschii* are major components of age-0 pollock diets (Feldmann, 2007; Moss *et al.*, 2009; Coyle *et al.*, 2011), and the pollock have high levels of lipids (Hunt *et al.*, 2011; Heintz *et al.*, 2013). In these years, overwinter survival of age-0 pollock can be high. In warm years (early sea-ice retreat), *Calanus* spp. are less abundant, and age-0 pollock lipid levels are low, as is their overwinter survival (Sogard and Olla, 2000; Duffy-Anderson *et al.*, 2016, 2017; Copeman *et al.*, 2017). Other commercially important species affected by these climate-driven changes in the southeastern Bering Sea food web include sockeye salmon (*Oncorhynchus nerka*) (Farley *et al.*, 2007) and Pacific cod (*G. macrocephalus*) (Farley *et al.*, 2016).

Here, we examine the impact of variations in the amount and location of southeastern Bering Sea winter and spring sea-ice cover on the abundance of large, lipid-rich copepods in the following late summer and early fall, and how this affects survival of age-0 pollock (Moss *et al.*, 2009; Duffy-Anderson *et al.*, 2017; Eisner *et al.*, 2020). We test hypotheses that the areal concentration of sea ice in winter and the timing of sea-ice retreat in the

spring of the age-0-year impact pollock recruitment. We seek evidence that the relationship between sea ice and pollock recruitment is location-specific (see also Smart *et al.*, 2012) and that it operates through effects on the timing of the availability of sea-ice algae for crustacean zooplankton.

We assume that prevailing currents carry larval pollock to the southern portion of the middle shelf and therefore hypothesize that sea-ice cover in the southern middle shelf will have a greater impact on pollock recruitment through the support of *Calanus* spp. than sea ice in either the northern middle shelf or the outer shelf. Because *Calanus* spp. require food (ice-associated algae) in mid-winter as they break diapause and begin egg production, we also hypothesize that the concentration of sea ice in February over the southern middle shelf will be correlated with the abundance of *Calanus* spp. there the following summer/fall. In addition, we hypothesize that the greater the number of days with ice cover after February, the greater the abundance of *Calanus* spp. in the following summer, and hence the more food for age-0 pollock. We also test the hypothesis that the biomass of zooplanktivorous jellyfish in the study area varies with respect to sea-ice cover and that the biomass of large medusae in this region impacts pollock recruitment.

The extent and duration of sea-ice cover also affects water temperatures in the southeastern Bering Sea (Stabeno *et al.*, 2012b, 2017; Sullivan *et al.*, 2014). Extensive melting of ice can cool the water column to less than -1.7°C , and a pool of cold-water forms at the bottom of the middle shelf. It has been hypothesized that this cold pool may provide a refuge for some forage fish, including juvenile pollock, from predators that avoid the cold, including adult pollock (e.g. Wyllie-Echeverria and Wooster, 1998; Ciannelli and Bailey, 2005; Kotwicki *et al.*, 2005; Spencer *et al.*, 2016). Ambient temperature also affects metabolic rates and Coyle *et al.* (2011) and Coyle and Gibson (2017) have hypothesized that, if bottom temperatures are too warm, diapausing copepods will consume their stored lipids before spring (Baumgartner and Tarrant, 2017). Testing of these hypotheses is beyond the scope of this paper.

Methods

The eastern Bering Sea shelf can be divided into oceanographic domains that reflect differences in their hydrographic structure: the Inner Shelf Domain, which is well mixed in summer; the Middle Shelf Domain, which has a two-layer structure in summer, and the Outer Shelf Domain, which has three layers (Coachman, 1986; Stabeno *et al.*, 2001). To ascertain the importance of location and timing of sea-ice cover over the eastern Bering Sea shelf, we defined eight regions, four over the outer shelf (regions 1, 3, 5, and 7), and four over the middle shelf (regions 2, 4, 6, and 8) (Figure 1 and Supplementary Table S1). We chose to have separate regions for the middle and outer shelf because ice cover differs considerably in the cross-shelf axis (Stabeno *et al.*, 1998). The landward edges of the middle-shelf regions were set to be seaward of the Inner Front (the 50 m isobath) (the boundary between the Inner Shelf and Middle Shelf Domains) and of the flow of the Alaska Coastal Current (Kachel *et al.*, 2002); the seaward side of the middle-shelf regions was approximately the 100-m isobath. For the outer shelf regions, the landward edges were set at the 100-m isobath and the seaward edges at approximately the 170-m isobath just shoreward of the shelf edge. The axis of the northwest/southeastward divisions between regions was set perpendicular to the axis of the eastern shelf.

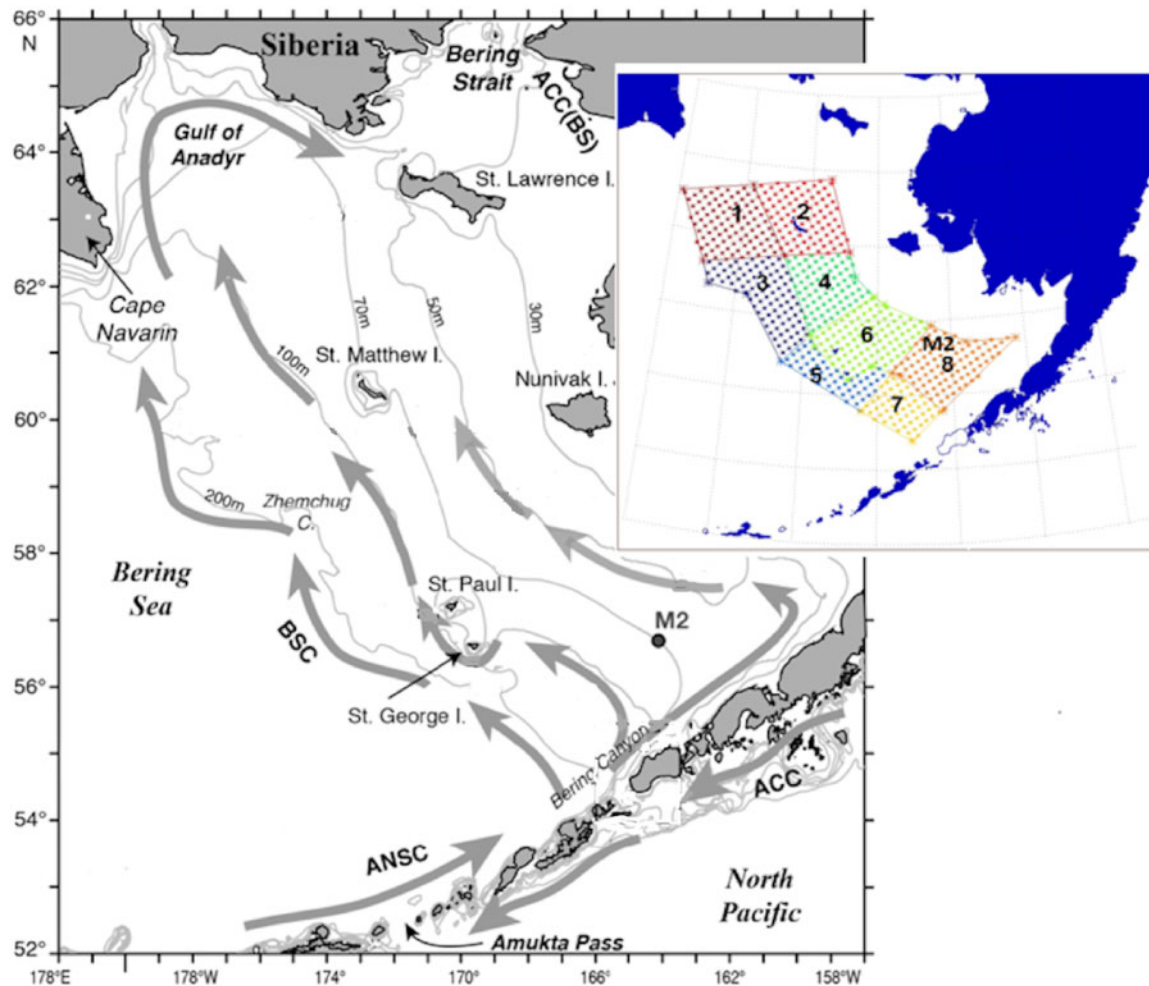


Figure 1. Currents on the eastern Bering Sea shelf with an inset showing our study area and eight regions in which sea ice cover was analysed (modified from [Stabeno et al., 2016](#)). The four regions to the right cover, approximately, the Middle Shelf Domain (50–100 m depth), while those on the left cover the Outer Shelf Domain (100–170 m depth). The dots within each region are the grid points from which the Special Sensor Microwave/Imager (SSM/I) ice data were obtained. Mooring 2 is indicated as M2. ANSC, Aleutian North Slope Current; BSC, Bering Slope Current; ACC, Alaska Coastal Current.

