



# The northern Bering Sea zooplankton community response to variability in sea ice: evidence from a series of warm and cold periods

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**ABSTRACT:** Recent, unprecedented losses of sea ice have resulted in widespread changes in the northern Bering Sea ecosystem, and this study explores the zooplankton community response. Time-series observations were used to identify zooplankton community changes in the northern (>60° N) Bering Sea (NBS) over a 17 yr period (2002–2018). The overall objective was to determine if the changes in zooplankton populations previously described for the southeastern Bering Sea shelf (<60° N) were also observed in the NBS over alternating warm and cold periods. Particular attention was paid to more recent (2014–2018) years that showed significant losses of sea ice in the NBS (2017/2018) in comparison to a prior warm period (2003–2005) and an intervening cold period (2006–2013). A multivariate framework (redundancy analysis) was used to explore correlations with environmental conditions, and differences in mean abundance across the differing warm and cold periods were tested. The NBS zooplankton community had different responses across each warm and cold period, and the primary driver for the differences in response was sea ice. Redundancy analysis demonstrated that the zooplankton community during the second warm period experienced greater variability compared to the prior warm period. The zooplankton community had higher abundances of small copepods and meroplankton and reduced abundances of *Calanus* spp. and chaetognaths during the most recent warm period. This suggests that the NBS zooplankton will not be impacted by reduced sea ice when the ice coverage extends south of 60° N, but show community change once a minimum threshold in ice extent and timing of retreat is reached. Shifts in the zooplankton community may have had cascading effects on higher trophic levels that were evident during the latter warm period.

**KEY WORDS:** Bering Sea · Zooplankton abundance · Zooplankton community composition · Climate · Sea ice

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## 1. INTRODUCTION

In the highly productive eastern Bering Sea ecosystem (Springer et al. 1996) the broad, shallow shelf provides a fertile ground for zooplankton production. Zooplankton form a vital link between primary producers and higher trophic levels by direct and indirect transfer of energy. Zooplankton are consumed by forage fish (Yasumiishi et al. 2020), seabirds (Piatt & Spring 2003), and marine mammals, including the

critically endangered north Pacific right whale *Eubalaena japonica* (Baumgartner et al. 2013). Zooplankton also provide nutrition for abundant, commercially exploited fish stocks, including walleye pollock *Gadus chalcogrammus* and Pacific cod *G. macrocephalus* (Strasburger et al. 2014, Buckley et al. 2016). In the Bering Sea, much work has been done to understand the population dynamics of key zooplankton taxa that appear most frequently in higher trophic level diets. These key taxa include the

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predominant euphausiid species on the middle and outer shelves, *Thysanoessa raschii* and *T. inermis*, respectively (Ressler et al. 2014, Bi et al. 2015, Hunt et al. 2016), as well as the calanoid copepod *Calanus marshallae/glacialis* (Coyle & Gibson 2017, Kimmel et al. 2018, Eisner et al. 2020a). Interannual shifts in overall zooplankton community composition, in addition to changes in these key taxa, have been linked to the environmental change in the Bering Sea (Vidal & Smith 1986, Coyle et al. 2008, Eisner et al. 2014, 2018). Understanding how zooplankton respond to contemporary environmental variability offers a glimpse into possible future response to predicted ecosystem change (Richardson 2008) and this understanding contributes to ecosystem-based management of fisheries.

In the eastern Bering Sea, zooplankton differ across bathymetric regions, with different communities being found in the inner (0–50 m), middle (50–100 m), and outer (100–180 m) shelf regions (Cooney & Coyle 1982) (see Fig. 1A). Differences in these communities are related to local oceanography and current patterns along the shelf. In addition to spatial variability, the community undergoes shifts in abundance and composition in relation to the environment. Distinct zooplankton communities inhabit particular water mass types that are related to atmospheric forcing and the cycle of annual ice formation and retreat (Coyle & Pinchuk 2002, Eisner et al. 2018, Kimmel et al. 2018). Most often compared are warm years characterized by early ice retreat, a later spring phytoplankton bloom, and higher overall temperatures; and cold years characterized by late ice retreat, an earlier ice-associated bloom, and lower overall temperatures (Hunt et al. 2011). In the southeastern Bering Sea, *Calanus* spp. populations have reduced abundance and lower lipid content during warm periods in contrast to colder years that have increased abundance, persistence on the shelf into fall, and higher lipid content (Heintz et al. 2013, Eisner et al. 2018, Kimmel et al. 2018).

The northern Bering Sea (NBS) shelf is characterized by seasonal sea ice cover and high water column production that typically goes ungrazed, resulting in tight benthic–pelagic coupling (Grebmeier 2012). The region also has reduced salinities at the surface, cold bottom temperatures, and a stronger pycnocline compared to the southern shelf (Stabeno et al. 2012a). Three water mass types predominate in the NBS: Anadyr Water that is cold, saline, and nutrient-rich and found in the western, outer shelf and north of St. Lawrence Island; Alaska Coastal Water that is warmer and fresher and found near the Alaskan

coast; and Bering Shelf Water that is intermediate in salinity and temperature and is located on the middle shelf (Coachman et al. 1975). Danielson et al. (2017) have noted the role that seasonality plays in influencing these water masses, and winds may redirect typical flow patterns during particular times of the year, with not well-understood biological consequences (Danielson et al. 2017, Eisner et al. 2020b). Differences among fauna are related to these differences in hydrography (Siddon et al. 2020), and zooplankton show correlations to particular water masses or temperature and salinity characteristics (Eisner et al. 2013, Pinchuk & Eisner 2017). These correlations appear to be robust and have been tracked as water moves into the Chukchi Sea (Hopcroft et al. 2010, Ershova et al. 2015, Kim et al. 2020).

The NBS has been predicted to remain strongly influenced by persistent seasonal ice cover (Hermann et al. 2016), albeit with interannual variability until at least 2050 (Stabeno et al. 2012a). However, recent years of unprecedented low ice coverage have occurred, resulting in shifts in oceanographic conditions across the NBS (Stabeno & Bell 2019, Basyuk & Zuenko 2020) that have been linked to ecosystem-wide responses (Duffy-Anderson et al. 2019, Siddon et al. 2020). The recent low ice event of 2018 was determined to be the lowest ice extent in the last 5500 yr, based on peat cellulose oxygen isotopes from St Matthew Island, AK, USA (Jones et al. 2020). Most notable was the significant reduction in cold pool (<2°C bottom water) extent (Stabeno & Bell 2019) and weakened stratification (Duffy-Anderson et al. 2019). This was related to a delayed spring phytoplankton bloom (Kikuchi et al. 2020) and a shift in phytoplankton (Fukai et al. 2020) and zooplankton community composition (Kim et al. 2020, Kimura et al. 2020). Other ecosystem effects were also noted; these included northward movement of demersal fish populations (Stevenson & Lauth 2019, Eisner et al. 2020b), shifts in spatial location of forage fish (Yasumiishi et al. 2020), sea-bird die-offs (Romano et al. 2020, Will et al. 2020), poor body condition of seals (Boveng et al. 2020), and an unusual mortality event that was declared for bearded *Erignathus barbatus*, ringed *Pusa hispida*, and spotted seals *Phoca largha* (Boveng 2019).

Past studies of the NBS have focused on short time frames of zooplankton distributions in relation to water mass characteristics (Eisner et al. 2014, Yamaguchi et al. 2021). Here, we seek to build on these studies and provide a time-series perspective of how the NBS zooplankton community has changed over a 17 yr period (2002–2018) in response to alter-

nating warm and cold periods (Duffy-Anderson et al. 2017, Duffy-Anderson et al. 2019). The extremely low ice cover in the winters of 2017/2018 and 2018/2019 suggests warming may be occurring more rapidly in the NBS than has been predicted. The overall objective of this study was to determine if the changes observed in zooplankton populations in the southeastern Bering Sea also occurred in the NBS over this period of changing climate conditions (warm, cold, warm). We focused on comparing the zooplankton response of the more recent years with minimal ice cover (Stabeno & Bell 2019) to that of a prior warm period to determine if warm period responses were similar. We chose to examine the zooplankton variability in a multivariate framework to discover overall community patterns and then chose to focus on individual taxa belonging to specific groups. Understanding the zooplankton community response to short-term warming events may provide a window into predicting the future community structure and function in a warmer Bering Sea and its impact on the broader ecosystem.

## 2. MATERIALS AND METHODS

### 2.1. Study area

Based on physics and biology, Stabeno et al. (2012a) placed the dividing line between the NBS and southern Bering Sea at 60°N. The NBS is seasonally covered in ice, with maximum extent occurring between January and May, but typically peaking in March (Clement Kinney et al. 2022), and with ice extending south of 60°N (Stabeno et al. 2012a). The NBS shelf is typically ice-free by June, and the retreating ice leaves behind a large region of bottom water <2°C, referred to as the 'cold pool' (Clement Kinney et al. 2022), that can extend well into the southeastern Bering Sea. As ice melts and the region warms, the southeastern Bering Sea middle shelf region stratifies, resulting in a 2-layer system with a mixed layer depth of approximately 25–30 m (Danielson et al. 2011, Stabeno et al. 2012a). This stabilization of the water column results in the spring phytoplankton bloom (Danielson et al. 2011, Sigler et al. 2014). The inner shelf remains vertically mixed or only partially stratified, and a sharp transition occurs between the inner and middle shelf waters, known as the inner front, which occurs at or near the 50 m isobath (Stabeno et al. 2001). This inner front often prevents the movement of low-salinity water onto the

middle shelf, but may be eroded by winds, resulting in cross-shelf transport. Danielson et al. (2011) notes that this cross-shelf transport is impacted by the relative location of the Aleutian Low, either trapping waters near the coast or advecting them onto the middle shelf. As previously mentioned, the zooplankton community differs across the inner (0–50 m), middle (50–100 m), and outer (100–180 m) shelf regions (Fig. 1A). These cross-shelf regions are less pronounced north of 60°N; however, the inner-front is reported as occurring along the 50 m isobath north of Nunivak Island, AK (Coachman 1986).

We focused on the middle and inner shelves, as the outer shelf region had few samples for comparison. We used the polygons developed by Ortiz et al. (2012) to define the inner shelf using the North Inner Shelf (Region 11 in Ortiz et al. 2012), and the middle shelf as a combination of the St Matthews and the North Middle Shelf regions (Regions 9 and 10 in Ortiz et al. 2012, respectively) (Fig. 1A). Zooplankton and CTD sampling varied within each region (Fig. 1B), but total stations occupied were similar between the 2 regions: middle (370 total stations) and inner (394 total stations) shelves. As is common with ecological data, stations often had missing data, thus the total sample number reported in the analysis is less than these totals. We also chose to group years together to reflect the current temporal occurrence of multiple warm or cold years in a row (Duffy-Anderson et al. 2017). We divided the time-series into 3 distinct periods: Warm 1 (2002–2005), Cold (2006–2013), and Warm 2 (2014–2018), based on cold pool area (see below).

