



Physical and biological drivers of zooplankton communities in the Chukchi Sea

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Abstract

The physical environments of high-latitude systems are rapidly changing. For example, the Chukchi Sea has experienced increased water temperatures, advection from the Bering Sea, declines in sea-ice concentration, earlier spring ice retreat, and delayed fall ice formation. This physical restructuring is expected to impact ecosystem structure and function. In this study, a series of bio-oceanographic research surveys were conducted in the summers of 2010, 2011, and 2012 to characterize the physical environment and to examine the influence of physical forcing on zooplankton community distribution and abundance. Results revealed yearly advection from the Bering Sea influenced zooplankton community structure, but this influence became less apparent in the northeastern Chukchi due to changes in current speeds and patterns. Decreased advection and later ice retreat in colder years resulted in zooplankton communities that exhibited more diversity, had higher abundances of the lipid-rich copepod *Calanus glacialis*, and were less closely related to water masses advected from the south. These findings suggest more localized processes are influencing zooplankton community structure in the Chukchi Sea. Increased inflow of water into the Chukchi is predicted with increased warming in the Arctic and changes in food-web structure and function are likely to result.

Keywords Zooplankton · Chukchi Sea · Advection · Sea-ice · Climate change

Introduction

In recent years, warm conditions and sea-ice minimums have been record-breaking in the Arctic; 2012 was a record sea-ice summer minimum, and more recently, 2016 was a record low in winter ice extent (nsidc.org; Perovich et al. 2013). This intensified warming in the Arctic exceeds global temperature rise, defined as Arctic amplification, and is driven by feedbacks associated with temperature, water vapor, cloud cover, and surface albedo (Serreze and Berry 2011; Pithan and Mauritsen 2014). Arctic warming and the decline in annual and multi-year sea-ice have had major impacts on marine mammals and birds through habitat loss and

changes in food availability (Bromaghin et al. 2015; Divoky et al. 2015; Laidre et al. 2015). Climate models predict that the entire Arctic will be ice-free in the summer beginning between 2040 and 2060 (Overland and Wang 2013). Relative to the entire Arctic, the Chukchi Sea has had significant reductions in sea-ice thickness and extent, as well as an earlier seasonal melt season (~ 10 days per decade), resulting in conditions that have already impacted the region (Grebmeier et al. 2006a, b) and will likely result in further disruption of biological processes and/or an ecosystem regime shift (IPCC 2013a, b; Serreze et al. 2016).

