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Copepod dynamics across warm and cold periods in the eastern Bering Sea: Implications for walleye pollock (*Gadus chalcogrammus*) and the Oscillating Control Hypothesis

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Abstract

Differences in zooplankton populations in relation to climate have been explored extensively on the southeastern Bering Sea shelf, specifically in relation to recruitment of the commercially important species walleye pollock (*Gadus chalcogrammus*). We addressed two research questions in this study: (i) Does the relative abundance of individual copepod species life history stages differ across warm and cold periods and (ii) Do estimated secondary production rates for copepods differ across warm and cold periods? For most copepod species, warmer conditions resulted in increased abundances in May, the opposite was observed in colder conditions. Abundances of smaller-sized copepod species did not differ significantly between the warm and cold periods, whereas abundances of larger-sized *Calanus* spp. increased during the cold period during July and September. Estimated secondary production rates in the warm period were highest in May for smaller-sized copepods; production in the cold period was dominated by the larger-sized *Calanus* spp. in July and September. We hypothesize that these observed patterns are a function of temperature-driven changes in phenology combined with shifts in size-based trophic relationships with primary producers. Based on this hypothesis, we present a conceptual model that builds upon the Oscillating Control Hypothesis to explain how variability in copepod production links to pollock variability. Specifically, fluctuations in spring sea-ice drive regime-dependent copepod production over the southeastern Bering Sea, but greatest impacts to upper trophic levels are driven by cascading July/September differences in copepod production.

KEYWORDS
Bering Sea, *Gadus chalcogrammus*, Oscillating Control Hypothesis, walleye Pollock

1 | INTRODUCTION

The southeastern Bering Sea is one of the most productive large marine ecosystems in the world (NRC, 1996). It supports large populations of invertebrates, finfish, seabirds, and marine mammals (Loughlin, Sukhanova, Sinclair, & Ferrero, 1999). It is home to some of the largest commercial and subsistence fisheries on the planet encompassing a wide range of target species, including walleye pollock (*Gadus chalcogrammus*, hereafter pollock), Pacific halibut (*Hippoglossus stenolepis*), Pacific salmon (*Oncorhynchus* spp.), snow crab (*Chionoecetes* spp.), king crab (*Paralithodes* spp.), and whales (National Research Council, 1996). Recent, large-scale climatic fluctuations have been observed in the Bering Sea (Danielson, Curchitser, Hedstrom, Weingartner, & Stabeno, 2011; Hunt et al., 2011; Stabeno et al., 2012; Yeo et al., 2014). The result was a period of warm and cold "stanzas" (anomalous temperatures that persist over multiple years) that affected the temporal and spatial coverage of sea ice (Duffy-Anderson et al., 2017; Stabeno et al., 2017).

Sea ice changes have been linked to shifts in phytoplankton bloom dynamics and total system productivity (Lomas et al., 2012; Niebauer, Alexander, & Henrichs, 1990, 1995; Sambroto, Niebauer, Goering, & Iverson, 1986). Zooplankton populations have also shown differences during warm and cold periods in the Bering Sea (Eisner, Napp, Mier, Pinchuk, & Andrews, 2014; Ohashi et al., 2013; Pinchuk, Coyle, Farley, & Renner, 2013; Volkov, 2012). Changes in the zooplankton community are relevant because the vast majority of fish species rely on zooplankton as prey during their early life stages when pre-recruitment mortality is at its highest and year-class strength is determined (Cushing, 1974, 1990; Hjort, 1914; Houde, 1989). Thus, plankton resources available to fish during the first year of life are critical and other recent work from the Bering Sea indicates that recruitment success is dependent upon zooplankton availability in summer and autumn (Siddon, Heintz, & Mueter, 2013). Specifically, quality, quantity, and distribution of zooplankton prey later during the first-year period, when fish are in the juvenile phase, have been linked to survivorship of pollock (Heintz, Siddon, Farley, & Napp, 2013; Siddon, Kristiansen, et al., 2013), a nodal food web species that supports a billion dollar fishing industry (Bailey, 2013). Adequate provisioning over summer through predation on large-bodied, lipid-rich zooplankton species appears to be critical to survival through the first overwinter period, a time of selective mortality of energy-poor individuals. As such, climate-mediated variations in zooplankton prey resources during summer-autumn, when juveniles are provisioning for winter, can manifest as large-scale fluctuations in cohort strength (Ianelli, Honkalehto, Barbeaux, Fissel, & Kotwicki, 2016).

Differences in zooplankton populations between warm and cold years have been observed in the southeastern Bering Sea since the 1980s. There is general consensus that *Calanus* spp. abundance increases on the middle shelf during cold periods (Baier & Napp, 2003; Coyle, Pinchuk, Eisner, & Napp, 2008; Eisner et al., 2014; Jin, Deal, Wang, & McRoy, 2009; Ohashi et al., 2013; Smith & Vidal, 1986); however, one study did find that *Calanus marshallae* abundance increased during June at locations along the inner shelf during warm conditions (Coyle & Pinchuk, 2002). Other copepod taxa (*Acartia* spp., *Oithona* spp., *Magnapinna pacifica* and *Pseudocalanus* spp.) appear to show greater variability in response to interannual variability in temperature. Warm conditions appear to result in increased abundances of *M. pacifica* (Smith & Vidal, 1986), *Oithona* spp. (Coyle et al., 2008; Eisner, Hillgruber, Martinson, & Maselko, 2013), and *Pseudocalanus* spp. (Coyle & Pinchuk, 2002; Coyle et al., 2008; Smith & Vidal, 1986). In contrast, Ohashi et al. (2013) and Eisner et al. (2014) reported higher abundances of *Pseudocalanus* spp. during a cold period. *Acartia* spp. abundances have been reported to both increase (Coyle & Pinchuk, 2002) and decrease (Ohashi et al., 2013; Smith & Vidal, 1986) in response to warm conditions. The discrepancies among taxa reported for these studies may be a result of sampling time and location differences; however, the majority of studies agree on the general copepod response on the middle Bering Sea shelf to warm and cold fluctuations. The two main items in agreement were (i) changes in copepod abundances are not thought to be related to cross-shelf advection (Coyle & Pinchuk, 2002; Coyle et al., 2008; Eisner et al., 2014; Smith & Vidal, 1986) and (ii) cold years appear to favor increased abundances of larger-sized *C. marshallae* whereas warmer conditions appear to result in increased abundances of smaller-sized copepods (*Oithona* spp. consistently and *Pseudocalanus* spp. in the majority of studies).

The mechanism that has been proposed to explain these observed patterns focuses on the atmosphere-ice-ocean dynamics that influence water temperature and phytoplankton production (Napp, Kendall, & Schumacher, 2000; Sigler et al., 2016). Cold years on the southeastern Bering Sea shelf have significant winter sea-ice extent, colder water temperatures, and an ice-associated spring algal bloom (Hunt et al., 2002; Sigler, Stabeno, Eisner, Napp, & Mueter, 2014; Stabeno, Bond, Kachel, Salo, & Schumacher, 2001; Stabeno, Schumacher, Davis, & Napp, 1998), although considerable variability within cold years is observed (Stauffer, Miksis-Olds, & Goes, 2015). Warm years are ice-free, have warmer water temperatures, and an open-water spring bloom as the water column stratifies (Hunt et al., 2002; Sambroto et al.,1986; Sigler et al., 2014; Stabeno et al., 2001). The combined effects of primary production and temperature have been hypothesized to drive the observed differences in the zooplankton community (Banas et al., 2016; Coyle et al., 2011; Hunt et al., 2011; Sigler et al., 2014; Stauffer et al., 2015).