### 2.2. Environmental data

Climate and environmental variables are listed in Table 1. The Arctic Oscillation (AO) index is obtained by projecting the AO loading pattern to the daily anomaly 1000 mb height field over 20°–90°N latitude (Thompson & Wallace 1998). Here, we show the index as a mean of the November through March values, as this period is the most influential in terms of ice formation. We also evaluate the North Pacific Index (NPI), an indicator of the Aleutian Low, since atmospheric phenomena over the Arctic (AO index) and Gulf of Alaska (NPI) can impact the NBS region (Trenberth & Hurrell 1994). Southeast (SE) and Northwest (NW) winds are the proportion of daily NCEP/NCAR reanalysis wind data at 60°N, 170°W blowing from each direction. These are used as an index for shifts in Bering Sea advection (Danielson et

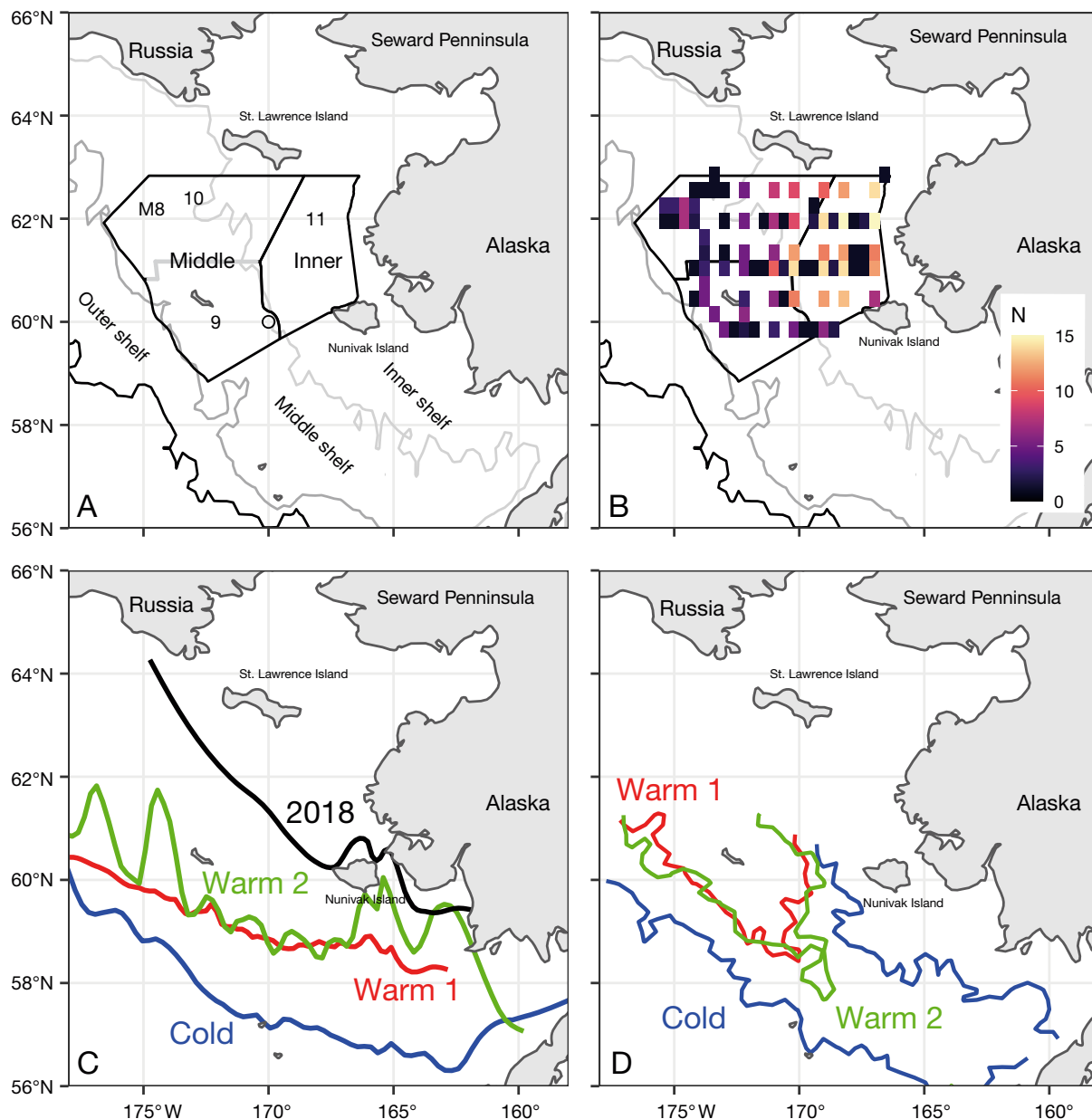


Fig. 1. (A) Location of the ‘middle’ (combined areas of the St Matthews and North Middle Shelf regions; Regions 9 and 10 in Ortiz et al. 2012, respectively) and the ‘inner’ (North Inner Shelf; Region 11 in Ortiz et al. 2012) study regions. Location of the M8 mooring site is indicated and the open circle represents the location used for wind data ( $60^{\circ}\text{N}$ ,  $170^{\circ}\text{W}$ ). Light gray, dark gray, and solid black line to the west represent the 50, 100 and 200 m isobaths, respectively, and are used as separators for the inner, middle, and outer shelves, respectively. (B) Sample count (N) for the entire study period. (C) Average ice extent (thick lines) as of 15 March and (D) average location of the  $2^{\circ}\text{C}$  bottom temperature isotherm (thick lines), indicator of the cold pool extent for the periods Warm 1 (2003–2005), Cold (2006–2013), and Warm 2 (2014–2018). Also shown in (C) ice extent in 2018, a year of record low ice cover in the Bering. The cold pool was not detected within the survey boundary in 2018

al. 2012). We report wind speed ( $\text{m s}^{-1}$ ) anomalies from 2 time-periods: February–May (spring), which covers the early season of zooplankton growth and production, and the June–September (summer) period preceding and including the sampling period for zooplankton. Finally, we compute a wind mixing index for June–September by taking the cube of the time-

period mean friction velocity at  $60^{\circ}\text{N}$ ,  $170^{\circ}\text{W}$ , as this measure is proportional to the rate of mechanical energy translated to mixing at the ocean surface (Bond & Adams 2002).

Total ice-covered area ( $\text{km}^2$ ) from January through April for the entire Bering Sea (south of Bering Strait) was acquired from the National Snow and Ice Data

Table 1. Climate and environmental variables used to calculate standardized anomalies and conduct the redundancy analysis for the survey period 2002–2018, including abbreviation, source, reference, and hyperlink. NWS CPC: National Weather Service, Climate Prediction Center; NCAR: National Center for Atmospheric Research; NASA NSIDC: National Aeronautics and Space Administration, National Snow and Ice Data Center; NMFS: National Marine Fisheries Service; NCEP: National Center for Environmental Prediction

Variable	Abbreviation	Source	Reference	Link
Arctic Oscillation Nov–Mar mean index	AO	NWS CPC	Thompson & Wallace (1998)	<a href="https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao_index.html">https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao_index.html</a>
North Pacific Index Nov–Mar mean index	NPI	NCAR	Trenberth & Hurrell (1994)	<a href="https://climatedataguide.ucar.edu/sites/default/files/npindex_anom_ndjfm.txt">https://climatedataguide.ucar.edu/sites/default/files/npindex_anom_ndjfm.txt</a>
Ice area anomaly (Jan–Apr) (km <sup>2</sup> )	IA	NASA NSIDC	Stroeve & Meier (2018)	<a href="https://nsidc.org/">https://nsidc.org/</a>
Ice percentage around M8 mooring in March	M8I	NASA NSIDC	Stroeve & Meier (2018)	<a href="https://nsidc.org/">https://nsidc.org/</a>
Summer cold pool extent (km <sup>2</sup> )	CP	NMFS bottom trawl survey	Fedewa et al. (2020)	<a href="https://www.fisheries.noaa.gov/alaska/commercial-fishing/alaska-groundfish-bottom-trawl-survey-data">https://www.fisheries.noaa.gov/alaska/commercial-fishing/alaska-groundfish-bottom-trawl-survey-data</a>
Wind mixing Jun–Sep (summer) (m s <sup>−1</sup> )	WM	NCEP/NCAR reanalysis	Danielson et al. (2012)	<a href="http://apdrc.soest.hawaii.edu/erddap/griddap">http://apdrc.soest.hawaii.edu/erddap/griddap</a>
SE wind Feb–May (spring) (m s <sup>−1</sup> )	SpSE	NCEP/NCAR reanalysis	Danielson et al. (2012)	<a href="http://apdrc.soest.hawaii.edu/erddap/griddap">http://apdrc.soest.hawaii.edu/erddap/griddap</a>
SE wind Jun–Sep (summer) (m s <sup>−1</sup> )	SuSE	NCEP/NCAR reanalysis	Danielson et al. (2012)	<a href="http://apdrc.soest.hawaii.edu/erddap/griddap">http://apdrc.soest.hawaii.edu/erddap/griddap</a>
NW wind Feb–May (spring) (m s <sup>−1</sup> )	SpNW	NCEP/NCAR reanalysis	Danielson et al. (2012)	<a href="http://apdrc.soest.hawaii.edu/erddap/griddap">http://apdrc.soest.hawaii.edu/erddap/griddap</a>
NW wind Jun–Sep (summer) (m s <sup>−1</sup> )	SuNW	NCEP/NCAR reanalysis	Danielson et al. (2012)	<a href="http://apdrc.soest.hawaii.edu/erddap/griddap">http://apdrc.soest.hawaii.edu/erddap/griddap</a>
Mixed layer depth (m)	MLD	CTD	Present study	
Surface temperature (°C)	ST	CTD	Present study	
Bottom temperature (°C)	BT	CTD	Present study	
Surface salinity	SS	CTD	Present study	
Bottom salinity	BS	CTD	Present study	
Total chl <i>a</i> (µg l <sup>−1</sup> )	TC	Bottle samples	Present study	
Chl <i>a</i> >10 µm (µg l <sup>−1</sup> )	CG10	Bottle samples	Present study	

Center. A pixel was considered ice-covered if the ice cover exceeded 15 %. This cut-off was also used to estimate time-period average or annual ice extent on 15 March. A more localized picture of the ice coverage was obtained from the M8 mooring site where a sea-ice profiler allows the percent ice cover to be estimated (Stabeno et al. 2019), and we report this percentage for March. Summer cold pool extent measures the area (km<sup>2</sup>) of cold (<2°C) bottom water that persists on the Bering Sea shelf after ice retreat (Stabeno et al. 2001) and is associated with zooplankton variability (Thorson et al. 2020). We report values calculated after the methods of Fedewa et al. (2020) and use bottom temperature data collected by the NMFS bottom trawl survey (Table 1). The 2°C isotherm from these data was also used to estimate time-period average or annual cold pool extent. The

degree of total ice cover, wind direction and strength, and wind mixing impacts advection and timing of the spring phytoplankton bloom, which precedes the sampling of zooplankton populations in this study by 2–5 mo (Stabeno et al. 2001, Nielsen et al. 2020).

Water temperature, salinity, and density ( $\sigma_t$ ) were calculated from conductivity-temperature-depth measurements (Sea-Bird [SBE] 911 or SBE 25 CTD) made immediately prior to zooplankton sampling. The mean temperature and salinity above and below the surface mixed layer depth (MLD) was estimated at each station following Danielson et al. (2011) who defined the MLD as the depth where  $\sigma_t$  is 0.10 kg m<sup>−3</sup> greater than the value at 5 m depth. We did not compute MLD for the inner shelf as many of the stations were shallow and completely mixed.