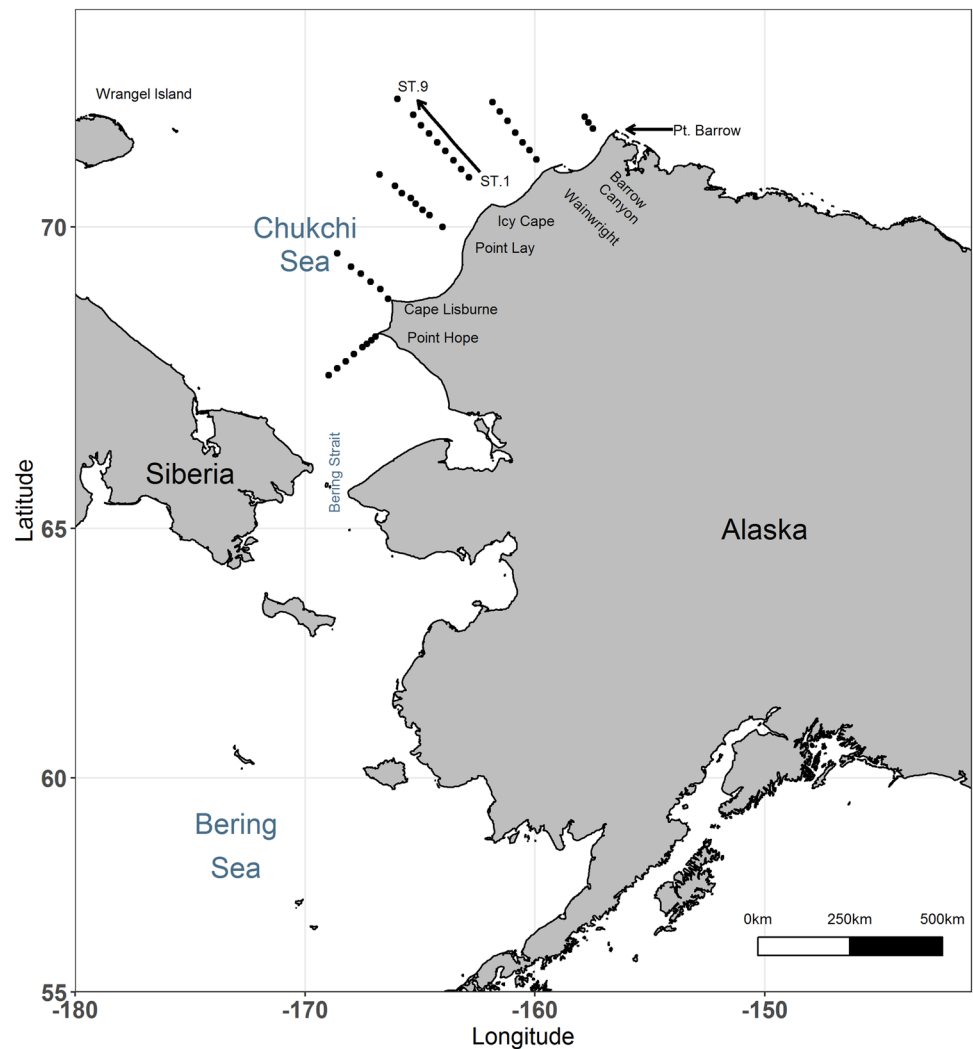
The Chukchi Sea is a marginal and mostly shallow (< 50 m) sea of the Arctic that is situated between Siberia and Alaska and extends from the Bering Strait in the south to the Chukchi shelf break in the north, and from Wrangel Island in the west to Pt. Barrow in the east (Fig. 1). The deep (> 250 m) Barrow Canyon extends 200 km long by 50 km wide and cuts through the northeastern-most section of the Chukchi Sea. The Chukchi Sea is considered a transition region between the north Pacific and the Arctic where the advection of warm, nutrient-rich water, as well as primary and secondary producers sourced from the Bering Sea, are

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Fig. 1 Map of study the area with station locations represented by black dots. Each transect is defined by its location: Barrow Canyon, Wainwright, Icy Cape, Point Lay, Cape Lisburne, Point Hope. Stations are numbered lowest to highest, inshore to offshore (black arrow)



mixed over the shelf (Grebmeier 2012). The main water masses that impact the Alaska-U.S. Chukchi Sea through the Bering Strait include the Bering Sea shelf water (BSW) and Alaska coastal water (ACW) which contribute about 1/3rd of the freshwater entering the Arctic Ocean (Aagaard and Carmack 1989; Serreze et al. 2006; Weingartner et al. 2013). Other water masses of importance are Anadyr water and Arctic winter water. Recently, a 50% increase in water volume transport was reported through the Bering Strait to the Chukchi Sea over the time period of 2001–2014, resulting in a substantial increase in freshwater within the Chukchi Sea and heat flux that is a potential trigger for Arctic sea-ice melt and retreat (Woodgate et al. 2010, 2015; Woodgate 2018). In addition to ice melt, the increased transport decreases the residence time of water and plankton over the shelf, potentially altering the physical and biological environment of the region for several months (Woodgate et al. 2015; Woodgate 2018).

Zooplankton distributions and taxonomic composition can be indicators of climate change, particularly in rapidly

changing ecosystems, because few species are commercially exploited and their short life cycles facilitate rapid responses to temperature changes that manifest as expansion or contraction of geographic distribution (Hays et al. 2005; Richardson 2008). Moreover, zooplankton populations and communities are sensitive to changes at a wide range of spatial (kilometers) and temporal scales (days to several years) (Haury et al. 1978; Daly and Smith 1993; Prairie et al. 2012) and have been previously used as indicators of large-scale climate variability (e.g. Pacific Decadal Oscillation, North Atlantic Oscillation) (Keister et al. 2011; Beaugrand et al. 2015).