The variability in sea-ice extent and zooplankton production has been linked to pollock variability through the Oscillating Control Hypothesis (OCH) (Coyle et al., 2011; Hunt et al., 2002, 2011). Hunt et al. (2002), in the first presentation of the OCH, predicted the southeastern Bering Sea would oscillate between top-down control in warm periods and bottom-up control in cold periods and the production of zooplankton was the fulcrum on which the ecosystem oscillated. Hunt et al. (2002) predicted that a phytoplankton bloom in warmer waters would allow zooplankton populations to grow rapidly providing plentiful prey for fish, specifically pollock, thus warm years would enhance fish recruitment. Cold years, in contrast, would lead to decreased production of zooplankton due to temperature limitation on growth and fish recruitment would be reduced over time (Hunt et al., 2002). After a series of poor recruitment years of pollock (year classes 2001–2005) that occurred during warm water conditions, the OCH was revisited (Coyle et al., 2011; Hunt et al., 2011). Coyle et al. (2011) noted that the original OCH treated zooplankton as a single box; however, there was an evident shift to a predominance of smaller-sized taxa, particularly later in the year, in warm years that was accompanied by a reduction in *C. marshallae* and euphausiid abundance. Coyle et al. (2011) also reported that in the subsequent colder period from 2006–2009, populations of larger zooplankton increased and juvenile pollock disappeared from diets of larger pollock and salmon. Hunt et al. (2011) revised the OCH to link the conditions in spring to those later in the year and suggested that while warm years did produce good initial conditions for larval pollock; conditions later in the year were not favorable due to a lack of lipid-rich zooplankton available in summer and autumn. This results in a lack of storage lipid accumulation that leads to increased overwintering mortality due to juvenile starvation and predation (Heintz et al., 2013; Hunt et al., 2011).

While many aspects of the copepod community response to warm and cold oscillations are generally agreed upon, several areas of interest remain unexplored. In this paper, we examine abundance of individual life history stages over the year and estimate rates of secondary production. Examining changes in species abundance over the growing season may indicate which period is most relevant to pollock and coincides with particular life history stages of copepods (a proxy for size). Secondary production rates of copepods define the rate at which energy is incorporated into body mass (Banse, 1995; Poulet, Ianora, Laabir, & Breteler, 1995). This rate is one of the most important, and most difficult, to quantify for ecosystem models (Dolbeth, Cusson, Sousa, & Pardal, 2012). Knowledge of differences in rates of secondary production across warm and cold conditions can provide estimates of the impact of water temperature fluctuations on upper trophic level production. We had two research questions: (i) Does the relative abundance of individual copepod species life history stages differ across warm and cold periods? and (ii) Do estimated secondary production rates for copepods differ across warm and cold periods? We expected copepod development to proceed faster during warm periods, thus the distribution of life history stages would be altered with temperature changes leading to a phenological change in the timing of peak abundances. In addition, because secondary production rates differ for copepods with different life history strategies (Hirst & Bunker, 2003; Hirst & Lampitt, 1998), we expected secondary production rates to increase for smaller copepods during warm periods (increased abundance and temperature) and secondary production rates to increase for *Calanus* spp. during cold periods (increased abundance and larger body size). We interpret our results in the context of the OCH predictions regarding controls on pollock recruitment variability in the southeastern Bering Sea.

2 | MATERIALS AND METHODS

2.1 | Study area

The southeastern Bering Sea is a broad (500 km wide), shallow (<200 m) coastal shelf (Hunt et al., 2002) that has three recognized cross-shelf hydrographic domains (inner, middle, outer) during the summer-fall period (Coachman, 1986; Cooney & Coyle, 1982; Iverson et al., 1979). We selected three finer scale regions that were defined using hydrographic and oceanographic features (Ortiz, Weise, & Grieg, 2012) and were approximately bounded by 55–60°N latitude and 160–172°W longitude (Figure 1). These areas were chosen to represent a more northerly (Central Middle Shelf (CMS)) and a more southerly (Southern Middle Shelf (SMS)) region of the middle shelf domain (50–100 m), as well as an outer shelf region (Southern Outer Shelf (SOS)) of the outer shelf domain (100–200 m) (Hunt et al., 2002). To quantify the temperature and ice cover differences in the southeastern Bering Sea, we report observations for sea surface temperature anomalies from January–April (M2 mooring, Figure 1), ice cover index, and days of ice retreat after 15 March. Details on these data may be found at: http://www.beringclimate.noaa.gov/data/index.php. We defined the years 2001–2005 as warm years and 2007–2011 as cold years based on sea ice data and water temperatures.

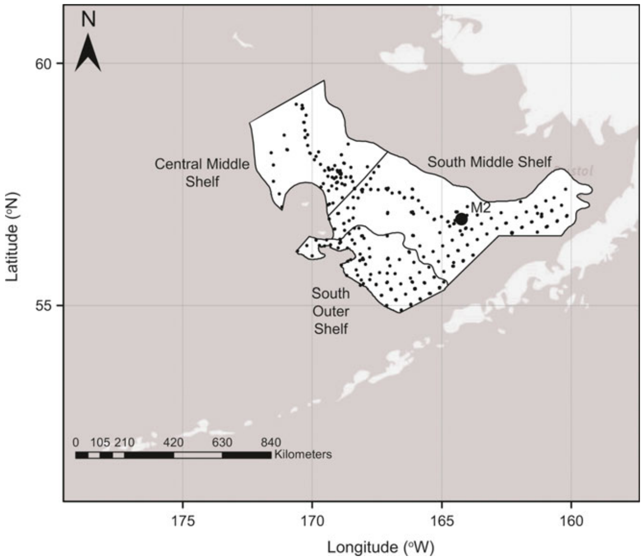

FIGURE 1 Southeastern Bering Sea showing locations of three geographic regions (Ortiz et al., 2012) and the location of mooring M2. Closed circles show sampling locations

2.2 | Copepod data collection

Copepods were collected using oblique tows of paired bongo nets (20 cm frame, 150 μm mesh and a 60 cm frame, 333 μm mesh) (Incze, Siefert, & Napp, 1997; Napp et al., 2002). The tows were within 5–10 m of the bottom depending on sea state. Net depth was determined in real-time using a SeaCat conductivity, temperature, and depth (CTD) sensor (Sea-Bird Electronics[1]). Volume filtered was estimated using a General Oceanics flowmeter mounted inside the mouth of each net. Samples were preserved in 5% buffered formalin/seawater. Copepods were identified to the lowest taxonomic level and stage possible at the Plankton Sorting and Identification Center (Szczecin, Poland), and verified at the Alaska Fisheries Science Center, Seattle, Washington, USA. We enumerated the following taxa and copepodites states from the 150 μm mesh net: *Acartia* spp. copepodite (C) 6, *M. pacifica* C1–C4, *Oithona* spp. C5–6 (combined), *Pseudocalanus* spp. C1–C6; from the 333 μm mesh net: *Calanus* spp. C2–C6, *M. pacifica* C5–C6 (Incze et al., 1997). It is important to note here that while we report *Calanus* spp. as a mixture of *C. marshallae* and *C. glacialis*, the exact proportion of each species on the southeastern Bering shelf is unknown as these species are difficult to distinguish (Campbell et al., 2016). Throughout the paper, we refer to this mixture as *Calanus* spp. A summary of the number of samples collected over space and time is shown in Table 1.

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[1] Use of trade names does not constitute an endorsement by NOAA.