### 2.3. Phytoplankton data

Water samples for total and size-fractionated chlorophyll *a* (chl *a*) were collected with Niskin bottles attached to the CTD. Samples were filtered through Whatman GF/F filters (nominal pore size 0.7  $\mu\text{m}$ ) to estimate total chl *a*, and through polycarbonate filters (pore size 10  $\mu\text{m}$ ) to estimate the large size fraction of the total chl *a*. Filters were stored frozen at  $-80^{\circ}\text{C}$  and analyzed within 6 mo with a Turner Designs benchtop fluorometer following standard acidification methods (Parsons et al. 1984).

### 2.4. Zooplankton data

Zooplankton were collected using multiple gear types over the sampling period (Table 2). Smaller zooplankton were collected using a vertically towed Juday net (37 cm diameter, 168  $\mu\text{m}$  mesh) (Shevelev 2004) from 2002 to 2011 and paired bongo nets (20 cm frame, 153  $\mu\text{m}$  mesh for the smaller net) (Kimmel et al. 2018) from 2012 to 2018. Larger zooplankton were collected with an obliquely towed ring net (60 cm diameter, 505  $\mu\text{m}$  mesh) from 2002 to 2011 for a subset of the samples and obliquely towed paired bongo nets (60 cm frame, 505  $\mu\text{m}$  mesh) for the majority of the samples. The mesh size (505  $\mu\text{m}$ ) and diameter (60 cm) was the same for the ring net and the bongo net and they were deployed in the same manner (oblique tow at  $0.5\text{--}0.75\text{ m s}^{-1}$ ), and we assumed these gears were comparable. A comparison of zooplankton abundance estimated from the different smaller mesh size gear deployed at the same location across 2 surveys conducted in the Chukchi Sea is presented in Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m705p021\\_supp.pdf](http://www.int-res.com/articles/suppl/m705p021_supp.pdf). Based on these comparisons, we suggest that the 2 gear types are comparable for most taxa, showing increases and decreases in abundance that covary (Figs. S2–S8). Additional information on gear comparisons may be found in Gorbatenko & Dolganova (2007). Vertical tows were within 5 m off the bottom and oblique tows were within 5–10 m of the bottom depending on sea state. Volume filtered was estimated from the distance (depth) towed for the Juday net assuming 100% filtering efficiency and

using a General Oceanics flowmeter mounted inside the mouth of each net for the 60 cm diameter nets. Filtration efficiency may vary considerably due to particle concentration, mesh size, diameter, and length of net (Skjoldal et al. 2019). Samples were preserved in 5% buffered formalin/seawater.

Zooplankton were identified to the lowest taxonomic level and stage possible at either the University of Alaska Fairbanks, the Plankton Sorting and Identification Center (PSIC) in Szczecin, Poland, and onboard ship (Juday net samples) by taxonomists from the Pacific Branch of the Russian Federal Research Institute of Fisheries and Oceanography (TINRO). Samples identified at the PSIC were verified at the AFSC, Seattle, Washington, USA. Hereafter, we will refer to *Calanus marshallae/glacialis* as *Calanus* spp., as the ability to distinguish between these sibling species morphologically is based on taxonomic characters that require significant processing time (Frost 1974). This appears to be a problem across the genus, as it has been suggested that the ability to distinguish between *C. glacialis* and *C. finmarchicus* in Atlantic waters can only be accomplished with DNA methods (Choquet et al. 2018). Recent results suggest that most *Calanus* in the Bering Sea may in fact be *glacialis* (Tarrant et al. 2021); however, these data are from one year only, so we will refer to *Calanus* spp. in this paper. We selected the taxa for inclusion in the analysis by ranking each

Table 2. Zooplankton data collection: year of survey, total number of net tows for each gear type: 37 cm diameter, 168  $\mu\text{m}$  mesh net (Juday); 20 cm diameter, 153  $\mu\text{m}$  mesh bongo net (20 cm); 60 cm diameter, 505  $\mu\text{m}$  mesh ring or bongo net (60 cm) within the middle and inner shelf regions, and dates when the surveys were conducted

Year	Juday (N)		20 cm (N)		60 cm (N)		Dates
	Inner	Middle	Inner	Middle	Inner	Middle	
2002					14	10	17–24 Sep
2003	7	4			16	8	28 Sep–2 Oct
2004	7	11			16	19	14–28 Sep
2005	7	9		2	16	16	17 Sep–4 Oct
2006	6	8		11	15	14	4 Sep–10 Oct
2007	7	8		17	13	12	17 Sep–11 Oct
2008							
2009	13	13	1	18	13	12	1 Sep–11 Oct
2010	16	8			9	3	14–25 Sep
2011	18	8		1	16	7	24 Aug–25 Sep
2012			13	1	13		29 Aug–28 Sep
2013					11	3	17–24 Sep
2014			16	27	16	26	14–24 Sep
2015			15	17	15	17	1 Sep–6 Oct
2016			16	10	16	10	28 Aug–18 Sep
2017			17	17	17	17	28 Aug–9 Sep
2018			16	8	17	8	1–10 Sep

taxa according to its percent contribution to the total abundance for each sample and each gear type. We estimated the percent contribution for each taxa across the entire data set and chose those taxa that made up at least 5 % of the total abundance on average (Table 3). We also grouped each individual taxon into a broader group for easier interpretation of the results. The 4 groups were: copepods >2 mm as adults, copepods <2 mm as adults, other holoplankton, and meroplankton (Table 3). It is important to note that a constituent of the zooplankton community, euphausiids, does not have abundance estimates reported here, as larger euphausiids are able to effectively avoid capture (Sameoto et al. 1993), thereby making euphausiid abundance estimates semi-quantitative. Accurate and precise measurements of euphausiid abundances in the Bering Sea remain the subject of debate (Hunt et al. 2016).

## 2.5. Statistical analysis

All statistical analyses were performed within the R computing environment, version 3.5.0 (R Core Team 2019). We compared average conditions across each of the 3 warm or cold time-periods using either 1-way ANOVA with the *anova* function, *stats* package or Kruskal-Wallis test (Kruskal & Wallis 1952) with the *kruskal.test* function, *stats* package. Prior to performing the comparison, the data were tested for normality using the Shapiro-Wilk test (Shapiro & Wilk 1965) with the *shapiro.test* function, *stats* package and homogeneity of variances using the Levene test (Lev-

ene 1965) with the *leveneTest* function, *car* package (Fox & Weisberg 2019). If neither assumption was violated, we used a 1-way ANOVA and tested for post-hoc differences using Tukey's HSD test (Tukey 1949) with the *TukeyHSD* function, *stats* package. If an assumption was violated, we used Kruskal-Wallis and tested for post-hoc differences using Dunn's test (Dunn 1964) with the *dunn.test* function, *dunn.test* package (Dinno 2017).

We conducted a multivariate redundancy analysis (RDA) (Borcard et al. 2011) using the *rda* function in the *vegan* package (Oksanen et al. 2019). We combined all taxa abundance estimates into the RDA, regardless of net size. Data were standardized prior to analysis using the *decostand* function in the *vegan* package using the 'range' method (Borcard et al. 2011). RDA included a stepwise-model selection step (*ordistep* function in *vegan* package) to identify variables for inclusion into the RDA model at a cutoff value of ( $p < 0.05$ ). Comparison of total model fit was done using Akaike's information criterion (AIC), and the model with the lowest AIC was considered the best fit. We also performed correlation analyses between environmental variables and zooplankton abundances using the *cor* function in the *stats* package.

## 3. RESULTS

### 3.1. Environment

The area of the Bering Sea covered by ice was less in both Warm 1 and Warm 2 compared to Cold

Table 3. Taxa considered in the multivariate analysis, abbreviation, gear type: 37 cm diameter, 168  $\mu$ m mesh net (Juday); 20 cm diameter, 153  $\mu$ m mesh bongo net (20 cm); 60 cm diameter, 505  $\mu$ m mesh ring or bongo net (60 cm), zooplankton stage or size limit, and group. For copepods, C refers to copepodite and the number to stage, with 6 being the adult stage

Taxa	Abbreviation	Gear	Stage/Size	Group
<i>Calanus</i> spp.	CA	20 cm/60 cm	C3–C6	Copepods >2 mm
<i>Epilabidocera longipedata</i>	EP	20 cm/60 cm	C1–C6	Copepods >2 mm
<i>Tortanus discaudatus</i>	TO	20 cm/60 cm	C1–C6	Copepods >2 mm
<i>Acartia</i> spp.	AC	Juday/20 cm	C1–C6	Copepods <2 mm
<i>Centropages abdominalis</i>	CE	20 cm/60 cm	C1–C6	Copepods <2 mm
<i>Oithona</i> spp.	OI	Juday/20 cm	C1–C6	Copepods <2 mm
<i>Pseudocalanus</i> spp.	PS	Juday/20 cm	C1–C6	Copepods <2 mm
Amphipoda	AM	60 cm	<20 mm	Other holoplankton
Appendicularia	AP	60 cm	<20 mm	Other holoplankton
Chaetognatha	CH	60 cm	<20 mm	Other holoplankton
Cnidaria	CN	60 cm	Medusa	Other holoplankton
<i>Limacina helicina</i>	LH	60 cm	<20 mm	Other holoplankton
Bivalvia	BI	Juday/20 cm	Larvae	Meroplankton
Cirripedia	CI	60 cm	Nauplius/Cypris	Meroplankton
Polychaeta	PO	Juday/20 cm	Larvae	Meroplankton

(Figs. 1C & 2A,B) and was markedly reduced in 2018, with maximum extent occurring north of 60°N (Fig. 1C). Warm 1 and Warm 2 differed from Cold, but not from each other in terms of total ice area or ice cover (Fig. 2A,B). The cold pool was also reduced in both Warm 1 and Warm 2 (Fig. 2C) and extended much further south, on average, during the Cold period (Fig. 1D). As with ice, the cold pool area differed between Warm 1 and Warm 2 and the Cold periods, but not when comparing Warm 1 to Warm 2 (Fig. 2C). The 2 climate indices, the AO, NPI, wind mixing, and seasonal wind speeds showed variability over the warm and cold periods (Fig. S9), but did not differ on average (data not shown).