Sea-ice cover

Seasonal sea ice in the Bering Sea is initially formed, primarily in the north, in polynyas located in the lees of islands and promontories ([Pease, 1980](#); [Niebauer, 1998](#); [Sullivan et al., 2014](#)). The ice is blown south, where it melts in the relatively warm waters of the southeastern Bering Sea. Ice retreat in spring occurs when the rate of melting is greater than the rate of southward advection, or when southerly winds blow the ice northward ([Pease, 1980](#)). Spring melt-back may occur quickly, or it may be characterized by periods of little movement, with short retreats northward and surges southward, termed “loitering” by [Steele and Ermold \(2015\)](#). Sea-ice retreat may occur “early”, or it may linger until May or even June ([Stabeno et al., 2012b](#)). Seasonal sea-ice cover was a defining characteristic of eastern Bering Sea shelf waters until the winters of 2017/2018 and 2018/2019, when little or no ice was present, even in the northern Bering Sea ([Overland et al., 2019](#); [Stabeno and Bell, 2019](#); [Thoman, 2019](#)). Prior to the winter of 2017/2018, seasonal sea ice covered a variable amount of the eastern shelf in winter, with the southern extent ranging from the Alaska Peninsula northward to near the southern shores of St.

Matthew Island in region 2. In general, the middle shelf receives more ice than the outer shelf, except in the northernmost regions of our study area, regions 1 and 2.

For each of the eight regions, we obtained daily records of sea-ice cover from the National Snow and Ice Data Center Special Sensor Microwave/Imager and included the years 1979–2017. We used the National Snow and Ice Data Center Bootstrap algorithm on a 25-km grid ([Comiso, 2017](#)). The ice data were reported semi-daily before 1987, and daily since then. Using these data sources, we calculated the daily mean sea-ice cover in each region based on the percentage of the region covered by pixels that were filled with sea-ice concentrations of $\geq 20\%$ sea ice. For data before 1987, we used a linear interpolation of semi-daily data to provide an estimate of daily sea-ice cover within the study regions. From these data, we developed three metrics of ice cover: (i) the last day in spring with $\geq 20\%$ of the region covered with $\geq 20\%$ areal ice (hereafter, LastDay); (ii) the mean percentage of a region covered with $\geq 20\%$ areal ice over the period from days 32 to 60 (roughly February) (hereafter, MeanIce); and (iii) the cumulative number of days after day 60, up to day 180, with $\geq 20\%$ of the

region covered by $\geq 20\%$ areal ice (hereafter, IceDays). We chose $\geq 20\%$ cover within a pixel to assure that there was sufficient ice present that the amount of sea ice was ecologically relevant. We recognize that this is an arbitrary percentage of coverage, but one that is a consistent indicator of ice presence in a region based on the field experience of the senior author.

Copepods

Data on the distribution and abundance of copepods (*Calanus* spp.) were gathered during the NOAA Fisheries Bering Arctic Subarctic Integrated Surveys (BASIS) during mid-August to September 2002–2014 (see Fig. 1 in Hunt et al., 2016) following methods in Eisner et al. (2014). Large copepods were collected with a 60-cm bongo frame with 505- μm mesh for 2002–2011 and with a 20-cm bongo frame with 153- μm mesh for 2012 and 2014. Abundance comparisons were made from stations where *Calanus* spp. were collected and enumerated from both net sizes deployed simultaneously (from the same bridle). Comparisons by copepodite stage C3 to adult for each cruise indicated no significant differences ($p < 0.05$) for C4, C5, or adults; there were underestimates for C3 (by approximately one half) using the 505- μm mesh, although C3 was only a small percentage of the counts (D. Kimmel, NOAA, Alaska Fisheries Science Center, pers. comm.). The bongo nets were towed obliquely from near bottom to the surface at 13–68 stations year⁻¹. Zooplankton were preserved in 5% formalin buffered with seawater. Samples were sent to the Polish Plankton Sorting and Identification Center (Szczecin, Poland) (2002–2004, 2012, and 2014), to the University of Alaska (Coyle et al., 2008) (2005–2010), or to NOAA Auke Bay Laboratories (2011), sorted, and counted to estimate abundances (no. m⁻³) of *Calanus* spp. All stages were combined for abundance estimates, although they were primarily copepodite stage C5, particularly in cold years.

Gelatinous zooplankton

The biomass of medusae (i.e. “large” jellyfish) was obtained from the NOAA Fisheries annual Bering Sea bottom trawl surveys (Brodeur et al., 1999). Collections were made at 356 stations during daylight hours from June through August of each year (Brodeur et al., 2008a; Decker et al., 2014). The trawl was towed above the bottom for 30 min at 5.4 km h⁻¹ (Hoff, 2006), but the trawl remained open and fished throughout the period of deployment and recovery. Since jellyfish are distributed throughout the water column (30–40 m mean depth; Brodeur, 1998; Brodeur et al., 2002), jellyfish biomass data used in our analyses are considered an index of relative abundance of the large medusae caught by the trawl and are comparable among stations and years. Catches, primarily *Chrysaora melanaster*, but also *Aequorea* sp., *Aurelia* sp., *Cyanea* sp., *Phacellocephora camtschatica*, and *Staurophora mertensi*. (Decker et al., 2014), were weighed and standardized to catch per unit effort (CPUE in kg ha⁻¹, where 1 ha = 10,000 m²) (see Brodeur et al., 1999, for details). Jellyfish biomass values were apportioned to the eight regions depicted in Figure 1.

Age-3 pollock

Data on the abundance of age-3 pollock recruits were obtained from Ianelli et al. (2018), which provides the estimated number of age-3 recruits based on the 2018 pollock assessment model. To account for the size of the spawning stock of pollock and its

impact on the number of young produced, the number of age-3 recruits was divided by the biomass of pollock spawners in the age-0 year (Ianelli et al., 2018, Table 30). We chose recruitment at age-3 because that is the first year that the pollock stock is well sampled.

Examination of linkages

We used simple linear least square regressions of the abundance indices for copepods, pollock, and jellyfish medusae in each region against each of the three sea-ice indices (LastDay, MeanIce, IceDays) for that region. We calculated r^2 and p values for each linear least square regression. Analyses were conducted using the linear model (lm) function in the stats package (version 3.5.3) with Microsoft open R (version 3.5.3) (R Core Team, 2016).

Results

Distribution of sea-ice cover

Sea-ice cover was greater over the middle shelf than over the outer shelf, and within each domain, greater in the north than in the south (Tables 1 and 2). The differences between ice cover in the middle shelf and outer shelf were proportionately greatest in the two southernmost regions (regions 7 and 8) (Tables 1 and 2). Between 1979 and 2015, in region 7, there were 10 IceDays spread over 3 years, vs. 531 IceDays spread over 20 years in region 8. In region 1, there were 1978 IceDays spread over 34 years with only 3 years in which there were zero IceDays. In comparison, in region 2 there were 2674 IceDays spread over 37 years (Tables 1 and 2).

From north to south, the steepest decline was a 93% reduction in the number of IceDays between regions 3 and 5; in the middle shelf, the steepest decline (52%) was between regions 4 and 6 (Table 1). As a result, regions 5 and 7 on the outer shelf had few IceDays, whereas there was a substantial number of IceDays in regions 6 and 8 over the middle shelf.

What one defines as a cold year with heavy ice cover or a warm year with relatively light ice cover may depend on the index of sea-ice cover employed. Indices of sea-ice cover were not consistently heavy or light within years (Table 2). For example, in region 8, in 1980, MeanIce was high, which suggested a relatively heavy ice year, whereas LastDay was relatively low (Table 2). Similarly, 1986 IceDays indicated a heavy ice year, whereas MeanIce was relatively light. In region 8, in only 10 of 37 years were all indices of sea-ice cover either very strong (top quartile) or very weak (bottom quartile).

From 1979 to 2015, there was a change in the pattern of inter-annual variability in sea-ice cover over the eastern Bering Sea shelf (particularly evident in region 8, Table 2). In region 8, prior to 1999, it was rare to have 2 years in a row in the same quartile for either IceDays or LastDay, though this was less true of MeanIce. After 2000, stanzas of years with heavy or light sea-ice

Table 1. Number of ice days after day 60 (IceDays) for the Outer and Middle Shelf Domain regions, 1979–2015 combined.

| | Outer Shelf Domain | | Middle Shelf Domain |
|----------|--------------------|----------|---------------------|
| Region 1 | 1978 | Region 2 | 2674 |
| Region 3 | 727 | Region 4 | 1764 |
| Region 5 | 55 | Region 6 | 841 |
| Region 7 | 10 | Region 8 | 531 |

See Figure 1 for a map of the regions.