TABLE 1 Sample sizes for each region, period, and month

Region	Period	Month	*N*
Central middle shelf	Warm	May	35
		July	2
		September	15
	Cold	May	48
		July	21
		September	61
South middle shelf	Warm	May	54
		July	26
		September	19
	Cold	May	158
		July	13
		September	109
South outer shelf	Warm	May	37
		July	30
		September	No data
	Cold	May	130
		July	16
		September	20

2.3 | Secondary production estimates

We calculated daily secondary production rates for each taxon and stage as P = NWg, where P is production (μg C m^{-3} d^{-1}), *N* is the number of individuals (m^{-3}), *W* is the individual biomass (μg C m^{-3}), and *g* is the growth rate (d^{-1}). Number of individuals (*N*) was measured using counts from net tows. Biomass (*W*) was estimated using literature values of dry weight for each taxon and stage (Table 1). Biomass was converted to Carbon (C) assuming 40% of dry weight (Båmstedt, 1986). Growth rate (*g*) was estimated using equations from the literature (Table 3). Sea surface temperature (SST) data were acquired from NOAA High resolution Blended Analysis of Daily SST and Ice (http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html#detail). Data are at the resolution of 0.25° latitude and 0.25° longitudes in a global grid. Monthly SST values were computed for each oceanographic region using the following bounding coordinates: CMS (56–58°N, 168–172°W), SMS (56–58°N, 160–168°W and 54–56°N, 160–164°W), and SOS (54–56°N, 164–168°W). Chlorophyll-*a* concentrations in the water column were acquired using SeaWiFS remotely sensed data (http://oceancolor.gsfc.nasa.gov/cgi/browse.pl?sen=sw&typ=GAC). Using the same bounding coordinates for each oceanographic region as SST, we computed monthly mean chlorophyll-*a* concentrations.

A comparison of production estimates using different equations to calculate growth rates, revealed some differences in production estimates (Figure S1). The production estimates (μg C m^{-3}d^{-1}) based on the Huntley and Lopez (1992) growth rate equation were higher for most taxa (Fig. S1). For the majority of taxa, there were no significant differences among the remaining production estimates (Fig. S1). The lone exception was *M. pacifica* that had a higher production estimate based on the Hirst and Bunker (2003) growth rate equation (Fig. S1). Based on these results, we chose to report secondary production estimates using the Hirst and Lampitt (1998) growth equation for comparison consistency across taxa. We chose the Hirst and Lampitt (1998) equation because it did not rely on chlorophyll-*a* concentration, therefore we could include more estimates of secondary production as the chlorophyll-*a* data had more missing data. Also, reliance on chlorophyll *a* estimation from satellite in this region makes multiple assumptions that introduce error, including: cloud prevalence, fixed carbon to chlorophyll *a* ratio, and that chlorophyll *a* concentrations within one optical depth represent the phytoplankton community.

2.4 | Statistical analysis

We compared differences in abundances of copepod life history stages and estimated secondary production between warm and cold periods by using analysis of variance (ANOVA) (Sokal & Rohlf, 1995). All statistical analyses were conducted using R statistical analysis software (R Core Team, 2016). First, we fourth-root transformed all zooplankton abundance data (number m^{-3}) to approximate the normal distribution and stabilize variances. We tested the null hypotheses that relative abundance of life history stage for a particular month and region did not differ across warm and cold periods. We analyzed each taxon separately, designated warm/cold period as a fixed factor, and ran ANOVA for each species, nesting life-history stage within warm/cold period. This allowed us to test the portioned variance related to shifts in the abundance of life history stages across warm and cold years in particular months, i.e. our null hypothesis. For two taxa, *Acartia* spp. and *Oithona* spp., there was only one life history stage enumerated, therefore life history stage factor was not used in these models. Our analysis had unbalanced data across all factors in the form of different numbers of observations, though all factors did have observations. For *post-hoc* comparisons, we used Tukey's honest significant difference (HSD) test to examine pairwise comparisons of interest.

We compared estimated secondary production rates for each taxon, and unfortunately, estimates of secondary production resulted in lower samples sizes due to missing parameters in the growth rate equation (namely, chlorophyll-*a* estimates; Table 3). As a result, we could not examine individual life history stages with statistical power; therefore, we estimated secondary production by summing across life-history stages. We then compared warm and cold periods for each month and region. Secondary production highlights the consequences of any observed differences in abundance for each region as it incorporates the effect of temperature, body size, and food availability, depending on the model used to estimate growth rate (Hirst & Bunker, 2003; Hirst & Lampitt, 1998; Huntley & Lopez, 1992). As above, we used ANOVA to test the null hypothesis that estimated rates of secondary production did not differ across warm and cold periods designating warm/cold period as a fixed factor.

TABLE 2 Prosome length (μm) and dry weight (μg) of copepod species

Species	Stage	Prosome length (μm)	Dry weight (μg)	Source
Acartia spp.	C6	1,110[a]	11	Size: http://www.arcodiv.org/watercolumn/copepod/Oithona_similis.html Weight: (Peterson, Tiselius, & Kiørboe, 1991)
Calanus marshallae	C2	966 ± 22.56	4.27 ± 0.87	Liu and Hopcroft (2007)
	C3	1,331 ± 60.67	10.19 ± 5.09	
	C4	1,824 ± 99.43	38.06 ± 12.84	
	C5	2,684 ± 175.27	236.22 ± 97.70	
	C6	2,923 ± 83.30	248.85 ± 60.12	
Metridia pacifica	C1	428 ± 16.26	0.92 ± 0.27	Liu and Hopcroft (2006)
	C2	568 ± 19.27	2.25 ± 0.38	
	C3	779 ± 36.22	5.37 ± 0.75	
	C4	912 ± 126.71	9.02 ± 3.85	
	C5	1,311 ± 134.52	35.76 ± 13.08	
	C6	1,851 ± 133.22	112.33 ± 30.00	
Oithona spp.	C5–6	550[a]	0.9	Size: http://www.arcodiv.org/watercolumn/copepod/Oithona_similis.html Weight: (Vidal & Smith, 1986)
Pseudocalanus spp.	C1	415 ± 44.60	0.70 ± 0.18	Liu and Hopcroft (2008)
	C2	522 ± 37.7	1.39 ± 0.68	
	C3	652 ± 76.47	2.36 ± 1.05	
	C4	821 ± 110.28	5.69 ± 2.11	
	C5	981 ± 176.18	8.46 ± 3.68	
	C6	1,052 ± 137.90	10.21 ± 4.83	

[a] Adult female size reported.

3 | RESULTS

3.1 | Environmental conditions

The two time-periods differed in ice cover, timing of ice retreat, and January–April SST anomalies (Figure 2). Ice cover index was negative during the warm period (2001–2005) and positive during the cold period (2007–2011) (Figure 2a). Ice retreat occurred prior to 15 March during all years of the warm period, except 2004; whereas, ice retreat occurred >20 days after 15 March in all years during the cold period (Figure 2b). Finally, January–April SST anomalies were positive in all years during the warm period, with the exception of 2002, and negative during all years during the cold period (Figure 2c).

3.2 | Abundance of life history stages

Copepod abundances across species and life history stages showed differences during warm and cold periods (Figures 3–5). On the CMS, *Calanus* spp., *M. pacifica*, *Oithona* spp., and *Pseudocalanus* spp. all had higher abundances observed in May during the warm period (Figure 3a). The only species that had a higher abundance during the cold period was *Acartia* spp. (Figure 3a). Unfortunately, not enough samples were collected during July during the warm period for comparison (Figure 3b). In September, *Oithona* spp. had higher abundances in the warmer period, as well as two stages of *Pseudocalanus* spp (Figure 3c). In contrast, *Calanus* spp. had higher abundances in the cold period, particularly for stage C5 (Figure 3c). On the SMS, the same pattern was seen as on the CMS with *Calanus* spp., *M. pacifica*, *Oithona* spp., and *Pseudocalanus* spp. having higher abundances during the warm period in May (Figure 4a). Interestingly, *Acartia* spp. abundance was also higher on the SMS during May (Figure 4a). July abundances differed for *Calanus* spp. stages C3–4, *Acartia* spp., and *Pseudocalanus* spp. stages C5–6, all of which had higher abundances in the cold period (Figure 4b). September abundances were similar across taxa, with the exception of *Oithona* spp., which had higher abundances in the warm period and *Calanus* spp. which had very high abundances in the cold period, particularly for stage C5 (Figure 4c). On the SOS, the warm period was characterized by higher abundances of *Acartia* spp., *Calanus* spp. C5, *M. pacifica* C2–5, and *Pseudocalanus* spp. C4–6 in May (Figure 5a). No statistical differences were found between warm and cold periods on the SOS in July (Figure 5b). Note that no abundances were measured during the warm period in September on the SOS (Figure 5c).