The MLD was reduced during the Cold period on the middle shelf (Fig. 3A), and only Warm 2 had deeper MLD than the Cold period (Figs. 3A & S10). Surface temperatures did not differ between Warm 1

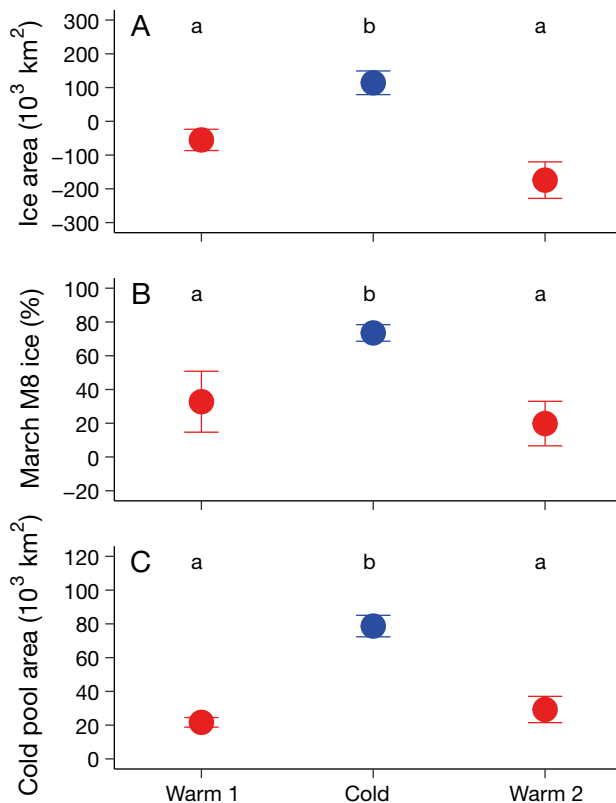


Fig. 2. (A) Comparisons of total ice area, (B) March percent ice cover around the M8 mooring, (C) and cold pool area across the Warm 1 (2002–2005), Warm 2 (2014–2018) and Cold (2006–2013) periods. Points represent time-period mean and error bars  $\pm 1$  SE of the mean (Warm 1: N = 4; Cold: N = 8; Warm 2: N = 5). Periods that have different lowercase letters had means that differed based on 1-way ANOVA ( $p < 0.05$ ) and Tukey HSD post-hoc tests ( $p < 0.05$ ) and periods with the same lowercase letter did not

and the Cold period, but both of these periods were statistically different from the higher temperatures that occurred in Warm 2 (Figs. 3B,C & S10). Bottom temperature anomalies differed across all 3 time-periods on the middle shelf (Figs. 3D & S10), but only the Cold period differed from Warm 1 and Warm 2 on the inner shelf (Figs. 3E & S10). As with bottom temperature, surface salinity differed across all 3 time-periods on the middle shelf (Figs. 3F & S10), whereas only Warm 1 and Warm 2 differed on the inner shelf (Figs. 3G & S10). Bottom salinities did not differ between any time-period (Figs. 3H,I & S10).

### 3.2. Phytoplankton

All 3 time-periods differed in total chl *a* concentration on the middle shelf with time-period average concentrations declining over time (Figs. 4A & S11). The same decline was observed on the inner shelf, but only Warm 1 differed in average concentration from the Cold period (Figs. 4B & S11). Chl *a* concentration anomalies for cells  $>10$   $\mu\text{m}$  in size mirrored the variability in total chl *a* concentration over time and resulted in significant differences across all 3 time-periods in both shelf regions (Figs. 4C,D & S11). The proportion of chl *a* found in cells  $>10$   $\mu\text{m}$  in size was highest Warm 1 and declined over time on both the middle and inner shelves, and all 3 time-periods also differed in the average proportion of cells  $>10$   $\mu\text{m}$  in size (Figs. 4E,F & S11).

### 3.3. Zooplankton

#### 3.3.1. Redundancy analysis

Redundancy analysis showed associations between environmental variables and zooplankton abundance in both shelf regions. The best fit model identified by stepwise selection for the middle shelf had ice area, total chl *a*, chl *a*  $>10$   $\mu\text{m}$  in size, cold pool extent, M8 ice cover, and bottom temperature as the variables correlated with zooplankton community variations (Table 4). Ice area was the first variable loaded into the model and explained the majority of the variance (Table 4). Similarly, the best fit model identified by stepwise selection for the inner shelf had M8 ice cover, bottom temperature, ice area, and cold pool extent (Table 4). M8 ice cover was the first variable loaded into the model and explained the majority of the variance (Table 4).



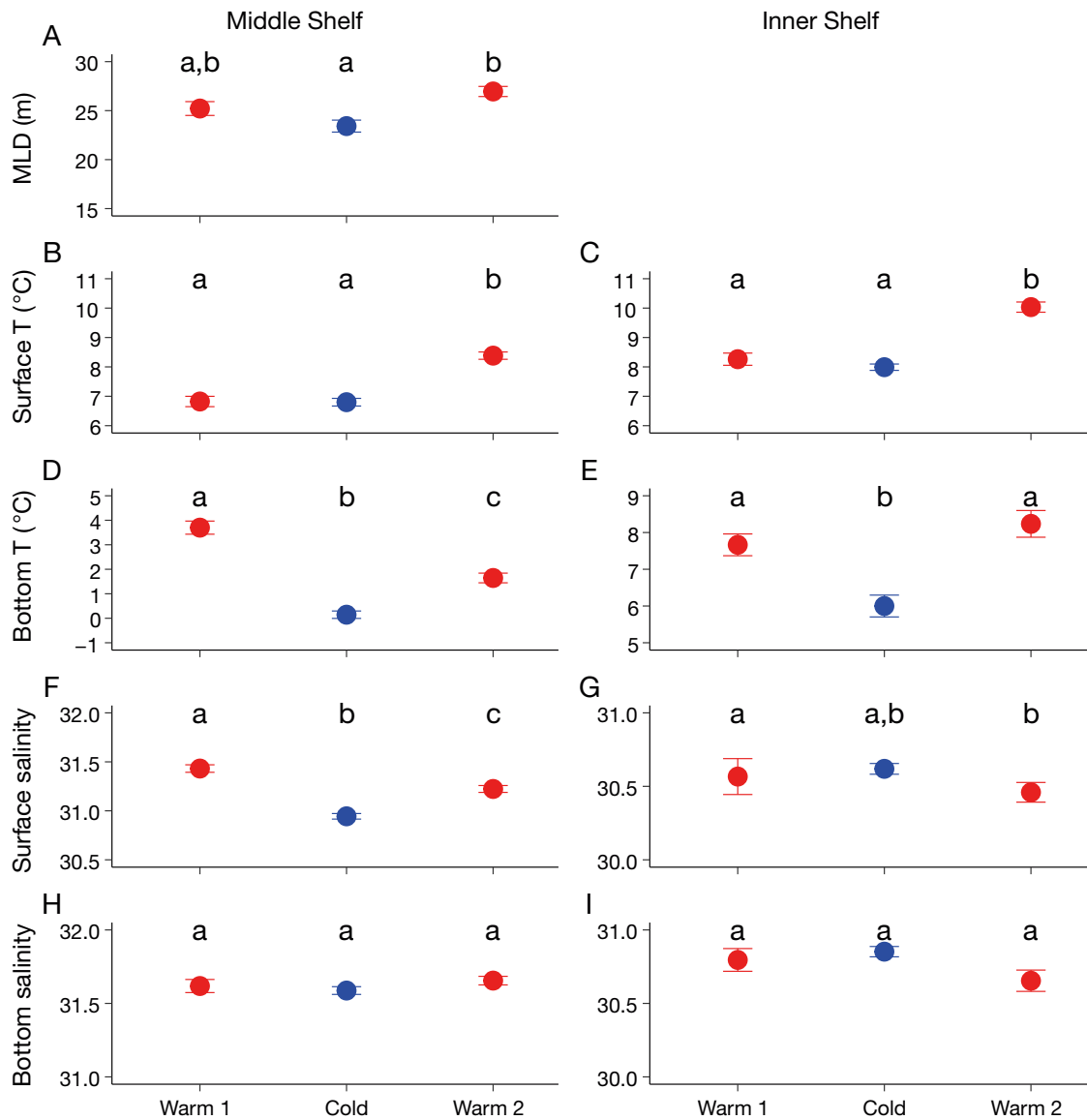


Fig. 3. (A) Mixed layer depth (MLD) on the middle shelf, and comparisons of (B,C) surface temperature, (D,E) bottom temperature, (F,G) surface salinity, and (H,I) bottom salinity between the middle and inner shelves across the Warm 1 (2002–2005), Warm 2 (2014–2018) and Cold (2006–2013) periods. Points represent time-period mean and error bars  $\pm 1$  SE of the mean (middle: Warm 1, N = 67; Cold, N = 108; Warm 2, N = 140; inner: Warm 1, N = 63; Cold, N = 110; Warm 2, N = 81). Periods that have different lowercase letters had means that differed based on Kruskal-Wallis ( $p < 0.05$ ) and Dunn's post-hoc tests ( $p < 0.05$ ) and periods with the same lowercase letter did not

### 3.3.2. Copepods > 2 mm

The 3 larger species of copepods showed differing responses to environmental variability. *Calanus* spp. were negatively associated with bottom temperature and positively associated with cold pool area (Figs. 5A & 6A). The correlation heat map showed *Calanus* spp. were positively correlated to ice area, M8 ice, and cold pool area on both shelves, and the opposite correlation patterns were observed for *E. longipedata* and *T. discaudatus* (Fig. 7). All 3 periods

had different, average *Calanus* spp. abundances, with Warm 1 having the lowest abundances, followed by Warm 2 and the Cold period (Fig. 8A,B). Both *E. longipedata* and *T. discaudatus* had positive association with bottom and surface temperature and total chl *a* concentration in both shelf locations (Figs. 5A & 6A). *E. longipedata* was nearly absent from the plankton during the Warm 1 and Cold periods (Figs. 8C,D & S12); however, this species was found in high abundances during Warm 2 (Figs. 8C,D & S12). *T. discaudatus* abundance was low on the

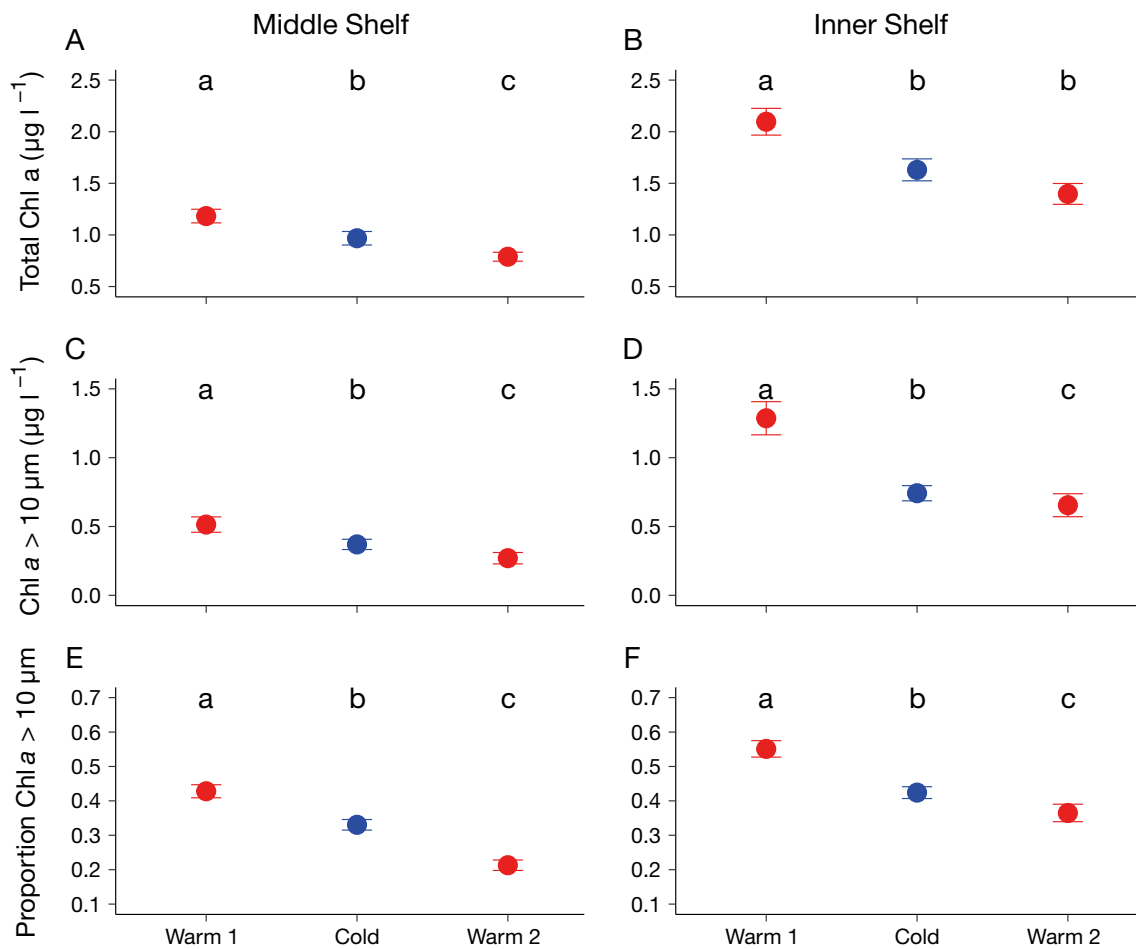


Fig. 4. Same as Fig. 3, but for comparisons of (A,B) total chl *a* concentration, (C,D) chl *a* > 10 µm cell diameter concentration, and (E,F) proportion of chl *a* > 10 µm