Table 2. Ice conditions and age-3 pollock recruitment, by quartile, for region 1 (upper left), region 2 (upper right), region 7 (lower left), and region 8 (lower right).

| Year | Region 1 | | | Region 2 | | | Age3/SSB |
|------|----------|---------|---------|----------|---------|---------|----------|
| | LastDay | MeanIce | IceDays | LastDay | MeanIce | IceDays | |
| 1979 | 82 | 0.51 | 10 | 104 | 21.97 | 30 | 7.892216 |
| 1980 | 135 | 26.93 | 75 | 130 | 96.1 | 70 | 8.396533 |
| 1981 | 117 | 45.17 | 52 | 115 | 91.69 | 55 | 2.825083 |
| 1982 | 0 | 1.29 | 0 | 146 | 55.35 | 84 | 5.662495 |
| 1983 | 126 | 34.86 | 65 | 128 | 96.1 | 61 | 1.270718 |
| 1984 | 151 | 41.99 | 91 | 154 | 93.3 | 94 | 2.841199 |
| 1985 | 140 | 0.06 | 64 | 145 | 18.49 | 82 | 1.054779 |
| 1986 | 119 | 3.82 | 53 | 145 | 76.51 | 85 | 0.523475 |
| 1987 | 126 | 17.05 | 41 | 137 | 76.8 | 76 | 0.371134 |
| 1988 | 125 | 16.46 | 65 | 145 | 67.77 | 85 | 0.711361 |
| 1989 | 30 | 0.92 | 0 | 102 | 23.67 | 30 | 3.478754 |
| 1990 | 127 | 49.63 | 59 | 132 | 95.3 | 72 | 2.26362 |
| 1991 | 141 | 71.16 | 79 | 140 | 97.12 | 79 | 2.677647 |
| 1992 | 131 | 5.79 | 71 | 146 | 81.69 | 86 | 5.298373 |
| 1993 | 130 | 15.02 | 70 | 123 | 93.38 | 63 | 1.290323 |
| 1994 | 145 | 1.99 | 84 | 150 | 63.47 | 90 | 0.799284 |
| 1995 | 137 | 89.26 | 77 | 137 | 97.85 | 77 | 1.639808 |
| 1996 | 118 | 1.8 | 2 | 124 | 63.25 | 59 | 2.245475 |
| 1997 | 121 | 28.99 | 61 | 132 | 95.17 | 72 | 1.164527 |
| 1998 | 145 | 82.9 | 85 | 137 | 97.61 | 77 | 1.369375 |
| 1999 | 142 | 28.82 | 67 | 152 | 90.71 | 92 | 2.116555 |
| 2000 | 129 | 20.12 | 69 | 133 | 84.54 | 73 | 2.852615 |
| 2001 | 0 | 2.5 | 0 | 129 | 0.01 | 39 | 1.90686 |
| 2002 | 111 | 85.41 | 23 | 122 | 97.53 | 62 | 1.23 |
| 2003 | 86 | 29.97 | 26 | 110 | 87.21 | 50 | 0.52698 |
| 2004 | 104 | 18.15 | 39 | 116 | 90.21 | 52 | 0.366524 |
| 2005 | 115 | 10.8 | 46 | 128 | 67.57 | 68 | 1.011311 |
| 2006 | 135 | 40.34 | 38 | 149 | 84.07 | 89 | 2.646104 |
| 2007 | 127 | 16.29 | 52 | 142 | 77.15 | 82 | 1.728697 |
| 2008 | 148 | 41.99 | 88 | 151 | 93.26 | 91 | 8.719632 |
| 2009 | 127 | 53.47 | 55 | 147 | 93.62 | 83 | 3.430341 |
| 2010 | 145 | 67.18 | 85 | 137 | 98.1 | 77 | 1.783987 |
| 2011 | 131 | 6.9 | 33 | 140 | 76.38 | 80 | 1.289462 |
| 2012 | 156 | 82.58 | 96 | 160 | 98.27 | 100 | 5.670262 |
| 2013 | 127 | 76.8 | 67 | 147 | 96.78 | 87 | 3.807866 |
| 2014 | 117 | 19.27 | 55 | 118 | 59.49 | 58 | 1.204687 |
| 2015 | 117 | 3.86 | 35 | 131 | 40.79 | 64 | 1.330032 |

cover were evident within all three ice indices for region 8 (Table 2). This shift in the pattern of interannual variability was not as evident in the other regions (Table 2 and Supplementary Tables S3–S6). In the two southernmost regions of the outer shelf, 5 and 7, there were many years with little or no sea ice present, despite there being plentiful sea ice over the middle shelf.

Sea-ice cover and *Calanus* spp. abundance

Over the outer shelf, our indices of sea ice explained little of the variance in copepod numbers, with only two cases (region 5, LastDay and region 7, MeanIce) in which p values were <0.05 (Figure 2a). For all outer shelf regressions, sample sizes were small, particularly in region 1 ($n=0$) and region 3 ($n=6$). There was no evidence of a north/south gradient in the relationships between sea-ice variables and *Calanus* spp. abundance on the outer shelf (Figure 2a).

In the middle shelf, spring sea-ice cover within a region explained a large proportion of the variation in the numbers of *Calanus* spp. copepods captured in the summer/fall plankton

surveys in that region (Figure 2b). Ice cover after February consistently explained variation in *Calanus* spp. numbers (particularly in regions 6 and 8), with IceDays having explained variances ranging from 0.69 to 0.86 (Figure 2b). The ice index that had the lowest values of explained variance was MeanIce.

Sea-ice cover and jellyfish medusa biomass

We found no statistically significant relationships between our measures of sea-ice cover and the biomass of jellyfish medusae in any of the middle or outer shelf regions (Supplementary Table S2). This result held whether we analysed data from 1979 to 1999, 2000 to 2015, or for the entire period 1979–2015.

Sea-ice cover and age-3 pollock recruits

The relationship between sea-ice cover and pollock recruitment varied depending upon the years analysed, the region, and the ice-metric used (Table 3 and Figure 3a and b). For the period 1979–2015, there was scant evidence that the amount or

Table 2. Continued

| Year | Region 7 | | | Region 8 | | | Age3/SSB |
|------|----------|---------|---------|----------|---------|---------|----------|
| | LastDay | MeanIce | IceDays | LastDay | MeanIce | IceDays | |
| 1980 | 0 | 0.55 | 0 | 0 | 0.15 | 0 | 7.892216 |
| 1981 | 0 | 0 | 0 | 78 | 43.73 | 11 | 8.396533 |
| 1982 | 0 | 0 | 0 | 0 | 1.09 | 0 | 2.825083 |
| 1983 | 0 | 0 | 0 | 123 | 7.1 | 19 | 5.662495 |
| 1984 | 0 | 0.9 | 0 | 21 | 3.53 | 0 | 1.270718 |
| 1985 | 0 | 0 | 0 | 80 | 18.31 | 20 | 2.841199 |
| 1986 | 0 | 0 | 0 | 120 | 0.13 | 21 | 1.054779 |
| 1987 | 0 | 0 | 0 | 91 | 3.26 | 26 | 0.523475 |
| 1988 | 0 | 0 | 0 | 0 | 0 | 0 | 0.371134 |
| 1989 | 0 | 0 | 0 | 101 | 0.42 | 19 | 0.711361 |
| 1990 | 0 | 0 | 0 | 34 | 3.63 | 0 | 3.478754 |
| 1991 | 0 | 1.11 | 0 | 74 | 5.66 | 5 | 2.26362 |
| 1992 | 0 | 0.17 | 0 | 58 | 34.85 | 0 | 2.677647 |
| 1993 | 0 | 0.03 | 0 | 106 | 14.67 | 42 | 5.298373 |
| 1994 | 0 | 0 | 0 | 41 | 15.06 | 0 | 1.290323 |
| 1995 | 101 | 0 | 1 | 86 | 0.11 | 8 | 0.799284 |
| 1996 | 0 | 0 | 0 | 103 | 5.61 | 30 | 1.639808 |
| 1997 | 0 | 0 | 0 | 0 | 2.38 | 0 | 2.245475 |
| 1998 | 0 | 0.58 | 0 | 93 | 5.52 | 22 | 1.164527 |
| 1999 | 0 | 0 | 0 | 62 | 41.18 | 2 | 1.369375 |
| 2000 | 14 | 0 | 0 | 94 | 16.63 | 31 | 2.116555 |
| 2001 | 0 | 0 | 0 | 36 | 8.31 | 0 | 2.852615 |
| 2002 | 0 | 0.16 | 0 | 0 | 0 | 0 | 1.90686 |
| 2003 | 0 | 0 | 0 | 52 | 13.76 | 0 | 1.23 |
| 2004 | 0 | 0 | 0 | 0 | 0 | 0 | 0.52698 |
| 2005 | 0 | 0 | 0 | 0 | 0.03 | 0 | 0.366524 |
| 2006 | 0 | 0 | 0 | 0 | 0 | 0 | 1.011311 |
| 2007 | 0 | 0 | 0 | 35 | 7.13 | 0 | 2.646104 |
| 2008 | 88 | 0.56 | 6 | 91 | 0 | 25 | 1.728697 |
| 2009 | 0 | 0.1 | 0 | 104 | 33.12 | 44 | 8.719632 |
| 2010 | 0 | 0.42 | 0 | 118 | 16.44 | 43 | 3.430341 |
| 2011 | 0 | 0 | 0 | 101 | 19.92 | 41 | 1.783987 |
| 2012 | 82 | 0.39 | 3 | 111 | 6.84 | 24 | 1.289462 |
| 2013 | 0 | 0.19 | 0 | 119 | 25.15 | 59 | 5.670262 |
| 2014 | 0 | 0 | 0 | 107 | 26.92 | 39 | 3.807866 |
| 2015 | 0 | 0 | 0 | 0 | 0.16 | 0 | 1.204687 |

Blue, B = 1st quartile; green, G = 2nd quartile; yellow, Y = 3rd quartile; and red, R = 4th quartile where B is highest years of pollock recruits and B is years with greatest ice cover. Ice indices collected during the age-0 pollock year include LastDay = last day of year with ≥20% sea ice cover; MeanIce = mean sea ice cover, days 32–60; IceDays = days of sea ice cover ≥20% after day 60; and Age3/SSB = number of age-3 pollock of that year-class in millions of fish divided by the spawning stock biomass in the age-0 year.

timing of sea-ice cover had much influence on the recruitment of pollock. MeanIce in February had the r^2 values of 0.12 and 0.26 in regions 7 and 8, respectively (Figure 3a), and IceDays had the r^2 values of 0.14, 0.27, and 0.12 in regions 5, 7, and 8, respectively (Figure 3b). In all cases, the explained variance was ≤27%.