3.3 | Estimated secondary production rates

Estimates of copepod secondary production across species and life history changes showed differences during warm and cold periods both by region and by month (Figure 6). On the CMS, *M. pacifica*,

TABLE 3 Copepod growth rate equations used in production calculations

Equation	Taxa	Source
$g = 0.0445e^{0.111T}$	All	Huntley and Lopez (1992)
$\log_{10}(g) = -0.6516 - 0.5244(\log_{10}(\mathrm{BW}))$	*Acartia* spp., *Calanus* spp. CVI, *M. pacifica* CVI,	Hirst and Lampitt (1998)
$\log_{10}(g) = 0.0111T - 0.2917(\log_{10}(\mathrm{BW})) - 0.6447$	*Calanus* spp. CIII–CV, *M. pacifica* CI–CV,	Hirst and Lampitt (1998)
$\log_{10}(g) = -1.7726 + 0.0385T$	*Oithona* spp., *Pseudocalanus* spp. CVI	Hirst and Lampitt (1998)
$\log_{10}(g) = -1.4647 + 0.0358T$	*Pseudocalanus* CI–CV	Hirst and Lampitt (1998)
$\log_{10}(g) = 0.0125T - 0.230(\log_{10}(\mathrm{BW})) + 0.729(\log_{10}(C_a)) - 1.348$	*Acartia* spp., *Calanus* spp. CVI, *M. pacifica* CVI,	Hirst and Bunker (2003)
$\log_{10}(g) = -0.0143T - 0.363(\log_{10}(\mathrm{BW})) + 0.135(\log_{10}(C_a)) - 0.105$	*Calanus* spp. CIII–CV, *M. pacifica* CI–CV,	Hirst and Bunker (2003)
$\log_{10}(g) = 0.0182T + 0.193(\log_{10}(\mathrm{BW})) + 0.729(\log_{10}(C_a)) - 1.591$	*Oithona* spp., *Pseudocalanus* spp. CVI	Hirst and Bunker (2003)
$\log_{10}(g) = 0.0333T - 0.163(\log_{10}(\mathrm{BW})) - 1.528$	*Pseudocalanus* CI–CV	Hirst and Bunker (2003)
$\log_{10}(g) = -0.3659 + 0.0228T + 0.345(\mathrm{Chl}) + 0.4224\log_{10}(\mathrm{BW}) - 0.3891(\mathrm{Stg})$	*Calanus* spp. CIII–CV	Liu and Hopcroft (2007)
$\log_{10}(g) = 0.4033 + 0.0095T + 0.0549 \mathit{log}_{10}(\mathrm{Chl}) + 0.3689\log_{10}(BW) - 0.1694(\mathrm{Stg})$	*M. pacifica* CI–CVI	Liu and Hopcroft (2006)
$\log_{10}(g) = 0.12428 - 0.02953(\mathrm{Stg}) + 0.00404T + 0.0502\log_{10}(\mathrm{BW})$	*Pseudocalanus* CI–CVI	Liu and Hopcroft (2008)

T, temperature (C); BW, bodyweight μg C individual^{-1}; C_a, chlorophyll-*a* concentration (μg chl *a*/L); Chl, chlorophyll-*a* concentration (mg m^{-3}); Stg, initial stage.

Oithona spp., and *Pseudocalanus* spp. showed significantly higher secondary production rates during warm periods (Figure 6a). This was also observed on the SMS for *Oithona* spp. and *Pseudocalanus* spp. (Figure 6b). Estimated secondary production rates of *Acartia* spp. were higher during the cold period on the CMS (Figure 6a) and *Calanus* spp. rates were higher on the SMS during the cold period (Figure 6b). No significant differences in estimated secondary production rates were observed on the SOS, though *Calanus* spp. had higher production rates during cold years (Figure 6c). In May, estimated secondary production was higher in the warm period for all taxa excepting *Acartia* spp. (Figure 6d). Despite the differences, the production rates in May were the lowest rates observed over the year, even in warm years. In July, the estimated secondary production rates were higher for all taxa during the cold period, with the exception of *Oithona* spp. (Figure 6e). Finally, in September, *Calanus* spp. estimated secondary production rates remained higher during the cold period, whereas *Oithona* spp. rates remained greater during the warm period (Figure 6f).

4 | DISCUSSION

We found seasonal differences in both copepod abundances and estimated secondary production rates across the warm and cold periods in the southeastern Bering Sea. The magnitude of the warm–cold difference was much lower in May than subsequent seasons (Figure 6d) and this observation suggests that variability in spring zooplankton composition or secondary production is not related to the regime-dependent differences in recruitment strength observed among age-1 pollock populations (Hunt et al., 2002, 2011). Furthermore, it appears that spring copepod production occurs at a level sufficient to support larval pollock survival, regardless of thermal regime. A study that examined larval pollock condition in the Bering Sea in spring reported that larvae over the continental shelf were healthy, based on the percentage of muscle cells in the S phase of the cell cycle (Porter & Bailey, 2011). We showed that copepod production is an order of magnitude greater in July and nearly an order of magnitude greater in September (due to *Calanus* spp.), in cold years relative to warm, precisely at the critical period when pollock are provisioning their overwinter energy reserves (Figures 6e, f). This supports demonstrated relationships between large copepod abundances in summer/autumn, juvenile pollock condition as inferred from energy density in summer/autumn, and pollock recruitment to age-1 (Eisner & Yasumiishi, 2016; Heintz et al., 2013). As such, production rates of copepods in summer/autumn are critical to juvenile pollock that have switched allocation of energy from growth to storage for overwintering (Siddon, Heintz, et al., 2013) and require prey of sufficient quality and quantity to do so. We hypothesize that a size-based (Boyce, Frank, & Leggett, 2015) conceptual model of trophic interactions provides a mechanistic explanation for the