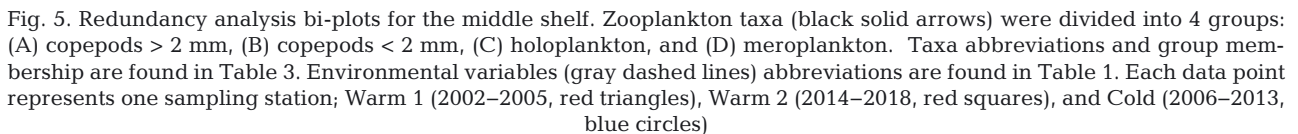
Table 4. Step-wise model selection results for the middle and inner shelf zooplankton community redundancy analyses. Columns show variables included in each iteration of the model selection, as well as the corresponding Akaike information criterion (AIC) values, *F* values, and *p*-values. The *r*<sup>2</sup> value represents the result for the full model. Variable abbreviations can be found in Table 1

Variable	AIC	<i>F</i>	<i>p</i>
Middle shelf ( <i>r</i> <sup>2</sup> = 0.34)			
IA + TC + CG10 + CP + M8I + BT	-50.79	2.28	0.01
IA + TC + CG10 + CP + M8I	-50.25	2.12	0.03
IA + TC + CG10 + CP	-49.93	2.65	0.01
IA + TC + CG10	-49.09	2.83	0.005
IA + TC	-48.13	3.49	0.005
IA	-46.86	4.57	0.005
Inner shelf ( <i>r</i> <sup>2</sup> = 0.26)			
M8I + BT + IA + CP	-67.79	2.65	0.005
M8I + BT + IA	-67.001	3.34	0.005
M8I + BT	-65.55	5.03	0.005
M8I	-62.49	5.41	0.005

middle shelf overall and was highest during Warm 1 (Figs. 8E & S12) in contrast to the inner shelf, where abundances were higher overall and highest during Warm 2 (Figs. 8F & S12).

### 3.3.3. Copepods <2 mm

*Acartia* spp. was associated with colder conditions, in contrast with *Centropages abdominalis*, *Oithona* spp., and *Pseudocalanus* spp., which were associated with warmer conditions (Figs. 5B & 6B). Correlations for these species were strongest on the inner shelf and weaker on the middle shelf, as indicated by the correlation heat map (Fig. 7). Positive correlations were found between ice area, M8 ice cover, and cold pool area for *Acartia* spp. on both shelves (Fig. 7). Negative correlations for these same variables were observed on both shelves for *C. abdominalis* and *Oithona* spp. (Fig. 7). *Pseudocalanus* spp. had weak correlations on the middle shelf, but strong, negative



the highest mean abundance during Warm 2 in both shelf locations (Figs. 9G,H & S13).

Other holoplankton taxa showed less variability overall compared to copepods and meroplankton (Figs. 5C & 6C). Correlations with environmental variables were near zero for other holoplankton on the middle shelf and were stronger on the inner shelf (Fig. 7). Amphipoda showed no consistent relationship with environmental condition based on the RDA analysis (Figs. 5C & 6C), and on average, abundances

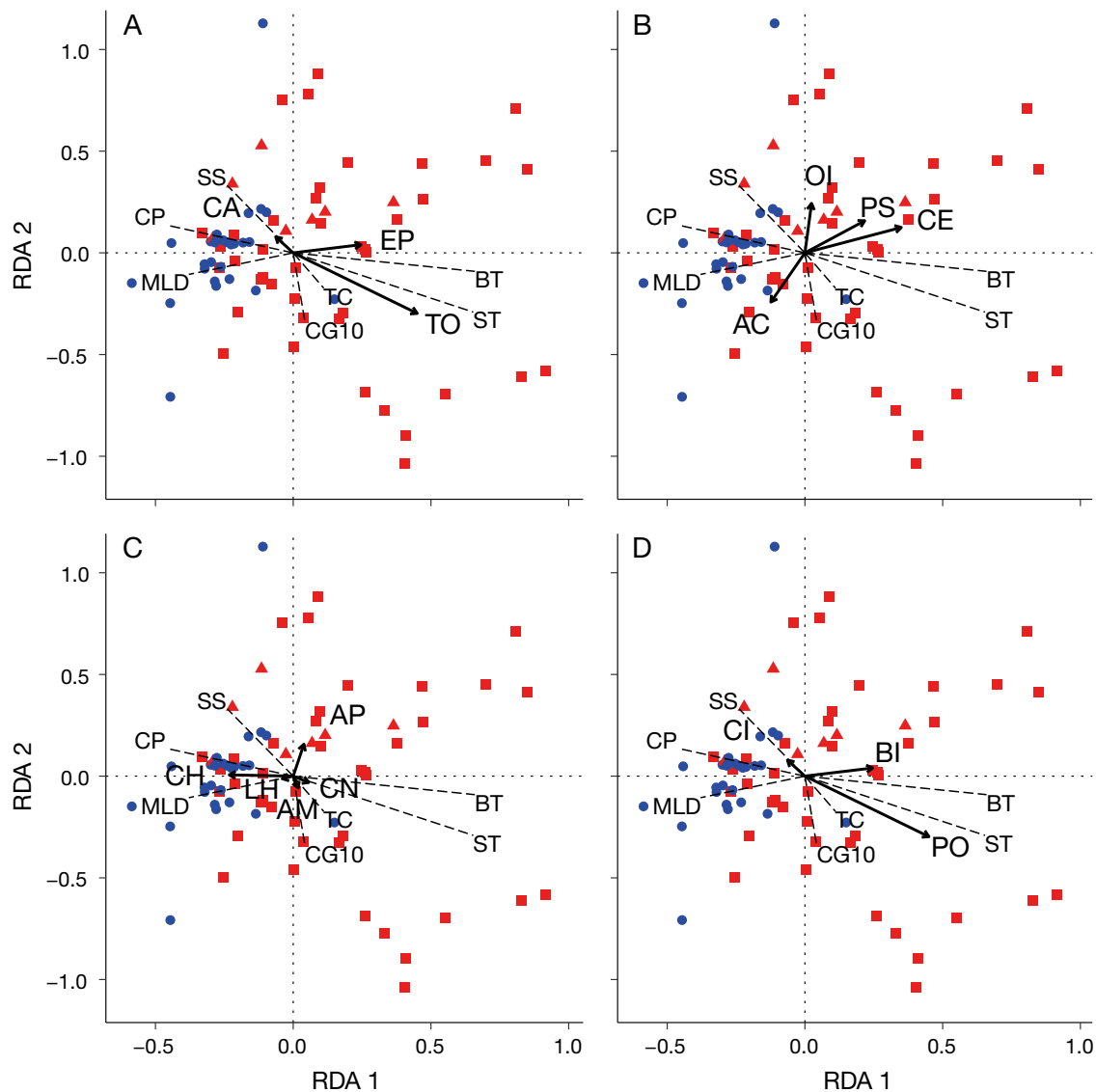


Fig. 6. Redundancy analysis bi-plots for the inner shelf. Further details as in Fig. 5

remained similar across warm and cold periods (Figs. 10A,B & S14). The exception was 2 abundance peaks (Fig. S14) that caused average abundances to be higher on the middle shelf in Warm 2 (Fig. 10A) and inner shelf in the Cold period (Fig. 10B). The peak on the inner shelf occurred during the Cold period and thus resulted in positive correlations with cold conditions (Fig. 7). Based on the RDA, Appendicularia was associated with warmer conditions (Figs. 5C & 6C), correlations between bottom temperatures were positive, and correlations between ice area, M8 ice, and cold pool area were negative on both shelves (Fig. 7). Appendicularia mean abundance was highest during Warm 2 on both shelves (Figs. 10C,D & S14), but was also elevated on the middle shelf during the Cold period (Fig. 10C). Chaetognaths were

associated with colder conditions (Figs. 5C & 6C) and had positive correlations with ice area, M8 ice cover, and cold pool area and negative correlations with bottom temperature (Fig. 7). Chaetognaths mean abundances were consistently higher during the Cold period (Figs. 10E,F & S14). Similar to Amphipoda, Cnidaria and *Limacina helicina* had no consistent association with environmental variables in the RDA (Figs. 5C & 6C). On the middle shelf, Cnidaria was negatively correlated with cold conditions in contrast with *L. helicina*, which was positively correlated with cold conditions (Fig. 7). These relationships were opposite on the inner shelf for Cnidaria, which was positively associated with cold conditions (Fig. 7). Cnidaria abundances were higher during Warm 1 and Warm 2 (Figs. 10G,H & S14), excepting Warm 2 on

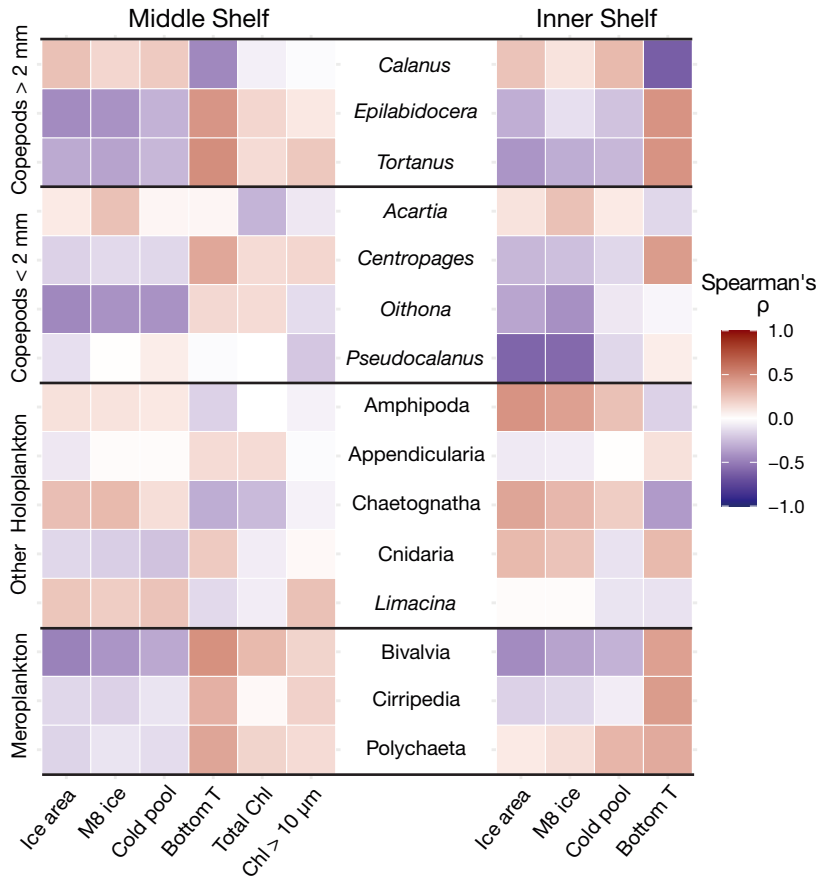


Fig. 7. Correlation (Spearman's  $\rho$ ) heat map for zooplankton identified by taxa and group and environmental variables identified by step-wise model selection during redundancy analysis (Table 4). Positive correlations are shown by the increasing intensity of red and negative correlations by the increasing intensity of purple. See Table 3 for full species names

the outer shelf (Figs. 10G & S14), and *L. helicina* did not differ across warm and cold periods in either shelf location (Figs. 10I,J & S14).