When we examined the relationship between sea-ice cover and pollock recruitment separately for the time periods 1979–1999 and 2000–2015, we obtained very different results (Table 3 and Figure 4). For the period 1979–1999, there were no significant ($p \leq 0.05$) relationships between pollock and ice metrics. The highest explained variance was 0.16. For 20 of 24 regressions, slopes were negative, though none were significantly so. By contrast, for the period 2000–2015, all regressions were positive and, across all eight regions, 17 of 24 were significant, with 11 having r^2 s ≥ 0.40. Although r^2 s were strongest on average in regions 7 and 8 (0.60 and 0.51, respectively), three r^2 s were above 0.40 in regions 1 and 2 (Table 3).

In region 7, the highest r^2 (0.80) between sea ice and pollock was with DaysAfter, whereas in region 8, the highest r^2 was between pollock and MeanIce. Pollock year-class strength in the period 2000–2015 over all regions was most strongly predicted by IceDays (mean $r^2 = 0.49$) followed by MeanIce (mean $r^2 = 0.29$).

The influence of sea-ice cover on pollock recruitment in the period 2000–2015 was similar in the outer and middle-shelf regions (9 of 12 vs. 8 of 12 regressions significant, respectively) (Table 3). The significant regressions in regions 5 and 7, however, may have been driven by the several “warm” years when sea-ice cover in those regions was zero (Figure 3a and b and Supplementary Table S5). The strong positive relationships between pollock recruitment and sea-ice cover for the period 2000–2015 were in stark contrast to the generally weak relationships seen when the data set from 1979 to 1999 or the full data set from 1979 to 2015 was used (e.g. Table 3 and Figure 4).

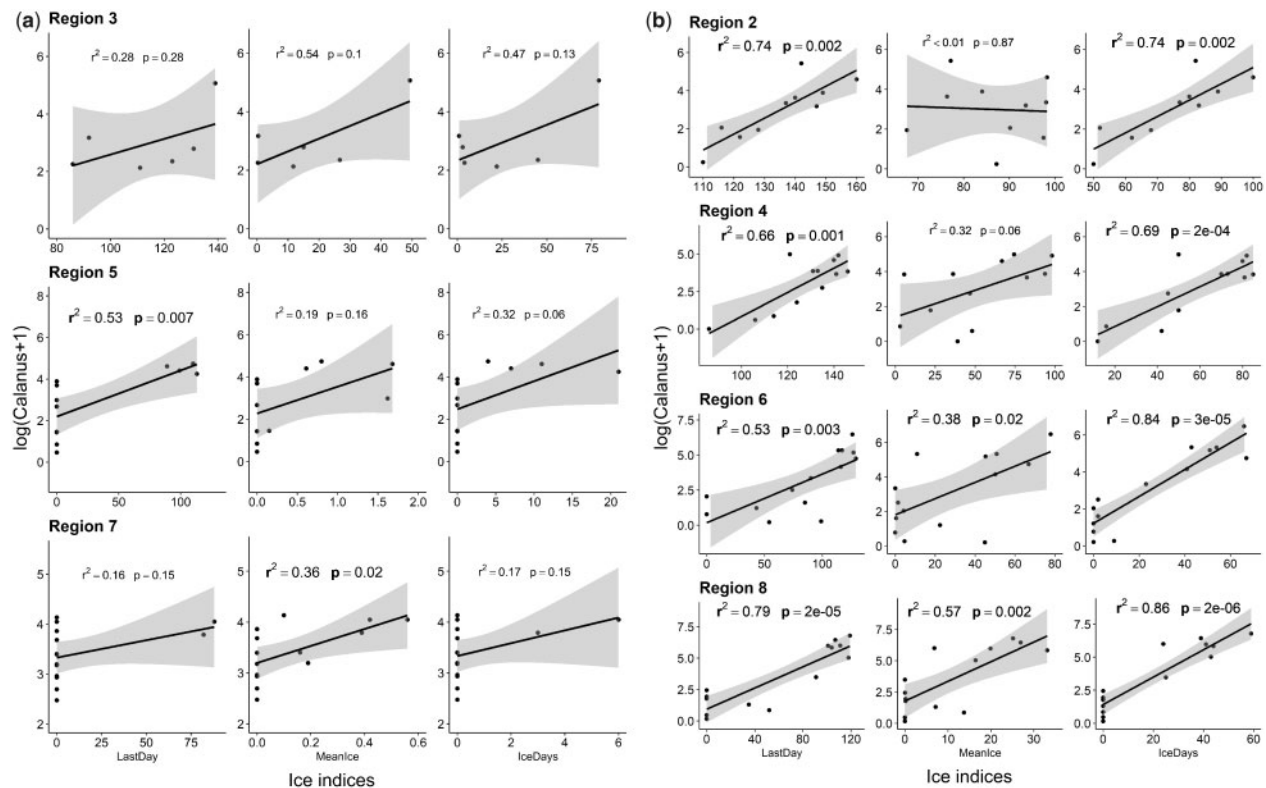


Figure 2. (a) *Calanus* spp. natural log abundance (number m^{-3}) in late summer as a function of sea-ice cover metrics by region over the Outer Shelf Domain (3, 5, 7 from top to bottom). Vertical scale is the natural log number of copepods plus 1; horizontal scales are the three indices of sea ice cover. There were no data available for region 1. (b) *Calanus* spp. natural log abundance (number m^{-3}) in late summer as a function of sea-ice cover metrics by region over the middle shelf (4, 6, 8 from top to bottom). Vertical scale is the natural log number of copepods plus 1, and the horizontal scales are the three indices of sea ice cover. Statistically significant regressions are indicated in bold. There were no data available for region 1.

Copepods and age-3 pollock recruitment

Regressions between age-3 pollock recruitment and the abundance of *Calanus* spp. copepods in mid-August to late September during the age-0 year varied in strength from an r^2 of 0.21 in region 7 to an r^2 of 0.47 in region 4 (Figure 5). Unlike the regressions between pollock and sea-ice cover metrics in the period 2000–2015, for which relationships between pollock and sea-ice cover were strongest in the southern middle shelf, regressions between pollock and copepod abundance were similar and ≥ 0.36 throughout all regions in the middle shelf. In the outer shelf, the only significant regression was for region 5 (Figure 5).

Jellyfish medusa biomass and pollock recruitment

We found no statistically significant relationships between the biomass of jellyfish medusae in the age-0 year of pollock and pollock recruitment to age-3 (Figure 6).

Discussion

Here, we have documented relationships between the timing, extent, and location of sea-ice cover and its impacts on pollock recruitment in the southeastern Bering Sea. The ecological impacts of sea ice depended on when and where in the middle or outer shelf the ice occurred. Our results were sensitive to the metric used to assess the amount or timing of ice cover. During the period 1975–1999, there was a neutral to negative relationship between sea ice and pollock year-class strength. After 2000, pollock

year-classes were stronger in years with heavy sea-ice cover. Although we lacked data on copepods prior to 2002, after that date we found strong correlations between sea-ice cover in spring and the abundance of *Calanus* spp. in late summer/fall. The abundance of these copepods was a good predictor of pollock year-class strength. We sought, but failed to find, a relationship between sea-ice cover and the biomass of jellyfish medusae, or between jellyfish biomass and pollock recruitment. Below, we suggest a new hypothesis that most of the large *Calanus* spp. in the southeastern Bering Sea are *C. glacialis* and that they have been transported south in association with annual sea ice cover.

Sea ice to copepods

For copepods in the outer shelf regions (3, 5, 7), the ice metrics that yielded the strongest correlations were MeanIce (region 7) and LastDay (region 5). Eisner *et al.* (2014) also found ice-retreat timing explained significant inter-annual variability in southern outer shelf *Calanus* spp. abundance. Regions 5 and 7 only rarely had sea-ice cover, and ice cover there may be an indicator of unusually heavy ice years during which there were strong recruitments of large copepods (see also Kimmel *et al.*, 2018).