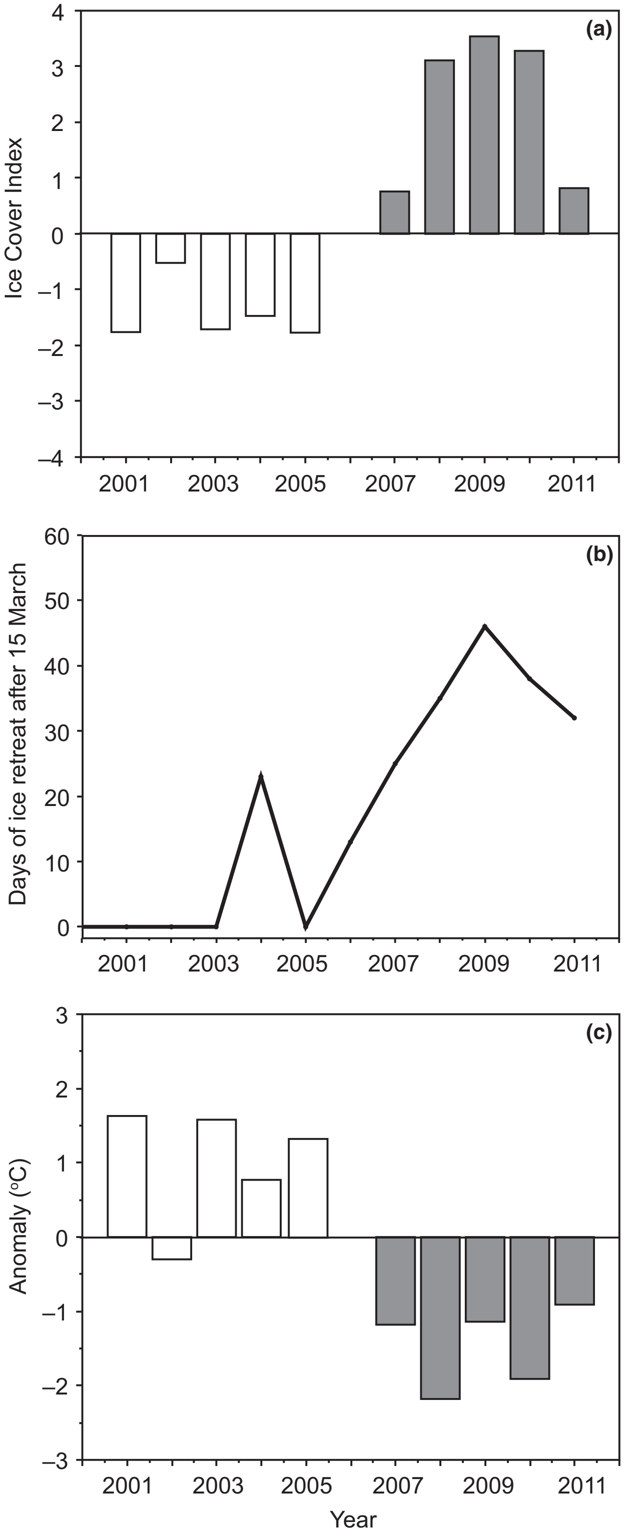

FIGURE 2 Ice cover index (a), Days of ice retreat after 15 March (b), and January–April sea surface temperature anomalies (°C) at mooring location M2 (c). Solid bars represent the warm period of (2001–2005) and shaded bars represent the cold period (2007–2011)

variability in copepod abundance and secondary production we observed (Figure 7). It is important to note that this model also assumes that there is spatial and temporal overlap of pollock and copepods (Siddon et al., 2013), overlap that is subject to the oceanographic conditions described in relation to sea-ice extent and timing of retreat (Stabeno, Napp, Mordy, & Whitledge, 2010). Our conceptual model is founded upon the fundamental ecological relationship between predator-prey mass ratios (PPMR) and trophic transfer efficiency, such that when predator-prey mass ratios increase, trophic transfer efficiency declines (Barnes, Maxwell, Reuman, & Jennings, 2010). We first discuss our observational findings compared to other studies in the Bering Sea and then describe the empirical evidence that led to the model.

Our observations are largely in agreement with other studies conducted on copepods in the region. The increase in *Calanus* spp. abundance during cold periods had been observed when comparing short time periods, usually one warm year to a cold year (Coyle et al., 2008; Vidal & Smith, 1986), or shorter time periods of several years within one season (Baier & Napp, 2003; Coyle & Pinchuk, 2002; Eisner, Siddon, & Strasburger, 2015; Eisner et al., 2014; Napp et al., 2002). One of our more interesting observations was that *Calanus* spp. abundances appeared to increase during warm periods compared to cold periods in May and the reverse was observed during July and September (Figures 3–5). We also found abundances of *M. pacifica*, *Oithona* spp. and *Pseudocalanus* spp. increased during the warm period, *Oithona* spp. abundances were higher over the course of the entire year, whereas *M. pacifica* and *Pseudocalanus* spp. only differed during May (Figures 3–5). *Metridia pacifica* is more abundant on the outer shelf (Cooney & Coyle, 1982; Vidal & Smith, 1986), thus the increased abundance during May could be the result of on-shelf transport. We conclude that the observed differences across warm and cold periods in *Calanus* spp. during May are the result of warmer temperatures increasing development rate, as *Calanus* spp. produce eggs very early in the year (January/February) after emergence from diapause (Baier & Napp, 2003). In cold periods, development is slower and the higher observed abundances later in the year must be fueled either by recruitment of more copepods from the previous year's cohort or summer growth and survival of the cohort produced in spring, as hypothesized by Coyle et al. (2008). We hypothesize that the observed increase in *Calanus* spp. abundance during July and September is the result of local production being higher in cold years rather than influence of the previous year's cohort.

Our estimated secondary production rates are more difficult to place in context, as there are few prior estimates and even fewer direct measurements. Vidal and Smith (1986) estimated whole copepod community secondary production ranged from 40–150 mg C m^{-2} d^{-1} as determined from estimated growth rates. This was similar to our measurements (Table 4) and our range of all estimates was 5.03–324.98 mg C m^{-2} d^{-1} (mean = 49.66 ± 65.94 SD) when integrated over depth. A more direct comparison of methods can be made using the results of Coyle and Pinchuk (2002) who also estimated calanoid secondary production using the growth equations of Hirst and Lampitt (1998) across spring and summer of 1997–1998 on the inner shelf of the Bering Sea. Coyle and Pinchuk (2002) estimated copepod secondary production to range from 0.69–

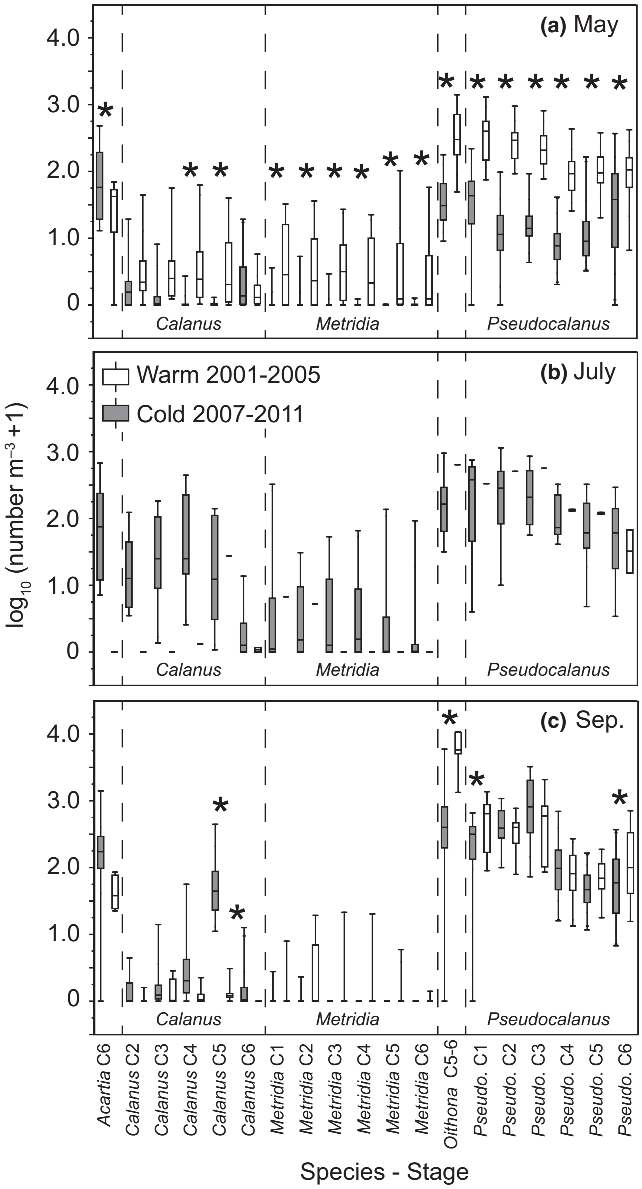

FIGURE 3 Central Middle Shelf. Monthly, copepod abundance ($\log_{10}$ [number m^{-3} + 1]) during cold (2007–2011) and warm periods (2001–2005). Taxa and abundances from May (a), July (b), and September (c) are shown. Middle line in box represents the median and whiskers represent the minimum and maximum values recorded. Asterisks indicate statistical differences between warm and cold periods (ANOVA, Tukey's HSD post-hoc test $p < .05$)

37.15 mg C m^{-2} d^{-1} in spring and 6.44–35.68 mg C m^{-2} d^{-1} in summer and production was lowest during spring of the cold year, 1999. Our estimates are higher overall (Table 4) and this could be due to differences in location or methods, or lower abundances of *Calanus* spp. present on the inner shelf. Direct measures of the zooplankton community secondary production have also been estimated using the chitobiase assay method (Sastri & Dower, 2006, 2009). Sastri et al. (2012) estimated secondary production on the outer SE Bering shelf in 2008 and 2009 and found rates to range from 0.39–1.47 mg C m^{-3} d^{-1}, comparable to our range from 0.05 to 5.42 (mean = 0.67 ± 1.06 SD).