Across the world's oceans, zooplankton communities are influenced by regional (large-scale: advection, upwelling), meso-scale (eddies, convergence/divergence), and local scale factors (stratification, light, species interactions), but polar zooplankton communities are uniquely influenced by additional features as well. Sea ice, inclusive of ice edges, melting, timing and extent of ice retreat, influences community composition, seasonality and timing of production,

diel vertical migration, and trophic interactions. Recent studies in the Chukchi Sea (Hopcroft et al. 2010; Eisner et al. 2013; Questel et al. 2013; Ershova et al. 2015a, b; Pinchuk and Eisner 2017) have found that during ice-free periods, zooplankton communities are vulnerable to influence by differently sourced water masses that flow into polar regions from southern latitudes. Water masses from the Bering Sea dominate over the shelf such that there is little contribution from Arctic species and these are typically confined to the northeastern Chukchi shelf.

To better understand the responses of Arctic zooplankton community dynamics to changes in advective transport, warming, and the timing and extent of sea ice coverage, we examined zooplankton communities in the U.S. Arctic (Chukchi Sea) over three successive years (2010, 2011, and 2012). These years represented a wide range of temperatures, transport patterns and volume through the Bering Strait, as well as spatial and interannual differences in the extent of sea-ice and the timing of ice retreat. In this study, we asked whether or not zooplankton abundance patterns would differ during years that had different sea-ice extents and rates of advection through Bering Strait. A strong relationship between hydrography and zooplankton community structure would suggest that observed changes in the region are primarily driven by regional physical oceanographic processes. Conversely, a lack of relationship introduces the possibility that localized biological processes may be major driver of zooplankton species assemblages that would need to be further explored. This study represents an investigation of the relationship between Chukchi Sea zooplankton communities and advection from the Bering Sea, current speeds across the region, as well as the timing of ice melt.

Methods

Measurements

As a component of the Chukchi Acoustic, Oceanographic, and Zooplankton (CHAOZ) project, a series of multi-disciplinary, oceanographic (physics, chemistry, plankton and marine mammal) research surveys in the U.S. Chukchi Sea were conducted in the August of 2010, 2011, and 2012. Broadly, data collected during the surveys included water column properties, and zooplankton abundance and species composition. Samples were collected along six transect lines (Fig. 1). The Barrow Canyon transect was not sampled in 2010. Oceanographic moorings and satellite-tracked drifters were deployed to obtain continuous measurements of ocean currents.

We quantified broad scale patterns in sea-ice concentration and sea surface temperature (SST) using satellite data. Sea-ice concentration (percentage of ocean covered

by sea-ice) and extent data were obtained after the surveys from a Scanning Multichannel Microwave Radiometer (SMMR) on the Nimbus-7 satellite and from the Special Sensor Microwave/Imager (SSM/I) sensors on the Defense Meteorological Satellite Program (Comiso 1999). Optimum Interpolation Sea National Oceanic and Atmospheric Administration (NOAA) High Resolution SST data were acquired from NOAA in Boulder, Colorado, USA (<https://www.esrl.noaa.gov/psd/>; Reynolds et al. 2007).

Satellite-tracked oceanographic drifters were deployed during mid-summer to mid-fall across several locations in the southern Chukchi Sea, with a drogue depth of 25–30 m (Stabeno et al. 2018). Drifter data were averaged across 2010–2015 to determine the most common current pathways, and current speed. Bering Strait and Icy Cape volume transport data were collected from moored Acoustic Doppler Current Profiler (ADCP) measurements (Woodgate et al. 2015; Stabeno et al. 2018; Woodgate 2018). Data were not available at the Icy Cape transect prior to September 2010.