The duration of middle shelf ice cover in spring strongly influenced the abundance of *Calanus* spp. The length of time in spring that ice lingers is important for secondary production because the ice supports the growth of ice-associated algae on which the copepods can feed (Runge *et al.*, 1991; Durbin and

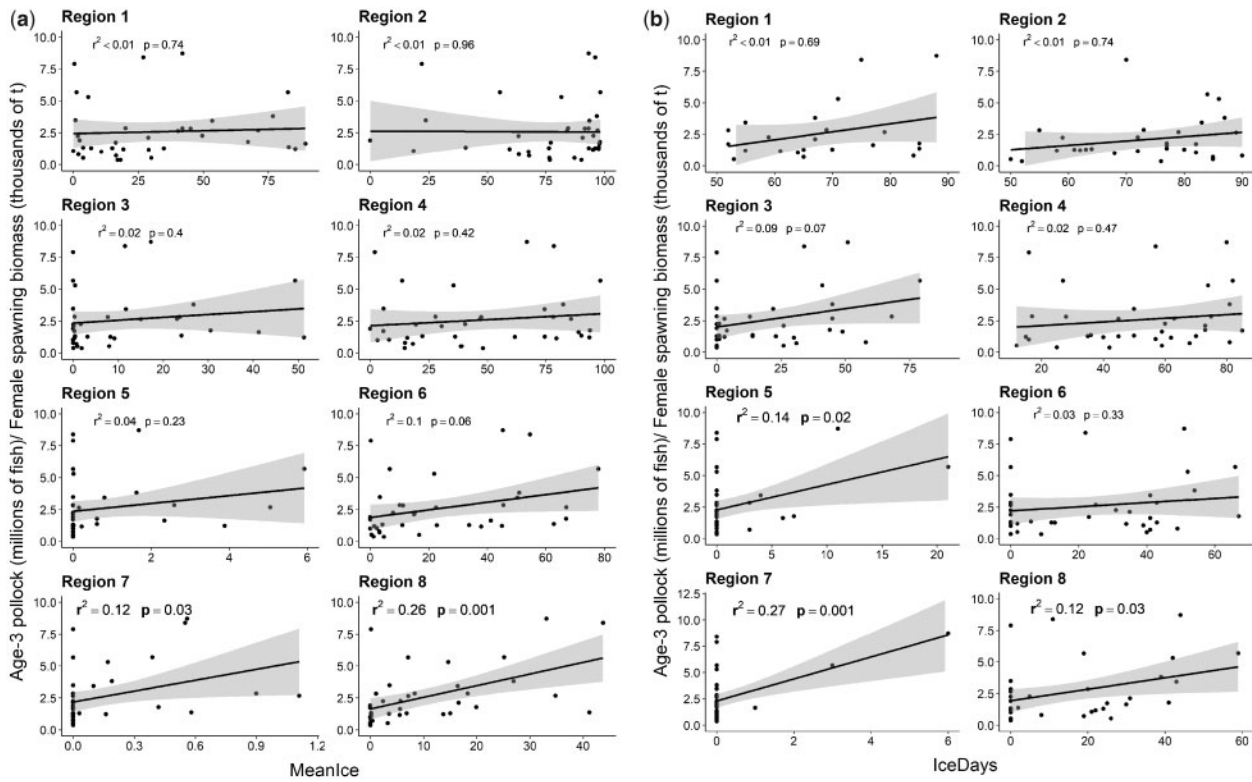


Figure 3. (a) Regressions of age-3 pollock recruitment in millions of fish, divided by spawner biomass in thousands of tons in the age-0 year, vs. February MeanIce in the age-0 year, 1979–2015. (b) Regressions of age-3 pollock recruitment in millions of fish, divided by spawner biomass in thousands of tons in the age-0 year, vs. IceDays in the age-0 year, 1979–2015. Statistically significant regressions are indented in bold.

Table 3. Least squares linear regression coefficient of determination (r^2) values relating the estimates of age-3 pollock recruits per spawner biomass to three metrics of sea-ice cover during the age-0 stage over three time periods in eight regions of the southeastern Bering Sea (see Figure 1).

| Outer Shelf Domain 1979–2015 | | | | Middle Shelf Domain 1979–2015 | | | |
|------------------------------|---------------------|---------------------|---------------------|-------------------------------|---------------------|---------------------|---------------------|
| Region | Pollock vs. LastDay | Pollock vs. MeanIce | Pollock vs. IceDays | Region | Pollock vs. LastDay | Pollock vs. MeanIce | Pollock vs. IceDays |
| 1 | <0.01 | <0.01 | <0.01 | 2 | 0.01 | <0.01 | 0.01 |
| 3 | 0.01 | 0.02 | 0.09 | 4 | 0.03 | 0.02 | 0.02 |
| 5 | 0.04 | 0.04 | 0.14* | 6 | <0.01 | 0.10 | 0.03 |
| 7 | 0.12* | 0.12* | 0.27** | 8 | 0.06 | 0.26** | 0.12* |
| Outer Shelf Domain 1979–1999 | | | | Middle Shelf Domain 1979–1999 | | | |
| Region | Pollock vs. LastDay | Pollock vs. MeanIce | Pollock vs. IceDays | Region | Pollock vs. LastDay | Pollock vs. MeanIce | Pollock vs. IceDays |
| 1 | 0.16 | 0.03 | 0.11 | 2 | 0.11 | 0.05 | 0.13 |
| 3 | 0.06 | <0.01 | <0.01 | 4 | 0.01 | <0.01 | 0.04 |
| 5 | 0.03 | <0.01 | <0.01 | 6 | 0.14 | <0.01 | 0.06 |
| 7 | <0.01 | 0.04 | <0.01 | 8 | 0.01 | 0.11 | <0.01 |
| Outer Shelf Domain 2000–2015 | | | | Middle Shelf Domain 2000–2015 | | | |
| Region | Pollock vs. LastDay | Pollock vs. MeanIce | Pollock vs. IceDays | Region | Pollock vs. LastDay | Pollock vs. MeanIce | Pollock vs. IceDays |
| 1 | 0.17 | 0.17 | 0.47** | 2 | 0.56** | 0.09 | 0.46** |
| 3 | 0.32* | 0.14 | 0.58** | 4 | 0.13 | 0.19 | 0.26* |
| 5 | 0.42** | 0.25** | 0.51** | 6 | 0.18 | 0.36** | 0.36* |
| 7 | 0.60** | 0.41** | 0.80** | 8 | 0.35* | 0.69** | 0.48** |

The number of years with ice data >0 in regions 5 and 7 was 8 and 4 years, respectively. Red font denotes a regression that was negative; that is there was a tendency for years with less ice to support larger year-classes of pollock.

* $p \leq 0.05$;