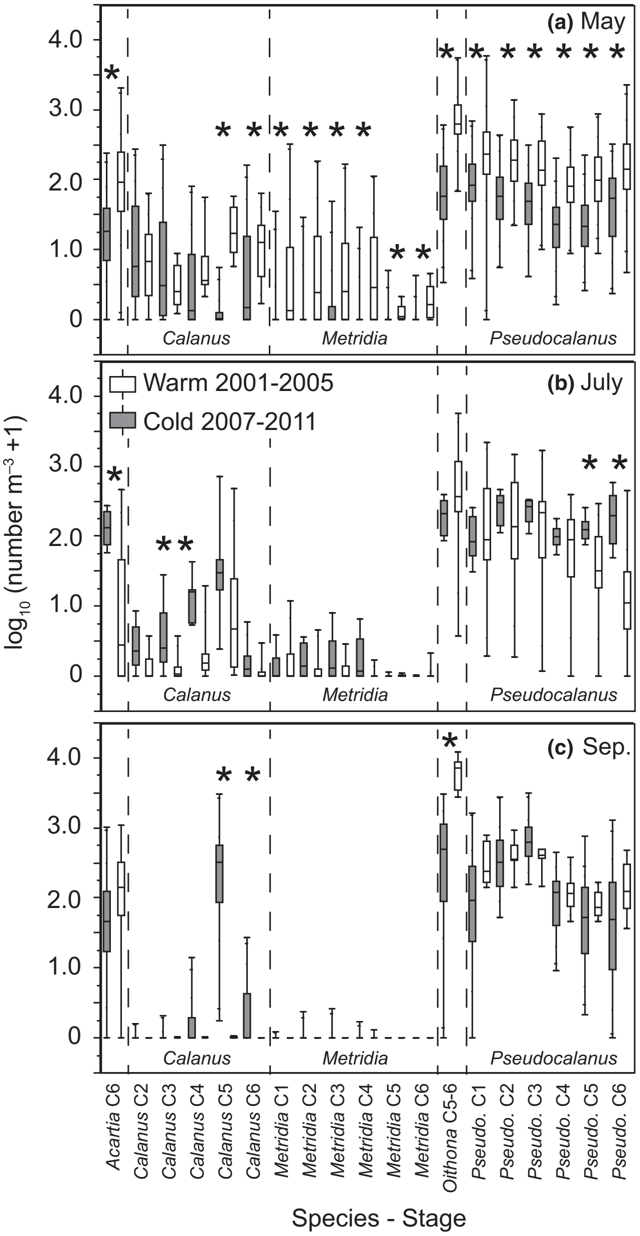

FIGURE 4 South Middle Shelf. Monthly, copepod abundance ($\log_{10}$ [number m^{-3} + 1]) during cold (2007–2011) and warm periods (2001–2005). Taxa and abundances from May (a), July (b), and September (c) are shown. Middle line in box represents the median and whiskers represent the minimum and maximum values recorded. Asterisks indicate statistical differences between warm and cold periods (ANOVA, Tukey's HSD post-hoc test $p < .05$)

Cold years are characterized by spring blooms that are associated with the ice edge (Sambrotto, Burdloff, & McKee, 2016; Sigler et al., 2016). The majority of the phytoplankton cells are microplankton (20–200 μm diameter) (Stauffer, Goes, McKee, Gomes, & Stabeno, 2014) and are diatoms (Baumann et al., 2014; Stauffer et al., 2014). Copepods that are grazing within this bloom experience favorable PPMR that increases trophic transfer efficiency (Barnes et al., 2010) (Figure 7). Campbell et al. (2016) showed that though both *M. pacifica* and *Calanus* spp. had strong preference for microzooplankton

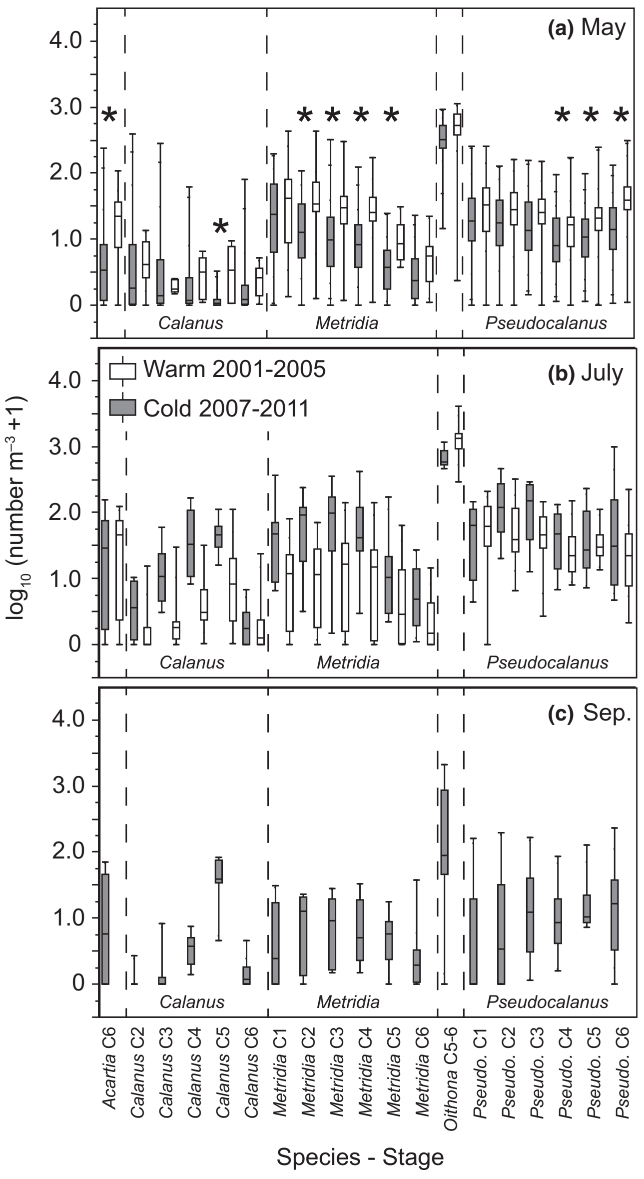

FIGURE 5 South Outer Shelf. Monthly, copepod abundance ($\log_{10}$ [number m^{-3} + 1]) during cold (2007–2011) and warm periods (2001–2005). Taxa and abundances from May (a), July (b), and September (c) are shown. Middle line in box represents the median and whiskers represent the minimum and maximum values recorded. Asterisks indicate statistical differences between warm and cold periods (ANOVA, Tukey's HSD post-hoc test $p < .05$)

prey, ice-associated algae were large components of their diets in the ice edge region. This is likely because microzooplankton grazing rates were found to be low in the spring (Sherr, Sherr, & Ross, 2013) and the microzooplankton declined in proportional abundance as chlorophyll *a* concentration increased (Campbell et al., 2016). Smaller phytoplankton cells were ingested by copepods only when chlorophyll concentrations were very low (Campbell et al., 2016). This observation, combined with the low temperatures that reduce growth rates, may explain the low abundances of smaller-bodied taxa observed in May during the cold period (Figures 3–5a). Furthermore, *Calanus* spp. can initiate reproduction after emergence from diapause by consuming ice-associated algae, as has been observed for *C. glacialis* in Rijpfjorden, Svalbard (Søreide, Leu, Berge, Graeve, & Falk-Petersen, 2010) and Hudson Bay, Canada (Runge, Therriault, Legendre, Ingram, & Demers, 1991) and the northern Bering Sea (Durbin & Casas, 2014). Ice edge phytoplankton blooms made up of large size phytoplankton would provide the necessary primary production and fatty acids for *Calanus* spp. to produce eggs (Søreide et al., 2010; Wang, Budge, Gradinger, Iken, & Wooller, 2014; Wang et al., 2015). As the *Calanus* spp. develop, the ice will begin to retreat, and in the post-spring bloom period during cold years, chlorophyll-*a* concentrations are low (<1 μg/L), but in the marginal ice zone, chlorophyll-*a* concentrations exceed 5 μg/L (Baumann et al., 2014). These large cells would continue to provide favorable PPMR and enhance trophic transfer for developing *Calanus* spp.