Hydrographic data, including temperature, salinity, and chlorophyll fluorescence, were collected from the surface to 3–5 m from the bottom using a Sea-Bird Electronics SBE 911plus conductivity-temperature-depth (CTD) profiler and a WET Labs WETStar fluorometer. Water samples were collected using Niskin bottles for discrete depth sampling and to calibrate the instruments on the CTD. Salinity calibration samples were analyzed using a laboratory salinometer. Chlorophyll samples were filtered through Osmonics glass fiber filters (nominal pore size 0.7- μm), and stored in the dark at -80°C for several months before extracting in 90% acetone for 24 h. Fluorometric determination of chlorophyll concentration using the acidification method (Lorenzen 1966) was made with a Turner Designs TD700 laboratory fluorometer calibrated with pure chlorophyll-*a* (Chl-*a*). Sea-Bird Data Processing software was used for quality control, processing, and to bin continuous CTD profiler data in 1-m depth bins. To account for stratification and different water masses while separating the water column into surface and bottom groups, near-surface temperature and salinity were averaged from 5–10 m depths; near-bottom values were averaged from the maximum-recorded depth to 5 m above that depth.

There was a mechanical failure of the CTD deck unit in 2010, thus hydrographic samples could not be completed using the SBE 911plus CTD. Since data could no longer be logged real-time, a Sea-Bird SeaCAT (SBE19plus) with internal memory was lowered to a maximum depth of 25 m. Niskin bottles were used for discrete depth (1, 15 and 25-m) samples. Bottom temperatures and salinities were sampled using the SeaCAT attached to the Tucker Sled described below.

Zooplankton samples were collected, mostly during daylight hours, using a multiple-opening and closing 1-m²

Tucker Sled. The Tucker Sled was equipped with 1-m², 333- μ m mesh nets for larger taxa and a 20-cm diameter (0.04 m²), 150- μ m net for smaller taxa. One larger net sampled while the sled was towed at a speed of 1.5–2.0 knots for several minutes to sample the entire water column from the bottom to the surface (20 m min⁻¹ wire retrieval rate). The 20-cm net was mounted inside the mouth of the larger water column net. A calibrated General Oceanics mechanical flowmeter was mounted along the centerline of each 1-m² net to measure volume filtered. It should be noted that this setup is not ideal in cases where clogging in the 20-cm net occurs, thus the possibility of inaccurate volume filtered readings still exist in this study. Samples that appeared questionable (e.g. low flowmeter readings, large jellyfish in the net) were not used in the analysis. A SeaBird SeaCAT (SBE 19plus) or SeaBird FastCAT (SBE 49) was attached to the top of the frame immediately behind the net for real-time depth associated with zooplankton collections. Net samples were preserved with sodium borate-buffered 5% formalin. Copepods were identified to the lowest taxonomic level and stage at the Polish Sorting and Identification Center in Szczecin, Poland, followed by verification at the Alaska Fisheries Science Center in Seattle, Washington, USA. Briefly, plankton samples are processed by splitting the samples to obtain at least 150 individuals. Generally, smaller species of copepods including their stages of copepodites were enumerated from the 150- μ m mesh net (e.g. *Acartia* spp. copepodite (C) 1–5, *Oithona* spp., *Pseudocalanus* spp.); larger zooplankton species such as euphausiids, amphipods, and copepods including copepodite stages (e.g. *Calanus glacialis*, *Calanus hyperboreus*) were enumerated from the 333- μ m mesh net. In contrast to 2011 and 2012 where nets only sampled the upcast, a single net remained open during the entire downcast and upcast in 2010. Thus, we compared oblique samples in 2010 to the oblique, upcast-only, samples in 2011 and 2012.

Analyses

Spatial distribution plots of several ecologically important species were explored, including: *C. glacialis*, *Neocalanus* spp., and euphausiids (consisting mostly *Thysanoessa raschii* and *Thysanoessa inermis*). Both *C. glacialis* (a lipid-rich copepod) and euphausiids serve as an important food source for upper trophic levels in the region (Lowry et al. 2004; Berline et al. 2008; Moore et al. 2010). *Neocalanus* spp. are more southern associated species, and accordingly may indicate a response to temperature conditions or advection of Pacific water (Miller 1988; Springer et al. 1989; Hunt and Harrison 1990; Hunt 1997; Pinchuk and Eisner 2017).