** $p \leq 0.01$.

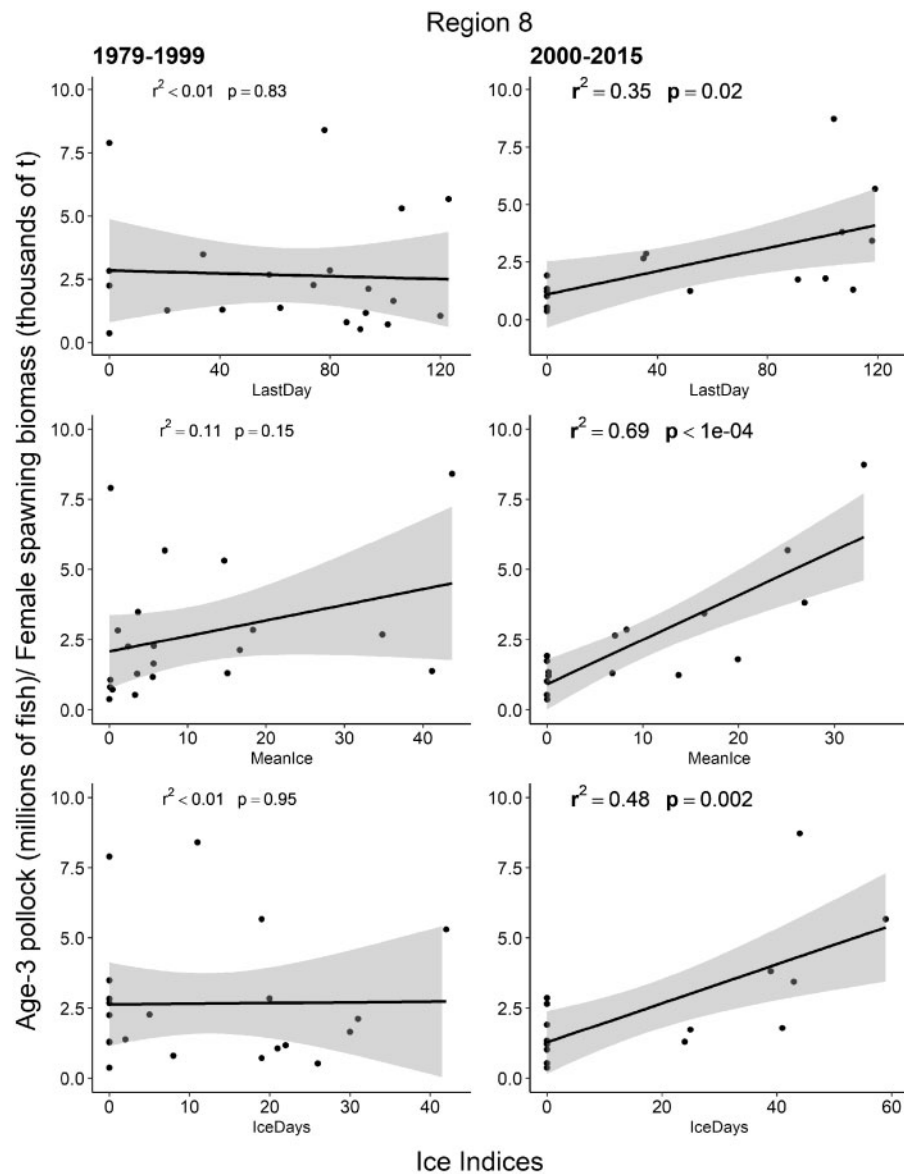


Figure 4. Comparison of results for the periods 1979–1999 and 2000–2015 for regressions of pollock age-3 recruitment in millions of fish divided by spawner biomass in thousands of tons against three ice metrics in region 8. Statistically significant regressions are indicated in bold.

Casas, 2014; Wang *et al.*, 2015). *Calanus* spp. in the Bering Sea also feed on microzooplankton, which in turn have fed on ice algae, as well as open water phytoplankton (Wang *et al.*, 2015; Campbell *et al.*, 2016). Ice cover in February is also important, as that is when adult female *Calanus* spp. seek ice algae to fuel the production of eggs (e.g. Conover, 1988; Runge *et al.*, 1991; Søreide *et al.*, 2006, 2013; Leu *et al.*, 2011; Daase *et al.*, 2013; Durbin and Casas, 2014).

The relationship between *Calanus* spp. abundance and sea-ice cover changed pre- and post-2000. In the period 1979–1999, there were examples of weak-to-positive relationships between water temperatures and crustacean zooplankton abundance (Smith and Vidal, 1986; Coyle and Pinchuk, 2002; Napp *et al.*, 2002). More recent studies, based primarily on data from 2002 to the present,

have emphasized that “cold years” have led to increased abundances of large crustacean zooplankton and “warm years” to reduced abundances (Ohashi *et al.*, 2013; Eisner *et al.*, 2014; Sigler *et al.*, 2016; Kimmel *et al.*, 2018).

The period pre-2000 was characterized by annual change between warm and cold years in contrast to the post-2000 period with stanzas of warm and cold years that may interact with the life histories of *Calanus* copepods and the euphausiid *T. raschii* (Pleuthner *et al.*, 2016). Stanzas of warm and cold years allow for lag effects, with multiple years of a similar level of ice cover allowing zooplankton populations to continue to decline, or conversely to have longer-term increases in abundance (Eisner *et al.*, 2014). Eisner *et al.* (2014) noted lags of 1–2 years between changes in climate and copepod abundance. For a shift from

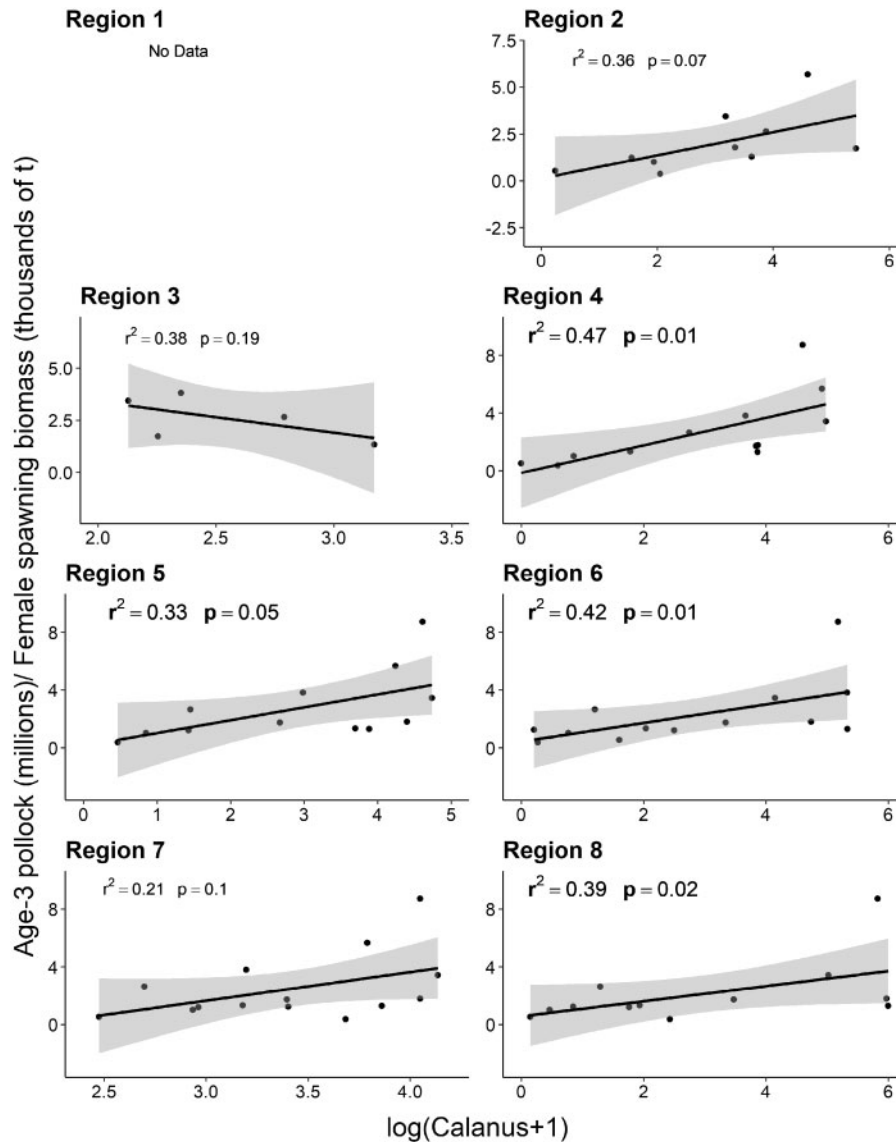


Figure 5. Age-3 pollock recruits in millions of fish divided by female spawning biomass in thousands of tons as a function of *Calanus* spp. natural log abundance (number m^{-3}), by region, 2002–2015. Statistically significant regressions are indicated in bold.

warm years (2001–2005) to cold with an average year, 2006 in between, there were modest increases in *Calanus* spp. in the first cold year 2007 and substantial increases in abundance of *Calanus* spp. in 2008. Eisner *et al.* (2020) also noticed lags in the decline in *Calanus* spp. numbers between cold (2012) to warm (2014) years with an average temperature year in between (2013). It was not until the second warm year (2015) that very low abundances of *Calanus* spp. were seen.

Are *Calanus* spp. in the southeastern Bering Sea mostly *Calanus glacialis*?

Prior to the determination of genetic differences between *C. marshallae* and the two genotypes (Arctic and northern Bering Sea) of *C. glacialis* by Nelson *et al.* (2009) (see also Bucklin *et al.*, 1995), it was assumed that there was one species of large *Calanus* in the southeastern Bering Sea, and most authors specified only *C. marshallae* as present (e.g. Frost, 1974; Vidal and Smith, 1986;

Baier and Napp, 2003). Because *C. marshallae* and *C. glacialis* are difficult to differentiate morphologically, many studies have lumped the two species together as *Calanus* spp. (e.g. Eisner *et al.*, 2014; Wang *et al.*, 2015; Sigler *et al.*, 2016; Kimmel *et al.*, 2018), as is the case in the present study.