Primary production needs to continue into the summer to support the populations of *Calanus* spp. that are developing and Zhou et al. (2015) suggests that ice edge phytoplankton act as a "seed bank" for further phytoplankton production in open water. Blooms in the wake of sea ice retreat have long been reported along the southeastern Bering Sea shelf (Alexander & Niebauer, 1981; Niebauer et al., 1990; Schandelmeier & Alexander, 1981). Indeed, the timing of ice retreat has been found to be negatively correlated with the fraction of chlorophyll-*a* derived from cells >5 μm in size (Fujiwara et al., 2016). Evidence suggests that secondary blooms can occur later in the year and be maintained by storm driven injections of nitrogen to surface waters (Eisner, Gann, Ladd, Cieciel, & Mordy, 2016; Goes et al., 2014; Rho & Whitledge, 2007; Sambroto et al., 1986). While these secondary blooms should rapidly deplete the available surface nitrogen, Goes et al. (2014) hypothesized that the formation of the cold pool (waters < 2°C) during cold years prevents these larger cells from sinking, allowing continued trophic transfer to zooplankton. Indeed, Odate (1996) found microplankton (>10 μm) were a persistent feature in the middle shelf during summer and Lomas et al. (2012) found that large cell (>5 μm) primary production continued in the southern Bering Sea during a cold period. Microzooplankton are the primary grazers of these cells during summer (Stoecker, Weigel, & Goes, 2014) and thus significant trophic transfer occurs through the microzooplankton fraction (Figure 7). The larger sized microzooplankton maintain favorable PPMR for *Calanus* spp. The result is the increased abundance of *Calanus* spp. observed into September (Figures 3c–5c). These *Calanus* spp. have high rates of estimated secondary production (Figure 6) and this assimilated carbon is accumulated as storage lipid when *Calanus* spp. reaches stage C5.

In the southeastern Bering Sea, warm years are characterized by open-water blooms in spring that are not associated with the ice edge (Brown & Arrigo, 2013; Sigler et al., 2014, 2016; Stabeno et al., 2012). Satellite-derived data suggest that the amount of chlorophyll-*a* represented by the > 5 μm cell size fraction (Fujiwara et al., 2016) decreases compared to ice-associated blooms. The open water spring bloom likely consists of larger-sized diatoms and possibly dinoflagellates (Moran et al., 2012), although observational data are limited. The phytoplankton community prior to the bloom is light-

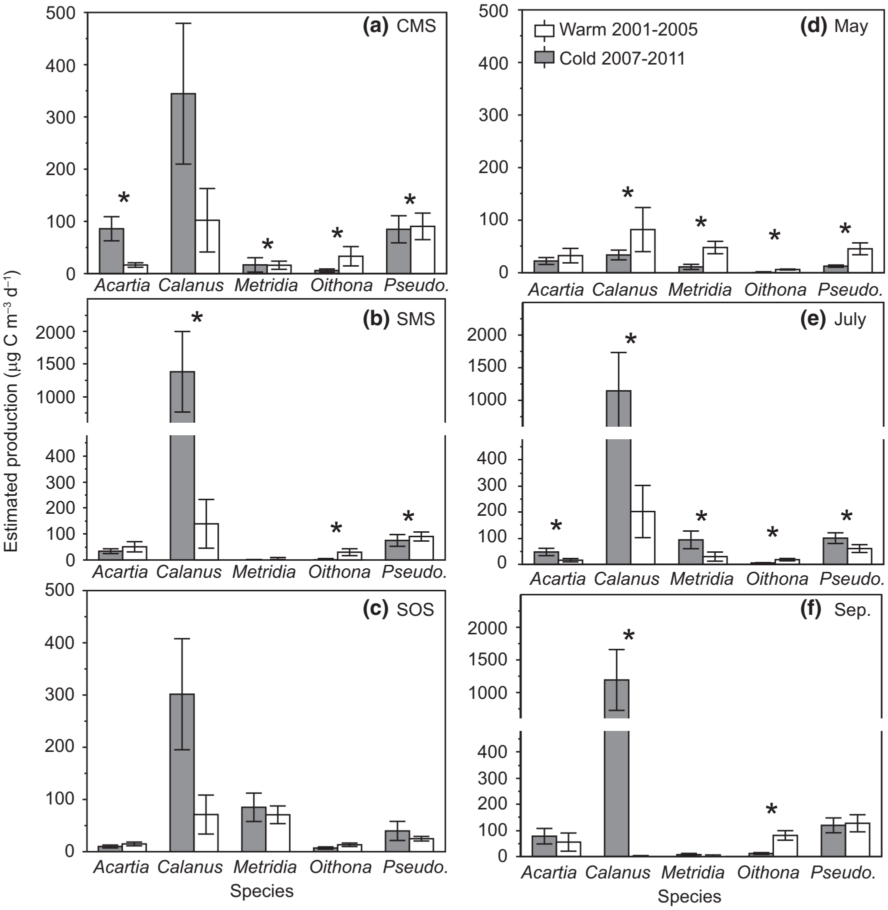

FIGURE 6 Copepod secondary production rates (µg C m^{-3}/d) for each species during cold (2007–2011) and warm (2001–2005) periods by region (all months combined): Central Middle Shelf (CMS) (a), South Middle Shelf (SMS) (b), and South Outer Shelf (SOS) (c) and by month (all regions combined): May (d), July (e), and September (f). Asterisks indicate statistical differences (ANOVA, Tukey's HSD post-hoc test $p < .05$) between warm and cold period

limited and is assumed to consist mostly of small cells (<5 µm or 10 µm in diameter) (Duffy-Anderson et al., 2017; Lomas et al., 2012). Under these conditions, smaller-bodied copepods would have a more favorable PPMR with smaller phytoplankton cells and all copepods would benefit from preying upon microzooplankton that graze on these smaller phytoplankton (Figure 7). It is not known if microzooplankton grazing rates differ overall in warm and cold periods (Stoecker et al., 2014); however, grazing rates in the cold spring months are reduced (Sherr et al., 2013) compared with summer observations (Liu, Suzuki, & Saino, 2002; Olson & Strom, 2002; Stoecker et al., 2014; Strom & Fredrickson, 2008). This suggests tighter coupling of phytoplankton and microzooplankton communities in warmer waters prior to the arrival of the larger size phytoplankton present in the spring bloom (Figure 7). The main beneficiary of these conditions would be the small, predatory copepod *Oithona* spp., and *Oithona* spp. numbers increase during warm springs on the middle shelf (Figures 3–4a, b). *Oithona* spp. are ambush predators whose lack of movement and small size reduces encounters with predators (Kiørboe, Andersen, Langlois, Jakobsen, & Bohr, 2009). *Oithona* spp. feed primarily on microzooplankton (Nakamura & Turner, 1997) and have much lower metabolic rates compared to similar-sized zooplankton (Castellani, Robinson, Smith, & Lampitt, 2005). Thus, warmer conditions in the southeastern Bering Sea are ideal for *Oithona* spp. to increase throughout the year (Figures 3–5).