Nonparametric, multivariate analyses were conducted using PRIMER-E (Clarke and Warwick 2001) and R (version 3.3.1)

vegan package (version 2.5-2; Oksanen et al. 2018). Developmental stages of each species that were counted separately were pooled together under one species category. Only species that had at least 2% occurrence across stations and years were included in the analyses. The zooplankton abundances were 4th root transformed so that the less abundant taxa were more equally represented in the analyses (Clarke and Warwick 2001). Bray–Curtis similarity matrices were used to conduct a hierarchical, group averaged, cluster analysis for each individual year, and to produce a non-metric multidimensional scaling (NMDS) plot to visualize and to compare to similarities in species assemblages from the cluster analysis. A similarity percentage analysis (SIMPER) was used to determine the percent contribution of each species to the observed similarity between samples.

Canonical analysis of principal coordinates (CAP) is a constrained ordination that produces principal coordinate values scores based on the chosen constraint (Anderson and Willis 2003). Cluster analysis groups were used as a constraint on the ordination to produce the principal canonical coordinate scores for each sampling station. To determine the influence of water column properties on species assemblages, the first two principal coordinate scores were used, along with temperature and salinity values, to calculate correlation values for each group. Using the above method, correlation coefficients were also calculated for the Icy Cape, Wainwright, and Barrow Canyon transects (Fig. 1) as well as inner stations (e.g. station 1) vs. outer stations (e.g. station 9) within those same transects. Inner and outer station designations were based on distance from shore as well as the general/direction location of the dominant currents (i.e. inner ACW; outer BSW; Danielson et al. 2017; Stabeno et al. 2018) in this region. Inner stations were located > 7 km and < 130 km from land. Outer stations were located > 130 km and < 233 km from land.

Development times (κ) of *C. glacialis* stages were estimated from the equation (Kiørboe and Hirst 2008):

$$\kappa = \ln \left(\frac{CW}{EW} \right) / \hat{g}$$

where CW and EW are the copepod stage and egg carbon masses (μ g-carbon; Liu and Hopcroft 2007) respectively, and \hat{g} is constant specific growth rate calculated from a global model (Hirst and Lampitt 1998). Development times were then compared to drifter data in order to explore the possibility of recent reproduction in the Chukchi Sea.

Results

Physical properties

The concentration of ice in the study area during early August was low in 2010 and 2011 in comparison to 2012