### 3.3.5. Meroplankton

The 3 meroplankton groups had weaker associations with environmental variables on the middle shelf (Fig. 5D) compared to the inner shelf (Fig. 6D). The strongest relationships were found for Bivalvia, which had negative correlations with ice area, M8 ice, and cold pool area and positive correlations with bottom temperature (Fig. 7). Cirripedia and Polychaeta also had positive correlations with bottom temperature (Fig. 7), but the correlations between ice and cold pool area were not consistent across shelves for Polychaeta (Fig. 7). Average abundances of Bivalvia were lowest on the middle shelf during the Cold period (Figs. 11A & S15) and highest on the inner shelf in Warm 2 (Figs. 11B & S15). Cirripedia

average abundances were highest during Warm 1 on the middle shelf (Figs. 11C & S15) and equally as high during Warm 1 and Warm 2 on the inner shelf (Figs. 11D & S15). Average Polychaeta abundance was lower on the middle shelf overall, but highest during Warm 1 and Warm 2 (Figs. 11E & S15). Higher abundances of Polychaeta were observed on the inner shelf, and abundances during Cold and Warm 2 were higher than those of Warm 1 (Figs. 11F & S15).

## 4. DISCUSSION

The NBS zooplankton community had different responses across each warm and cold period. We attribute the difference in response to sea ice, the primary variable identified in the redundancy analysis for both shelf regions (Table 4). Of particular note was the dramatic reduction in sea ice observed in Warm 2 (Fig. 1C) (Stabeno & Bell 2019). Warm periods were characterized by reduced ice area and ice cover (Fig. 2A,B) that resulted in a reduction in cold pool area (Figs. 1D & 2C), positive temperature anomalies (Fig. 3B–E), and a shift to smaller phytoplankton cells (Fig. 4), though this occurred only in Warm 2 (Eisner et al. 2019, Siddon et al. 2020). Redundancy analysis demonstrated that the zooplankton community during Warm 2 experienced greater variability compared to Warm 1, as given by the wider spread of points in the RDA analyses (red squares, Figs. 5 & 6). This suggests that when the ice coverage extends south of 60° N, as was observed in 2002–2005 (Fig. 1C), the NBS zooplankton community will be less impacted. Once a minimum threshold in ice extent and timing of retreat is reached, as happened during Warm 2 (Fig. 1C), the community will show a response. In general, copepods < 2 mm (except *Acartia* spp.), meroplankton, and copepods > 2 mm (except *Calanus* spp.) abundance were all negatively correlated with colder conditions and positively correlated with warm conditions, in particular bottom temperature (Fig. 7). These local responses may be significantly altered by advection, though we found no relationships with



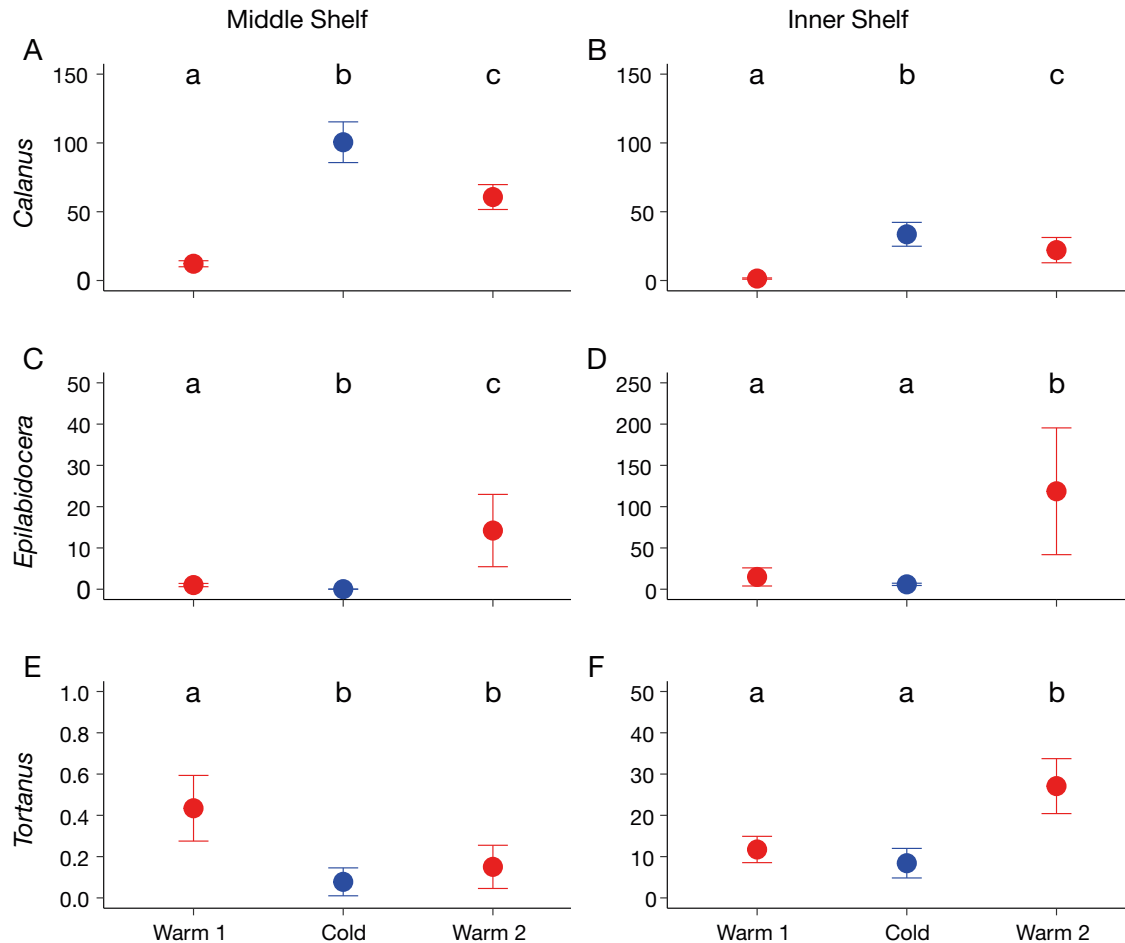


Fig. 8. Copepods > 2 mm. Differences in abundance (no. m<sup>-3</sup>) of (A,B) *Calanus* spp., (C,D) *Epilabidocera longipedata*, and (E,F) *Tortanus discaudatus* across the Warm 1 (2002–2005), Warm 2 (2014–2018) and Cold (2006–2013) periods for the middle and inner shelf. Points represent time-period mean and error bars  $\pm 1$  SE of the mean (middle: Warm 1, N = 58; Cold, N = 103; Warm 2, N = 83; inner: Warm 1, N = 62; Cold, N = 101; Warm 2, N = 81). Periods that have different lowercase letters had means that differed based on Kruskal-Wallis ( $p < 0.05$ ) and Dunn's post-hoc tests ( $p < 0.05$ ) and periods with the same lowercase letter did not

wind in this study as our proxy for advection. Cold years with ice-cover in the NBS may have experienced less advection of zooplankton populations into these waters, resulting in less overall variability in the zooplankton community, whereas warm years saw zooplankton populations advected into this region. This is supported by the observation that heat flux advection increased dramatically during 2014–2018 in the NBS and Chukchi Sea (Danielson et al. 2020). The shifts in the zooplankton community that we observed (e.g. an increase in smaller-sized copepods, neritic species, and meroplankton) may have contributed to the ecosystem response seen in higher trophic level organisms, such as seabird die-offs, as described in Siddon et al. (2020).

Average ice area, ice cover, and cold pool extent were higher in the Cold period compared to Warm 1 or Warm 2, whereas these same measures did not dif-

fer statistically when Warm 1 and Warm 2 were compared (Fig. 2). The lack of statistical difference was directly related to the impacts of the 2017/2018 winter on both ice and cold pool extent, increasing the magnitude of the standard deviation for these metrics for the second warm period. The NBS near M8 has experienced considerable variability in the timing of sea ice arrival/retreat over time, but it was largely ice covered for approximately 5 months of the year (Stabeno & Bell 2019, Stabeno et al. 2019). This changed in 2017/2018 with a late arrival and early retreat of the ice that was driven by shifts in wind (in particular, strong winds from the south during February) (Stabeno & Bell 2019, Thoman et al. 2020). We found no differences in spring or summer wind speed or mixing across time-periods, likely because we averaged wind speeds and mixing over discrete time-periods, rather than examining daily wind variability