Recent efforts, using genomic techniques, have increased our understanding of the distributions of these two closely related *Calanus* species in the eastern Bering Sea. Campbell *et al.* (2014) presented genetic data showing that *C. marshallae* primarily occupied the southern Bering Sea and outer shelf, while *C. glacialis* was dominant over much of the middle shelf, particularly in winter (R. G. Campbell, pers. com.). A second genetic investigation of *Calanus* identification showed that the majority of copepods identified as *Calanus* spp. in the southeastern Bering Sea were *C. glacialis* (Tarrant *et al.*, 2017). Of the 106 individual copepods they collected and tested in late summer 2015, 104 were *C. glacialis* and only 2 were *C. marshallae* and, surprisingly, those two

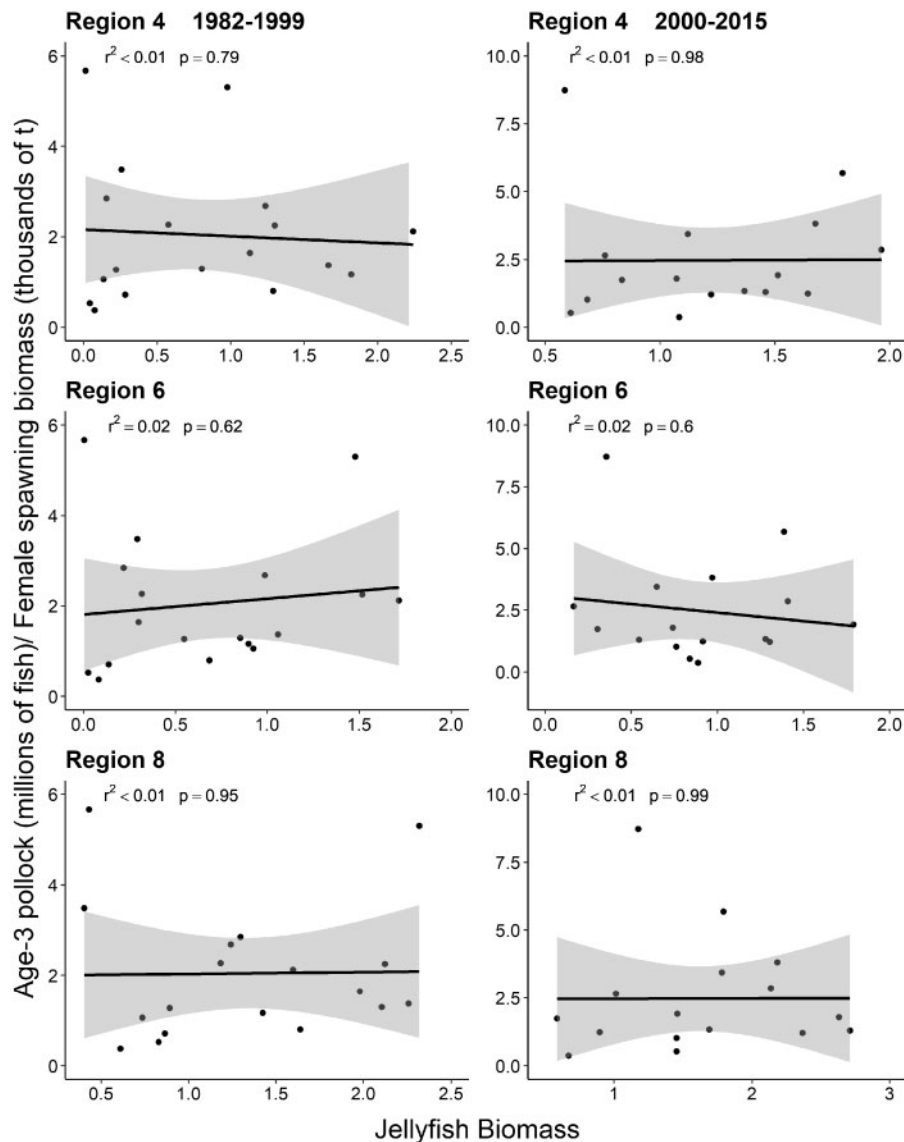


Figure 6. Age-3 pollock recruits in millions of fish divided by spawner biomass in thousands of tons vs. jellyfish biomass (CPUE, kg ha^{-1}) caught in the NOAA Fisheries Bering Sea Bottom Trawl Survey in the pollock age-0 year, by region, for the periods 1982–1999 and 2000–2015.

specimens came from one of the more northerly stations, at about $59^{\circ}30'N$, near the northern edge of the “southeastern” Bering Sea (Stabeno *et al.*, 2012a).

The 2015 dominance of *C. glacialis* in the southeastern Bering Sea was a surprising result, as 2015 was the second year in a row with light sea cover, and thus one might have expected the southern samples to be dominated by *C. marshallae*, the more temperate species. Note, however, that total mean abundance of *Calanus* spp. was low in 2015 and therefore overall counts of *C. glacialis* were low (Eisner *et al.*, 2020).

Calanus marshallae is a temperate species that is at the northern edge of its range, which extends from Cape Mendocino, California to the Bering Sea (Frost, 1974). *Calanus marshallae* is probably resident in the southeastern Bering Sea, supported by the advection of copepodites from the Gulf of Alaska via passes in the eastern Aleutian Islands (Coyle, 2005). *Calanus glacialis* is a pan-Arctic species that is at the southern extent of its range in the

Bering Sea (Frost, 1974; Nelson *et al.*, 2009). *Calanus marshallae* and *C. glacialis* have different life histories. *Calanus marshallae* can produce multiple generations before entering diapause in October (Peterson, 1998). By contrast, *C. glacialis* produces at most one generation in a year and in many locations has a 2-year life cycle (Tande *et al.*, 1985; Michel *et al.*, 2006), or even a 3-year cycle (Kosobokova, 1999). Both species feed before producing eggs (Peterson, 1998; Durbin and Casas, 2014). As noted above, in the Atlantic Arctic, *C. glacialis* forages on ice algae to fuel egg production, and the timing of the availability of ice algae is critical for its reproductive success (e.g. Runge *et al.*, 1991; Søreide *et al.*, 2010; Daase *et al.*, 2013).

We hypothesize that most of the *Calanus* spp. in the southeastern Bering Sea are *C. glacialis* and that at least some of these have been advected there while feeding on ice algae attached to, or recently released from, sea ice formed in the north and blown south (Pease, 1980; Durbin and Casas, 2014). *Calanus glacialis* eggs and

larvae could be transported to the south where they would continue to develop. With a 2-year life cycle, these *C. glacialis* might diapause in the southeastern Bering Sea. Pinchuk *et al.* (2013) evoked a similar wind-driven transport mechanism to account for the presence of the Arctic amphipod, *Themisto libellua*, in the middle shelf of the southeastern Bering Sea in cold years. The percent sea ice cover in February is an important predictor of *C. glacialis* numbers in summer because the ice supports the ice algae which the adult female *C. glacialis* need for egg production. Days of ice after day 60 are also a good predictor of *Calanus* spp. abundance because this is when *Calanus* will be feeding on ice algae.

The multi-year life cycle of *C. glacialis* could account for lags in their population responses to both stanzas of years with heavy and light sea-ice cover. A shift from a period with light sea-ice cover to heavy cover would result in a build-up of population size with a combination of “resident” copepods and new recruits from the north. Conversely, if sea ice is not advected south in February, then the population that may have overwintered in the south will not be augmented by new arrivals, nor have energy resources for reproduction because the open water phytoplankton bloom does not occur until months later (late April/May). The result would be a decline in *C. glacialis* numbers over time.

Figure 7 provides a cartoon summary of our present thinking. Adult female *C. glacialis* leave diapause and rise to feed on ice algae in February. They then lay eggs (not shown), and young feed on the ice algae and on the ice-edge bloom. The copepods mature

to stage C5 in late spring. In years when the ice retreats early, the mature female *C. glacialis* still come up and feed on ice algae if ice is present in February, but there is little algal food for their developing young. Under these conditions, the spring zooplankton community is dominated by smaller copepod species.

Sea-ice cover and pollock

The relationship between sea-ice cover and pollock recruitment varied through time. Between 1979 and 2015, the relationship was weakly positive, and from 1979 to 1999, we found either no relationship or a weak negative, as did Hunt *et al.* (2002). These authors analysed data from 1975 to 2000 and identified a positive relationship between warm years (presumably with less ice cover or earlier ice retreat) and strong year-classes of pollock. Had we had used ice data from before 1979, as was the case for the studies by Hunt *et al.* (2002), we would likely have found a negative relationship between pollock year-class strength and sea-ice cover in the 1975–1999 period. During the “cold” years of the early 1970s to 1976, pollock year-class strength was weak (Ianelli *et al.*, 2018). By contrast, during the warmer years of 1977–1983 (see Overland *et al.*, 2012), pollock year-classes were generally strong (Ianelli *et al.*, 2018).