During the summer/fall period of warm years, the phytoplankton community exhibits high rates of primary productivity, often 40%–50% higher compared to years with late sea ice retreat (Brown & Arrigo, 2013). Summer observations from 2004 (a warm, highly stratified year) showed that <20% of the phytoplankton observed near mooring M2 were >20 µm in size, particularly in the upper water column (Strom & Fredrickson, 2008). In contrast, ~75% of phytoplankton were >20 µm in size in summer 2011 (a cold moderately stratified year) (Stauffer et al., 2014). Thus, while warm period blooms were more productive, the amount of biomass in the larger (>5 µm) cell fraction appeared to be reduced. Under such conditions, the increased productivity of smaller phytoplankton cells creates a scenario that may benefit small copepod species, such as *Oithona* spp. and *Pseudocalanus* spp., due to favorable PPMR (Figure 7). Furthermore, this would be unfavorable PPMR for *Calanus* spp., reducing trophic transfer efficiency and causing *Calanus* spp. to fail to assimilate sufficient resources necessary to produce the larger populations observed in cold years (Figure 7). However, evidence for this is equivocal. A synthesis of long-term Bering Sea shelf observations of chlorophyll-*a* concentrations showed that overall chlorophyll-*a* concentrations in late summer/early fall were higher during warm years in some regions of the southeast shelf (Eisner et al., 2016). Additionally, Eisner et al. (2016) found that chlorophyll-*a* concentrations in the > 10 µm size fraction were 42% of the total chlorophyll-*a* in warm years and only 30% in cold years. Strom and Fredrickson

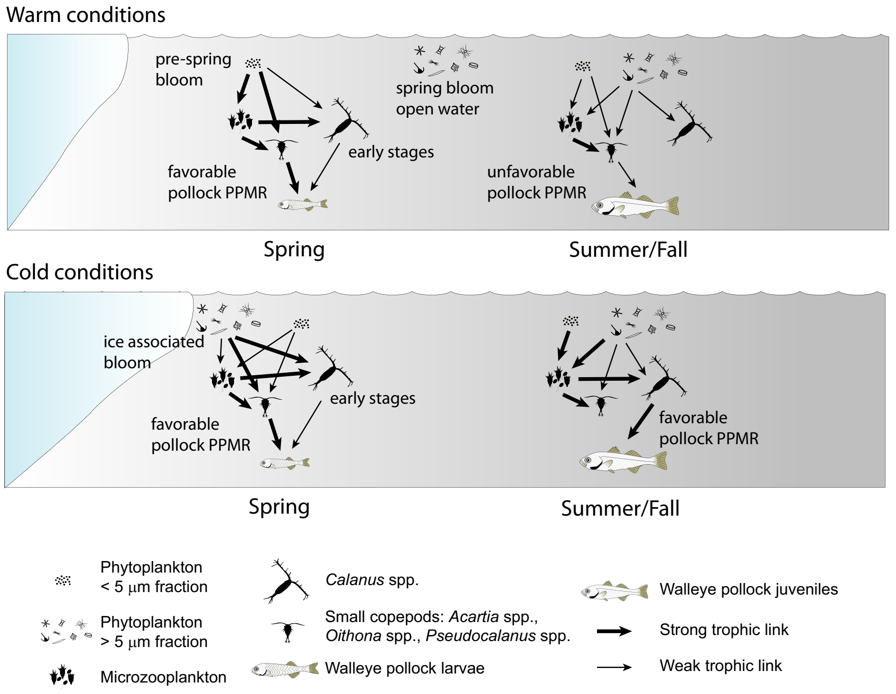

FIGURE 7 Conceptual model of the trophic interactions in the southeastern Bering Sea. See text for detail

(2008) showed that microzooplankton grazing rates on phytoplankton were reduced overall during the warm summer of 2004 and attributed this to a combination of high microzooplankton biomass and low grazing rates. The ambiguous results among these studies may in part reflect the influence of stratification and wind mixing on phytoplankton and microzooplankton biomass and production; August stratification near M2 in warm and cold years was not significantly different over the time series, 1996–2010 (Ladd & Stabeno, 2012). The dynamics of planktonic trophic interactions in warmer conditions need to be more resolved to test our hypotheses.

Our findings may be linked to directly to the Oscillating Control Hypothesis (Coyle et al., 2011; Hunt et al., 2002, 2011). The original prediction of the OCH that warm years are favorable for pollock is consistent with our findings for May conditions during the warm period because PPMR of larval fish would be favorable and trophic transfer efficiency would be high (Figure 7). For example, spring diet studies show that pollock prey upon *Metridia* spp. nauplii and *Pseudocalanus* spp. early stages (Brase, 1996; Clarke, 1984; Dagg, Clarke, Nishiyama, & Smith, 1984; Hillgruber, Haldorson, & Paul, 1995; Strasburger, Hillgruber, Pinchuk, & Mueter, 2014), both species that exhibited increased abundances (Figures 3–5a) and higher estimated secondary production rates (Figure 6d) during the warm period. High predation on copepods would therefore be sustainable by the higher estimated secondary production rates in warm springs, resulting in more turnover of the population to replace losses due to predation, and high trophic transfer (Figure 7). As pollock grow, they eventually must switch to feed on larger-sized prey (Brodeur, 1998; Strasburger et al., 2014; Wilson, Buchheister, & Jump, 2011) because PPMR increases to the point where trophic transfer efficiencies are too low to support growth (Barnes et al., 2010). In cold years, the sustained production and accumulation of *Calanus* spp. provides the necessary energy and favorable PPMR for pollock to grow and survive into the fall (Figure 7). This is based on the observed increase in *Calanus* spp. numbers in cold years (Figures 3–5) and the extremely high rates of estimated secondary production (Figure 6). Also of interest, is the minimal difference in estimated secondary production between *Pseudocalanus* spp. and *Acartia* spp. in warm and cold years during May (Figure 6d). This indicates that sufficient production to support larval pollock growth is present in cold years to supply enough juveniles to take advantage of the larger copepod prey present in the summer. Late in the year, *Calanus* spp. C5 provide the lipid-rich diet that Hunt et al. (2011) suggested and Heintz et al. (2013) demonstrated. Obviously, the dynamic is more complicated as we are neglecting to explore the role of other juvenile pollock prey, notably euphausiids a major diet item for pollock (Strasburger et al., 2014; Wilson, Jump, & Buchheister, 2009), as well as the role of predation and/or cannibalism as suggested in the OCH.

TABLE 4 Monthly mean (± standard deviation) of the estimated secondary production rates summed across each life history stage for each copepod species (see Table 2) included in the study for warm/cold period

Period	Month	Estimated production (mg C m^{-2} d^{-1})
Cold	May	6.95 ± 3.31
Cold	July	108.34 ± 97.20
Cold	September	94.5 ± 83.3
Warm	May	17.83 ± 7.59
Warm	July	28.5 ± 24.32
Warm	September	13.02 ± 9.94

5 | CONCLUSIONS

Significant seasonal differences in copepod life history stage abundance across warm and cold periods existed and were most pronounced among small-bodied taxa in May and *Calanus* spp. in July and September. Estimated secondary production values for dominant copepod species present in the southeastern Bering Sea demonstrated that cold periods show significant differences in estimated secondary production rates coincident with the increased *Calanus* spp. abundance of later life-history stages. These production estimates were used to formulate a conceptual, mechanistic model to explain how copepod abundance changes impact higher trophic levels. This model builds upon the predictions of the OCH and uses a size-structured approach to trophic interactions (Figure 7). We believe that further investigation into the size-based approach (Boyce et al., 2015) will continue to provide insight into ecosystem dynamics. Fully resolved size spectra (Kerr & Dickie, 2001) of the planktonic food web would provide significant insight into predator-prey dynamics. Reduction in organism body size as ecosystems warm has been hypothesized to be a universal response to global warming (Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011) and has been linked to dramatic changes in food webs in mesocosm studies (Peter & Sommer, 2012; Yvon-Durocher et al., 2015). As higher latitude systems continue to warm, the interplay between organism traits influenced by temperature, such as size (Forster, Hirst, & Atkinson, 2012) and metabolism (Bruno, Carr, & O'Connor, 2015), will have profound effects on ecosystem structure and function and warrant investigation.

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SUPPORTING INFORMATION

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