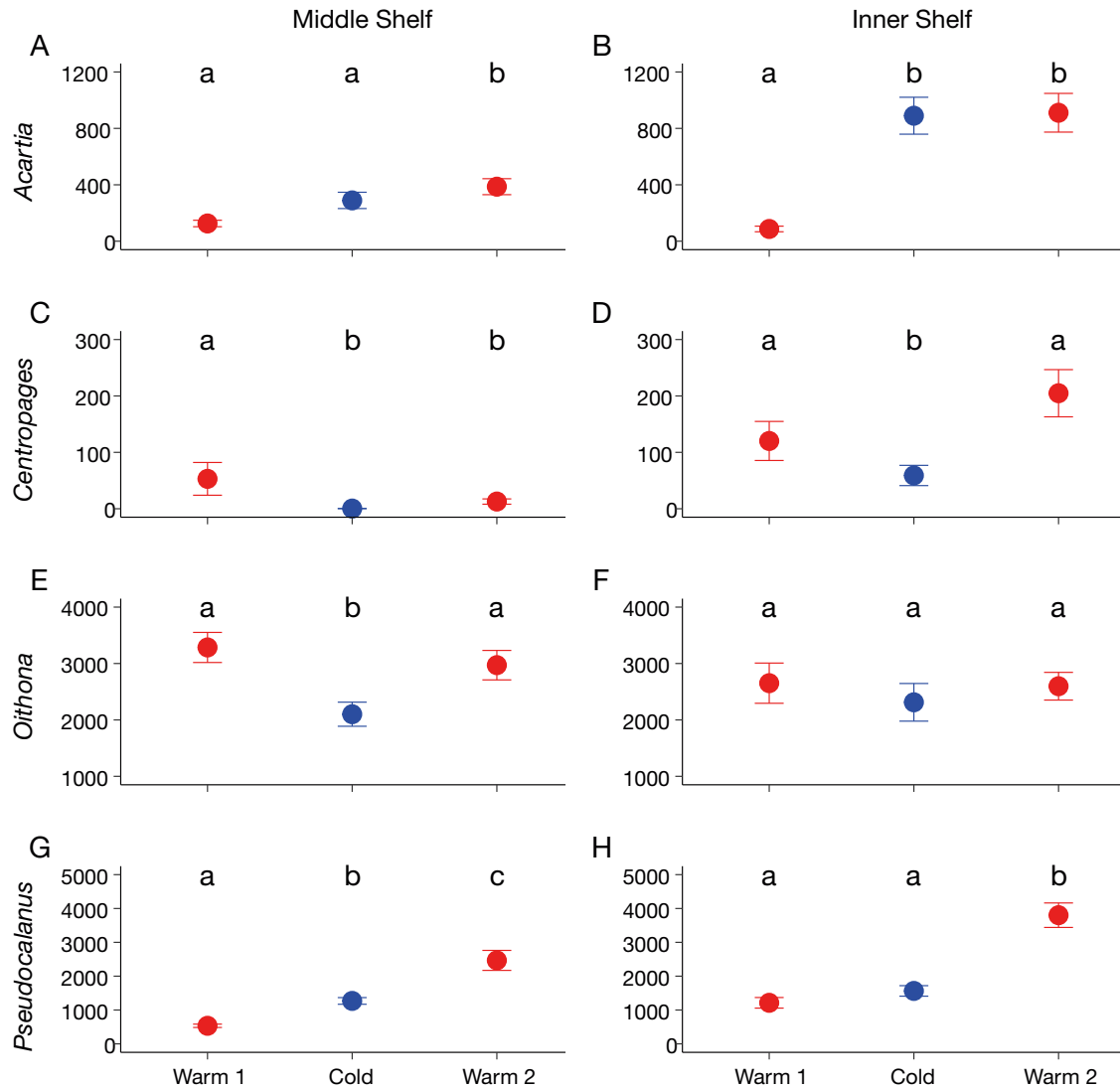


Fig. 9. Same as Fig. 8, but for copepods < 2 mm and differences in abundance (no. m<sup>-3</sup>) of (A,B) *Acartia* spp., (C,D) *Centropages abdominalis*, (E,F) *Oithona* spp., and (G,H) *Pseudocalanus* spp.

within a given year. The cold pool area was larger, on average, in Warm 2 (Fig. 2), but again this masked the smallest ever recorded cold pool extent in 2018 (Stabeno & Bell 2019), and the 2°C isotherm was not detected in the bottom trawl survey during 2018 (Fig. 1D). We could have separated the years 2017 and 2018 into a third warm period to explore these differences; however, the resulting sample size would have been too small for meaningful statistical comparison. We also suspect that a finer spatially resolved ice coverage index, rather than a Bering Sea-wide annual index, would show greater differences for the NBS in Warm 2, and we aim to explore this in a future study. We conclude that the warm periods present in this data set were similar in terms of average annual indices overall, but note that the winter

of 2017/2018 distorted the averages reported here as defining a 'warm' period. The winter of 2017/2018 represented a significant anomalous event resulting in large shifts in oceanographic conditions as has been widely reported (Stabeno & Bell 2019, Siddon et al. 2020).

The 2 warm periods had different water column characteristics relative to the cold period, and these also differed between the 2 shelf regions. The early ice retreat on the middle shelf resulted in increased mixing of more saline bottom waters with fresher water left after ice retreat, resulting in a greater MLD and higher salinities at the surface (Danielson et al. 2011). Temperatures increased in both surface and bottom waters during both warm periods, with the notable exception of the middle shelf during Warm 1,

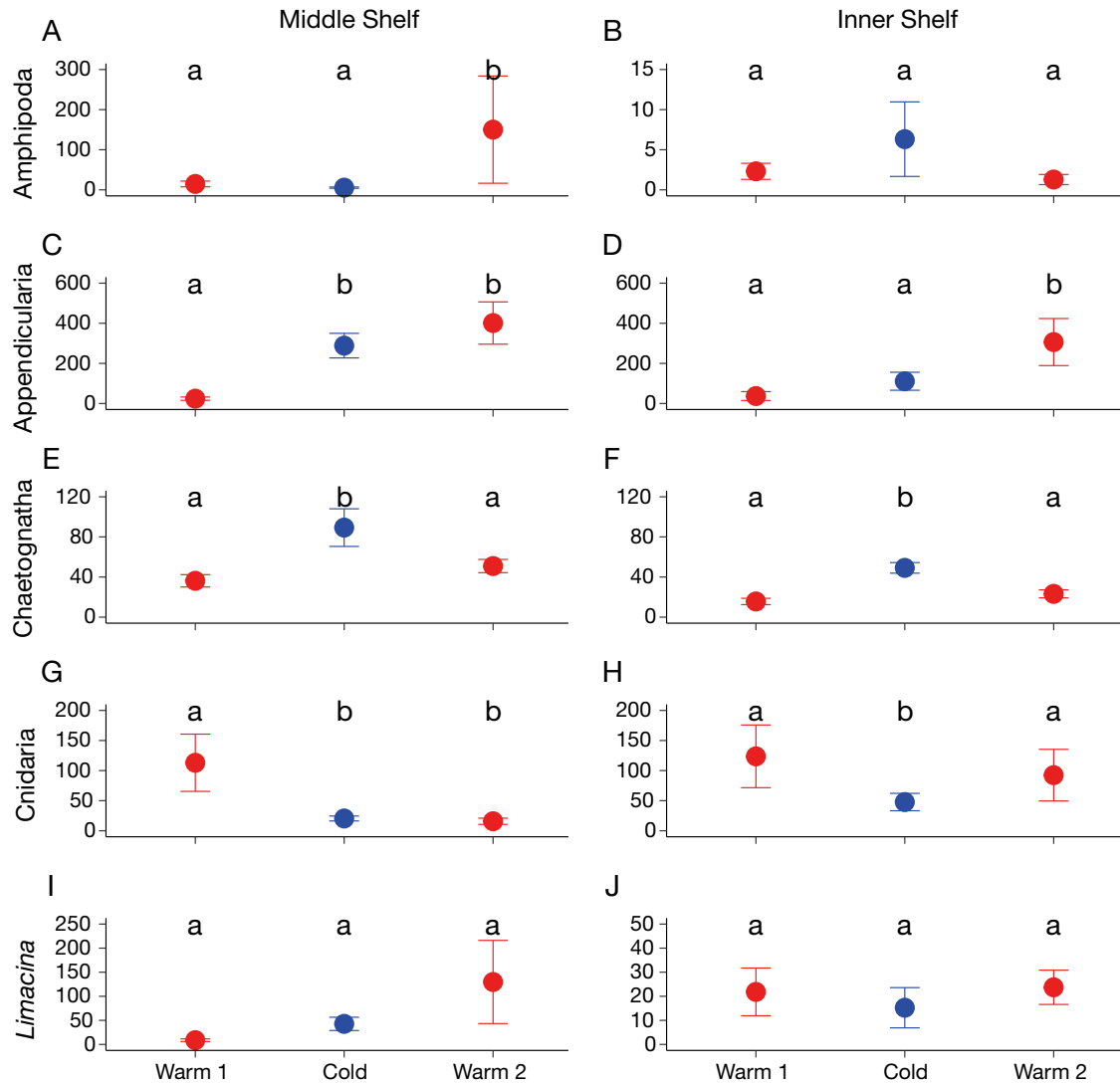


Fig. 10. Same as Fig. 8, but for other holoplankton and differences in abundance (no.  $m^{-3}$ ) of (A,B) Amphipoda, (C,D) Appendicularia, (E,F) Chaetognatha, (G,H) Cnidaria, and (I,J) *Limacina helicina*

which had lower average surface temperature relative to the subsequent Cold period (Fig. 3B). Bottom temperatures were much warmer on the middle shelf in Warm 1 relative to the other time-periods (Fig. 3). This difference in surface and bottom warming over contrasting warm and cold periods has been noted (Stabeno et al. 2012b) as stratification differences do not always impact bottom temperatures in a consistent manner (Ladd & Stabeno 2012). This highlights the difficulties in ascribing ‘warm’ and ‘cold’ to particular time-periods based solely on temperature in these layers. The salinity response also differed between the middle and inner shelves at the surface, with salinities increasing during warm periods on the middle shelf (Fig. 3F) and decreasing on the inner shelf, though only in Warm 2 (Fig. 3G). In contrast, the inner shelf was influenced by increased fresh-

water input as a result of warmer conditions, thus lower salinity waters left by retreating ice remained reduced in salinity (Ueno et al. 2020). This led to an inverse correlation between surface salinities on the middle and inner shelves (Danielson et al. 2011).

Total chl *a* and chl *a* > 10  $\mu m$  concentrations, as well as the proportion of cells > 10  $\mu m$ , were all highest in Warm 1 (Fig. 4). We expected both warm years to be characterized by smaller cell sizes due to the tendency for phytoplankton cell size to decrease in the Bering Sea as temperature increases (Fujiwara et al. 2011). Studies also report a decrease in phytoplankton cell size occurs during warming, though may be mediated or driven by other effects such as grazing or nutrient availability (Daufresne et al. 2009, Peter & Sommer 2013). The increased proportion of larger cells during Warm 1 may have been related to the