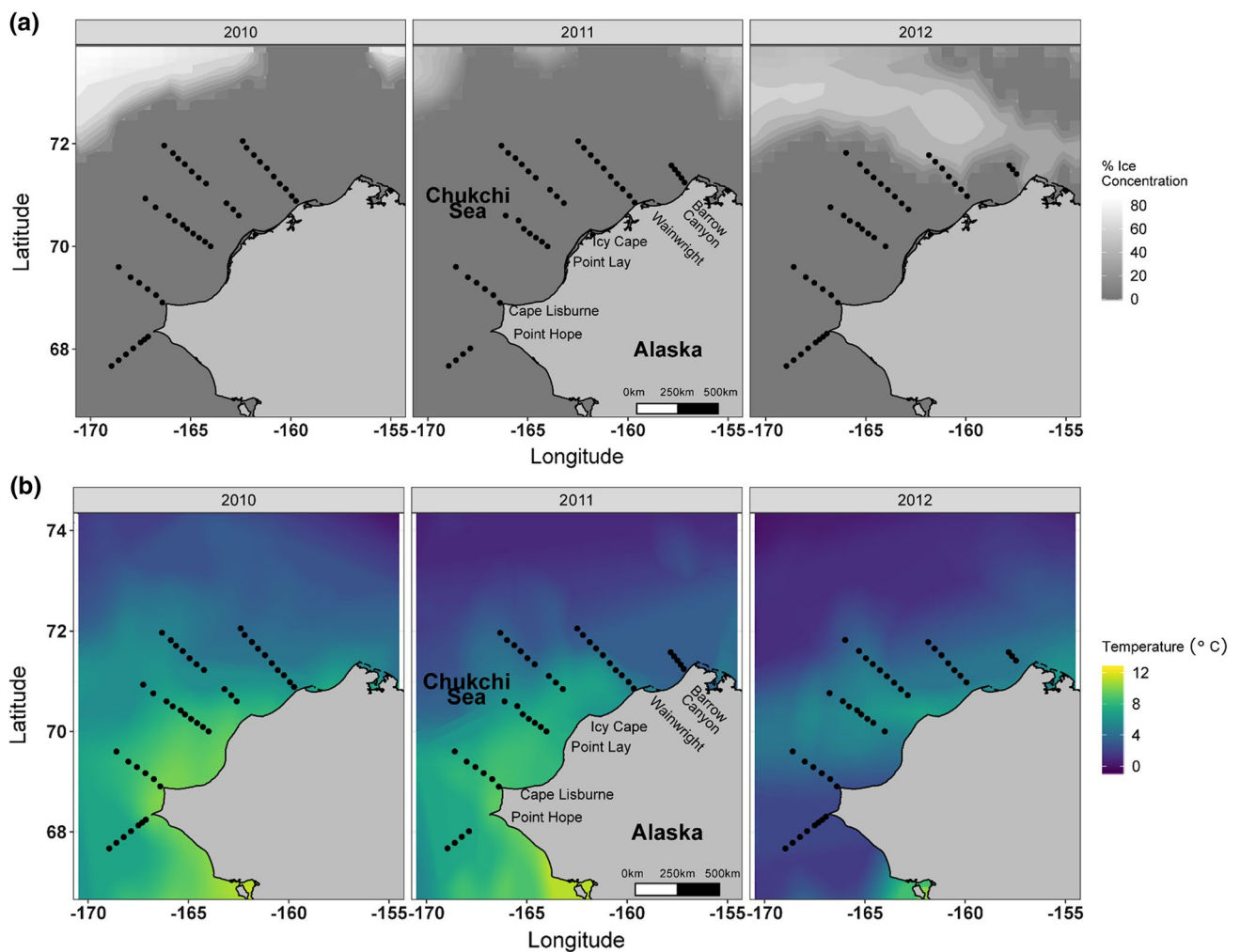


Fig. 2 Early August (just prior to the surveys) percent ice concentration (a) and satellite (b) observed sea surface temperature (°C) in colored contours. Circles indicate station locations

Table 1 Date at which ice concentration was less than 10% in two regions where stations were occupied

	Point Hope to Cape Lisburne	Wainwright to Point Barrow
2010	26-Jun	2-Aug
2011	3-Jun	15-Jul
2012	22-Jun	19-Aug

when ice was present within the study region near Barrow Canyon and Wainwright (Fig. 2a). Ice concentration of < 10% occurred the earliest in 2011 from the Point Hope/Cape Lisburne (June 3rd; Table 1) and Wainwright/Point Barrow regions (July 15th). Both 2010 and 2012 had similar melting rates (June 26th vs. June 22th, respectively) within the Point Hope/Cape Lisburne region, however ice melted 17 days later in the Wainwright/Point Barrow

region in 2012 (August 19th vs. August 2nd, respectively). Sea surface temperature (SST) patterns were similar in 2010 and 2011, with 8–10 °C water farther inshore from the Bering Strait up to Icy Cape and cooler temperatures (0–5 °C) offshore and northeast off Wainwright and Barrow Canyon (Fig. 2b). In 2012, SST was colder from Bering Strait through Point Hope, with a 6–8 °C warm tongue off Icy Cape extending eastward and cooler temperatures (0–2 °C) offshore of Wainwright and Barrow Canyon. Average SSTs over the region in 2010, 2011, and 2012 were 5.1 °C, 3.9 °C, and 2.4 °C, respectively. In 2011, mean integrated chl-*a* increased from the southwest to northeast direction from Point Hope to Barrow Canyon (Table 2). In 2012, mean integrated chl-*a* was highest near Point Hope and Wainwright transects. Both 2011 and 2012 had relatively high concentrations of chl-*a* in the Bering Strait.