Between 2000 and 2015, the recruitment of pollock was positively correlated with sea-ice cover and the timing of its retreat. We had expected strong correlations between pollock recruitment and sea-ice cover in the southern middle shelf, and we were surprised to find strong correlations between pollock year-class

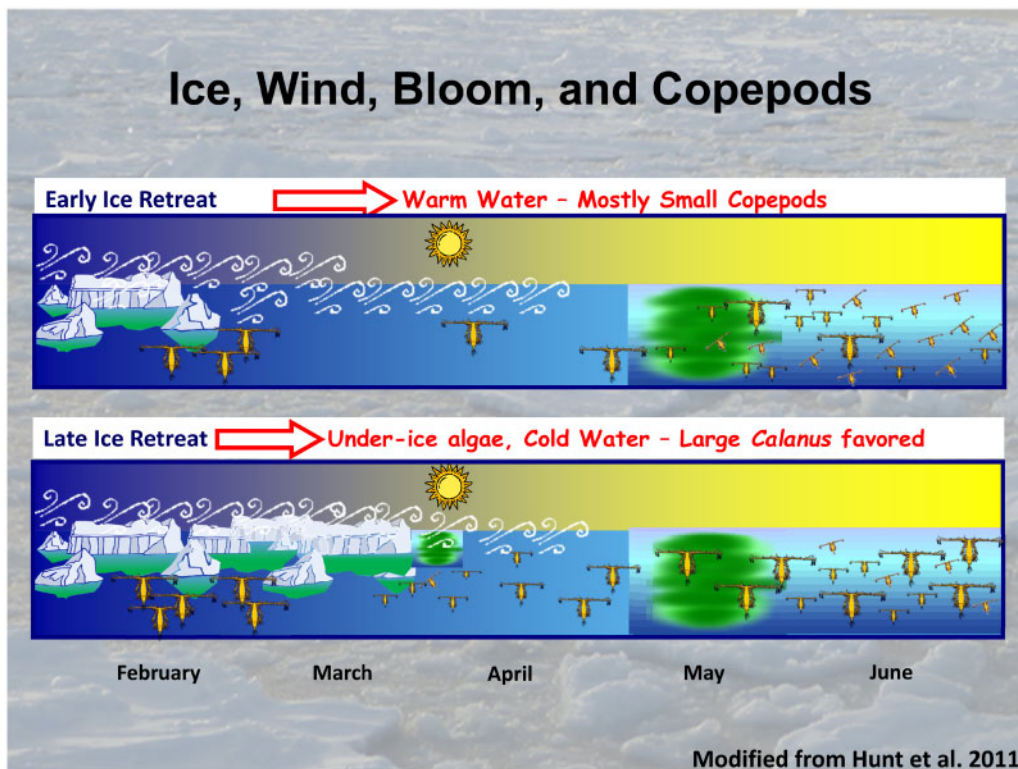


Figure 7. Conceptual model of relationships among sea ice, sea-ice algae, *Calanus* spp. copepods and ice-edge and open water spring blooms in the southeastern Bering Sea. Top: When there is little sea ice, copepods lack food for egg production and for feeding by developing nauplii. Few large copepods are produced, and small copepods reproduce to take advantage of the spring bloom. Bottom: When there is heavy sea-ice cover, the adult female *Calanus* spp. gain energy from ice algae to produce eggs. Nauplii then forage on sea ice algae (or microzooplankton) and large copepods dominate in spring. The spring bloom supports about the same abundance of small species of copepods under both sea-ice scenarios. For a cartoon of the impact of large zooplankton abundance on pollock recruitment, see Hunt *et al.* (2011).

strength and measures of sea-ice cover in region 2, the northernmost region in the middle-shelf portion of our study area. We had expected that ice there would have minimal influence on pollock survival. We have no explanation for this correlation, particularly given the weaker correlations found in adjacent region 4 to the south.

The strong correlations between all three measures of sea-ice cover in region 7, and to a lesser extent region 5, and pollock year-class strength for 2000–2015 may be the result of a few years with particularly heavy sea-ice cover. That said, sea ice in the southern outer shelf may be of importance to pollock larvae spawned near the Pribilof Islands. Although there is little information on the drift of eggs and larvae spawned around the Pribilof Islands (but see [Bacheiler et al., 2010](#); [Petrik et al., 2016](#)), the availability of abundant *Calanus* spp. in the outer shelf could enhance their survival.

Copepods to pollock

Copepods are an important component of juvenile pollock diets, and we had expected the relationship between pollock recruitment and copepod numbers to be stronger than those between sea-ice cover and pollock recruitment. But that was not the case. Similar relationships were found between pollock recruitment and copepods or mean sea-ice indices in both the outer and middle-shelf regions. However, using the same data, [Eisner et al. \(2020\)](#) found that pollock recruitment to age-3 was more strongly correlated with a spatially integrated estimate of large copepod abundance in the southeast Bering Sea than with the annual mean abundance of large copepods at stations sampled at different locations in different years. Thus, for the relationship between pollock recruitment and copepod abundance, an area-wide integrated assessment may be the most useful.

Regions 7 and 8, in the south, may be where age-0 pollock first begin feeding on copepods ([Duffy-Anderson et al., 2016](#)). The strong influence of sea-ice cover in regions 1 and 3 on pollock recruitment may reflect the importance of the availability of large (late stage) copepods there in the late summer/early fall ([Smart et al., 2012](#); [Eisner et al., 2018](#)).

Jellyfish

Although our analyses revealed no significant relationships among measures of sea-ice cover and jellyfish biomass, a generalized additive modelling analysis of Bering Sea jellyfish biomass, conducted on a larger regional scale during 1982–2004, identified sea-ice cover as a significant predictor of regional jellyfish biomass ([Brodeur et al., 2008a](#)). In addition, in periods of high zooplankton biomass when large species predominate, conditions are favourable for jellyfish, while jellyfish are not favoured when smaller crustacean species predominate ([Brodeur et al., 2008a](#); [Decker et al., in prep.](#)). Cyclical fluctuations of Bering Sea jellyfish suggest responses to multi-year changes in secondary productivity, as described above.

Jellyfish and pollock

Large medusae may negatively impact fisheries due to dietary overlap with zooplanktivorous forage fish and predation on fish eggs and larvae ([Brodeur et al., 2008b](#); [Shoji et al., 2009](#); [Robinson et al., 2014](#); [D'Ambra et al., 2018](#)). In our study, however, we found no statistically significant relationships between jellyfish biomass in the age-0 year of pollock and pollock

recruitment to age-3, even though there is considerable spatial overlap between jellyfish and age-0 pollock across the study area ([Decker et al., 2018](#)), and some prey overlap ([Duffy-Anderson et al., 2017](#); [Ruzicka et al., 2020](#)). However, jellyfish may benefit age-0 pollock by providing a refuge from predators among their tentacles ([Brodeur, 1998](#)). Interactions between jellyfish and young pollock are complex and change during their life cycles, which may explain why we found no effect of jellyfish biomass on pollock recruitment.

Importance of predicting meso-zooplankton

Of concern, based on present evidence, is what will happen to *C. glacialis* populations when ice cover is severely reduced due to climate warming ([Mueter et al., 2011](#); [Duffy-Anderson et al., 2016, 2017](#); [Hermann et al., 2016](#); [Stabeno et al., 2016](#)). These zooplankton play a key role in the southeastern Bering Sea ecosystem and are a significant portion of the diets of Pacific cod, pollock, sockeye salmon, and many species of forage fish ([Farley et al., 2007, 2016](#); [Moss et al., 2009](#); [Coyle et al., 2011](#); [Buckley et al., 2016](#)). They are also important prey for the planktivorous great whales (e.g. [Baumgartner et al., 2013](#)). An understanding of zooplankton population responses to climate warming and the loss of sea ice could provide an alert to how future changes will influence the eastern Bering Sea marine ecosystem and the fisheries that it supports. In the present study, our ability to examine the relationships among sea-ice cover, copepods, jellyfish biomass, and pollock year-class strength was compromised by the uneven availability of survey data. Examination of lags between years with or without sea ice and the complex responses of the ecosystem will require a longer time series of annual surveys of the zooplankton (see also [Duffy-Anderson et al., 2016](#)).

Post-script

The winters of 2017/2018 and 2018/2019 had very little sea-ice cover over the eastern Bering Sea shelf, and none below 67°N in either the middle or outer shelf ([Duffy-Anderson et al., 2019](#); [Stabeno and Bell, 2019](#)). In 2018, pollock produced a year-class that was only slightly below the long-term mean, despite the lack of sea ice, and a low abundance of large copepods in summer ([Yasumiishi et al., 2020](#)). In 2018, there was strong on-shelf advection in February, as well as a marked reduction in the biomasses of adult pollock and Pacific cod ([Hunt et al., in prep.](#)), and an increase in jellyfish ([Decker et al., in prep.](#)). There is the possibility that this advection transported zooplankton prey, in particular euphausiids, from the outer shelf to the middle shelf, thus augmenting what was likely a diminished production of zooplankton over the southern shelf. Alternatively, the reduced biomass of adult pollock and Pacific cod could have resulted in reduced predation pressure on those age-0 pollock that found sufficient food to survive their first winter. In winter 2018/2019, there was again strong on-shelf advection, but because of the cancellation of surveys in 2020, data on the size of the 2018 year-class are unavailable.

Supplementary data

[Supplementary material](#) is available at the *ICESJMS* online version of the manuscript.

Data availability statement

The data underlying this article will be shared on reasonable request to the corresponding author.

Acknowledgements

We thank the many people who participated in the multiple cruises to the eastern Bering Sea during which the data we have used were gathered. We give special thanks to Sigrid Salo who provided the sea-ice-cover data on which this paper is based, to Roger Hill for help with data manipulations, and to David Kimmel and Mike Sigler who provided insightful comments on earlier drafts. Their help in evaluating our hypotheses was greatly appreciated. We thank Bob Campbell and Ann Tarrant for sharing posters and other unpublished data on the genetic makeup and species designations of eastern Bering Sea *Calanus* spp. This paper was largely self-funded. The NOAA Eco_FOCI contribution number is EcoFOCI-0956.

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Handling editor: Rubao Ji