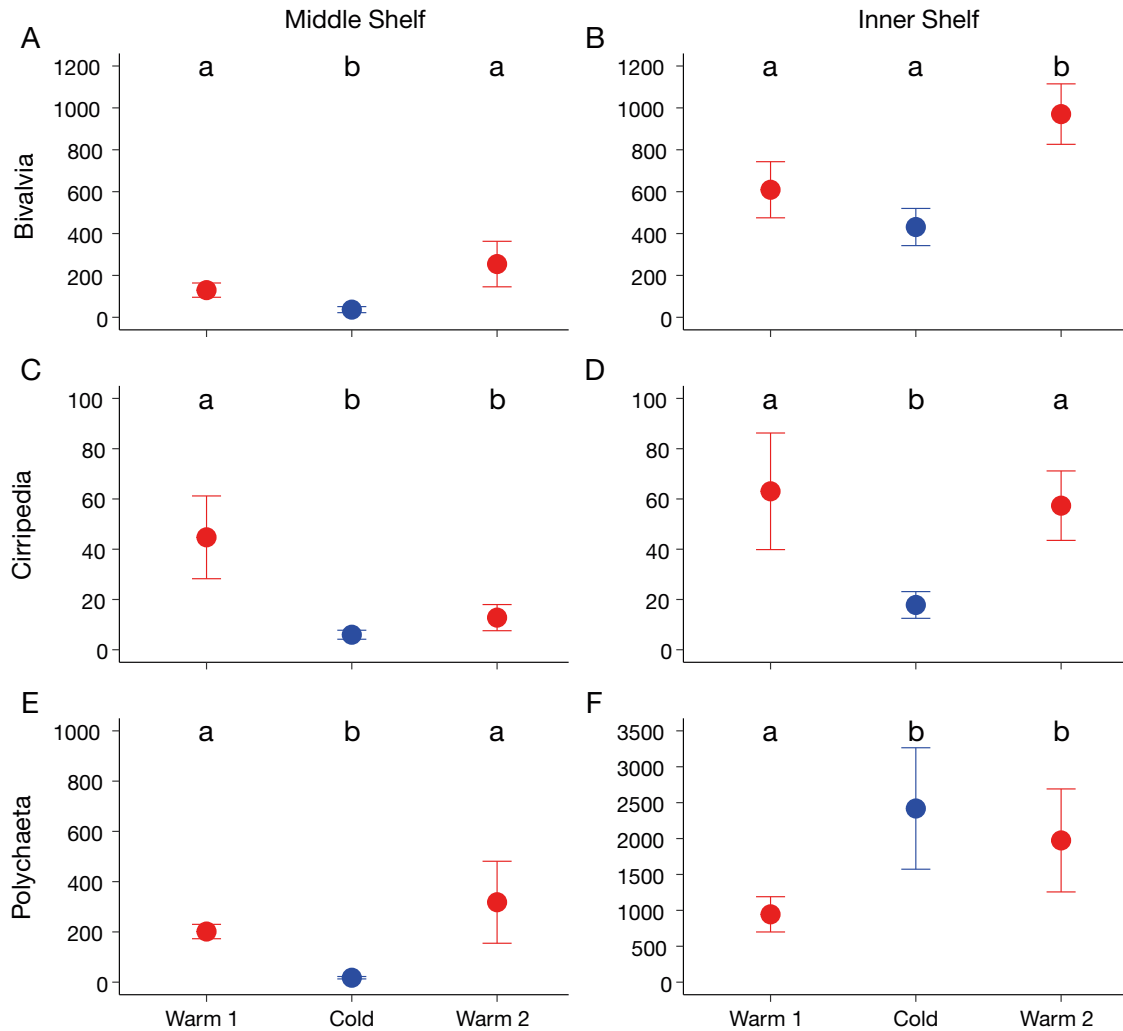


Fig. 11. Same as Fig. 8, but for meroplankton and differences in abundance (no. m<sup>-3</sup>) of (A,B) Bivalvia, (C,D) Cirripedia, and (E,F) Polychaeta

similar MLD and surface temperatures observed as occurred in the Cold period (Fig. 3A–C). However, other factors may be responsible for influencing phytoplankton community structure, including nutrient availability, grazing, or shifts in seasonal phenology. The reduction in cell size in Warm 2 likely indicated a reduction in large size diatoms that dominate the NBS phytoplankton community on average (Zhuang et al. 2014). The NBS community was characterized by smaller cells in 2018, particularly on the middle shelf (Fukai et al. 2020), and it also had very low proportions (~0.1) of large phytoplankton on the middle shelf in 2014, likely due to a bloom of coccolithophores (Ladd et al. 2018). While we did not measure primary production in our study, the lack of ice cover in Arctic waters has been suggested to lead to increased pelagic primary production (Arrigo & van Dijken 2015), increased influence of zooplankton

grazing, and a reduction in material flux to the benthos, thereby reducing overall benthic production (Lovvorn et al. 2005). A reduction in diatoms (both pelagic and sympagic) would result in reduced flux of carbon to the benthos, a situation that appears to be underway in the NBS (Grebmeier 2012).

Redundancy analysis showed a distinction between the zooplankton community during warm and cold periods. Communities from stations sampled during the Cold period clustered closely together, particularly on the middle shelf (Fig. 5), whereas warmer water communities had a wider spread of data points (Figs. 5 & 6). The copepod *Calanus* spp. and Chaetognatha increased in abundance during the cold periods and were positively correlated with increased ice area and negatively correlated with higher bottom temperatures (Fig. 7). Both taxa have been shown to associate with Bering Shelf Water

(Eisner et al. 2013, 2014), and Eisner et al. (2014) noted that the inner front bordered inshore by Alaska Coastal Water may be weaker during cold years, allowing these middle shelf species to enter onto the inner shelf. In contrast, warm periods were correlated with increased abundances of 2 neritic copepods >2 mm taxa (*Epilabidocera longipedata* and *Tortanus discaudatus*) (Pinchuk & Eisner 2017), Copepods <2 mm (with the exception of *Acartia* spp.), and meroplankton (Fig. 7). We hypothesize that Alaska Coastal Water (Danielson et al. 2017) expanded across both shelves during the warm periods, bringing the neritic zooplankton community with it. Eisner et al. (2020b) reported that distributions of walleye pollock followed a similar pattern, with a more narrow longitudinal distribution during 2010 (cold year) and wide longitudinal distribution during warm years (2017–2019). The increase in copepod numbers overall was likely a function of increased temperatures driving increases in growth rate, egg production, and reduced development times (Hirst & Bunker 2003), allowing abundances to accumulate. *Pseudocalanus* spp. has been found to be more responsive to temperature than food supply (Liu & Hopcroft 2008), and Warm 2 showed much higher *Pseudocalanus* spp. abundances (Fig. 9G,H), as well as increases in *E. longipedata* (Fig. 8C,D), *T. discaudatus* (Fig. 8F), and *Centropages abdominalis* (Fig. 9D).

The other members of the holoplankton community, aside from Chaetognatha, were less correlated to environmental conditions on the middle shelf, but colder conditions were associated with Amphipoda and Cnidarian on the inner shelf (Fig. 7). The amphipod *Themisto libellula* has been observed to increase in abundance during cold periods (Pinchuk et al. 2013); however, we did not observe an increase in this species probably because of different sampling techniques (night-time MOCNESS vs. day-time bongo). The 2 large peaks of amphipods were *T. pacifica* (2016, middle shelf) and *Corophium* spp. (2013, inner shelf). Since large increases in these taxa were not associated with any environmental variables, we may have simply sampled an anomalous patch of these organisms during the surveys. Cnidarian abundances are consistently problematic to interpret due to the destructive nature of net sampling; therefore, we do not draw major conclusions from these abundance estimates. More interesting was the increase in meroplankton observed during Warm 1 and Warm 2. Meroplankton may dominate the plankton at times, and release has been associated with the spring phytoplankton bloom in the NBS and the shallower Chukchi Sea (Matsuno et al. 2011, Questel

et al. 2013, Kimura et al. 2020). Kimura et al. (2020) found all 3 meroplankton groups which we identified had peaked on the NBS shelf inshore of 170° W during August of 2017, suggesting seasonal release of meroplankton may be later in the year in the NBS and tied to ice retreat timing. For example, earlier ice retreat and warmer bottom temperatures appeared to stimulate the release of Cirripedia in the Chukchi Sea (Matsuno et al. 2011).

Shifts in the zooplankton community have impacts on higher trophic level predators, often through the impact on key forage taxa such as *Calanus* spp. We found *Calanus* spp. variability in response to warm and cold periods to be similar to that observed over a shorter time-period (2003–2009) in the NBS (Eisner et al. 2014) and over the southeastern shelf (Baier & Napp 2003, Coyle et al. 2008, Eisner et al. 2018, Kimmel et al. 2018), with this taxon positively correlating with increased ice cover, cold pool area, and low bottom water temperatures (Fig. 7) (Eisner et al. 2013, 2014). Much remains to be learnt about *Calanus* spp. biology in this region, including which specific species of *Calanus* may be present (Nelson et al. 2009) and whether *Calanus* spp. diapause dynamics are changing in response to warming. We are seeing preliminary evidence that a second generation of *Calanus* spp. may be present on the Bering Sea shelf (Pinchuk et al. 2014), as has been shown at lower latitudes and has been predicted with life-history modeling (Banas et al. 2016). Our results suggest that continued warming of the NBS will result in a decline in *Calanus* spp. abundance in this region. This decline in *Calanus* spp. may impact adult fish that were seen to move northwards during the low ice events of 2017/2018 and 2018/2019 (Stevenson & Lauth 2019, Eisner et al. 2020b) as well as juvenile fish that rely on *Calanus* spp. as prey for lipid acquisition prior to overwintering (Heintz et al. 2013). We also observed a large increase in abundance of the copepod *E. longipedata*, a little-studied copepod that may be a significant portion of juvenile pink salmon *Oncorhynchus gorbuscha* diets at times (Armstrong et al. 2005). It remains to be seen whether this copepod species will become more prevalent in Bering Sea waters in the future.

The increase in smaller-sized zooplankton during Warm 2 may offer a glimpse into the future Bering Sea, which is projected to continue to warm (Hermann et al. 2019). Size decrease is thought to be a global response in ectotherms to increasing temperature (Gardner et al. 2011). A reduction in zooplankton size has been observed in mesocosms (Garzke et al. 2015) and in long-term time-series of zooplankton (Rice et al. 2015) in response to warmer tempera-



tures. Both the body size of individuals (Miller et al. 1992) and overall mean body size of the zooplankton community (Chiba et al. 2015) have been shown to decline during warm periods. A community of smaller-sized zooplankton grazing on smaller-sized phytoplankton would decrease trophic transfer efficiency (greater number of links in food web) and reduce the delivery of ungrazed phytoplankton to the benthos (Lovvorn et al. 2016). The result would be more carbon cycling in the pelagic, favoring the accumulation of small copepods. Smaller-bodied zooplankton are lower in energy density and are often lipid-poor relative to larger zooplankton (Siddon et al. 2013, Gorokhova 2019). The increase in smaller-sized zooplankton taxa may also accompany a decline in the lipid-rich *Calanus* spp., though it has been suggested that the increasing number of smaller zooplankton (with some lipid storage) may compensate for the loss of lipid-rich species of *Calanus* (Renaud et al. 2018). However, we must caution against overinterpretation of our results, as the reduced ice cover in 2017–2018 may be a single, infrequent event. Nevertheless, if the reduction of ice cover across the Arctic continues as predicted by some models (Peng et al. 2020), it will result in widespread ecosystem change.

## 5. CONCLUSIONS

We compared the NBS zooplankton community across 1 cold and 2 warm periods. Similar to prior studies, we found that the cold and warm periods differed in zooplankton community response; however, the community response was particularly striking during the 2017/2018 low ice event. The NBS zooplankton community had a weaker response to Warm 1, suggesting that the persistence of ice cover in this region, even during warm periods, appears to provide some buffer to broad-scale zooplankton community change. However, the low ice extent experienced in 2017/2018 resulted in positive abundance anomalies for small copepods, particularly on the middle shelf, which coincided with a decline in *Calanus* spp. abundance. This response is similar to what has been observed in the southeastern Bering Sea and suggests that the NBS zooplankton community will respond similarly if a particular minimum ice cover extent and retreat threshold is reached. It also suggests an increased role of smaller-bodied zooplankton in cycling of energy in the NBS if the open-water period increases substantially as ice retreats. The result would be a transition from tight benthic–pelagic coupling to a decoupled pelagic ecosystem.

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