Table 2 Integrated chl-*a* (mg m⁻²) ± *S.D* and (*n*)

	Bering Strait	Point Hope	Cape Lisburne	Point Lay	Icy Cape	Wainwright	Barrow Canyon
2011	108.35 ± 45.76 (2)	17.99 ± 13.41 (9)	27.33 ± 0.23 (6)	28.07 ± 9.06 (10)	41.32 ± 14.90 (19)	36.76 ± 11.39 (9)	38.47 ± 16.27(5)
2012	41.06 ± 9.78 (2)	48.21 ± 39.40 (7)	26.90 ± 5.84 (7)	20.06 ± 4.73 (9)	30.16 ± 8.09 (11)	48.10 ± 24.21 (9)	30.83 ± 12.34(5)



Fig. 3 Drifter transit time and direction averaged across 2010–2015. Dashed lines indicate more rare directions taken. Red boxes and numbers indicate each region and associated mean number of days to pass through. Numbers in parentheses indicate the number of drifters that were used to calculate the mean. (Adapted from Stabeno et al. 2018)

Satellite-tracked drifters (Fig. 3) measured dominant current patterns and speeds. The dominant current direction started north from Bering Strait, then split into three separate currents just prior to Point Hope, one headed northwest and the remaining two inner and outer currents headed northeast across the sampling area (indicative of the ACW and outer BSW currents respectively; Danielson et al. 2017). Eventually, both currents tended towards a single path just prior to Icy Cape and then continued northeast past Barrow Canyon. Only two drifters were found to split northward prior to Icy Cape and then switched direction towards Barrow Canyon (see Stabeno et al. 2018 for trajectories). The highest mean velocity ($\sim 25 \text{ cm s}^{-1}$) was along region five (Fig. 3; Stabeno et al. 2018). The lowest mean velocity measured from the drifters (5 cm s^{-1}) was in the region three, followed by region four and region two (10 and 11 cm s^{-1} respectively).

Mean velocities measured from ADCP's along Icy Cape decreased from inshore (7.3 cm s^{-1}) to offshore (3.9 cm s^{-1}) in the eastward direction. The lowest measured velocities ($\sim 2.4 \text{ cm s}^{-1}$) were in the eastward direction and occurred further offshore along the Wainwright transect. Bering Strait mean monthly volume transport several months prior to the survey was generally greater in 2010 and 2011, than in 2012 (Fig. 4; Woodgate et al. 2015; Woodgate 2018). The greatest monthly transport was May, June, and August of 2010 and 2011. July of 2011 also had greater transport compared to 2012. Volume transport across Icy Cape was similar in 2011 and 2012.

Zooplankton abundance and distribution

Mean copepod abundances were similar in 2010 and 2011, while 2012 exhibited marked differences in abundance among copepod taxa (Table 3). Most notable were the greater numbers of the larger copepod species, *C. glacialis*, in 2012 compared to 2010 and 2011. *Pseudocalanus* spp. abundance was lower and more variable in 2012 compared to previous years; however, the confidence intervals suggest that the means are not significantly different. *C. hyperboreus*, a much larger, Arctic basin copepod, was present in 2011 and 2012. The highest mean abundances of juvenile and adult euphausiids occurred during 2012 and furcilia were the most abundant euphausiid stage, with similar values across the 3 years. Abundances of the calyptopis stage were greatest in 2010. The mean abundance of gammarid amphipods was highest during 2012, while the highest abundance of hyperiid amphipods was in 2011. The separation of pteropods with and without shells was only determined in 2012, in which the shelled organism dominated, but abundances were greatest in 2010. Larvacean and cnidarian abundances were lower in 2012 than in the previous two years. In 2012, there were lower abundances of *Metridia pacifica/lucens*. Abundances of *Neocalanus* spp. were consistent across all years. *Eucalanus bungii* were most abundant in 2010.

In addition to general zooplankton abundances, several trophically important species showed differential spatial patterns among years (Figs. 5, 6). *C. glacialis* were most abundant along the Icy Cape, Wainwright, and Barrow transect lines across all three years, *C. glacialis* was more abundant across the entire sampling area in 2012, specifically across the Wainwright and Barrow Canyon transects (Fig. 5a). *Neocalanus* spp. was relatively rare, but most abundant in 2010,

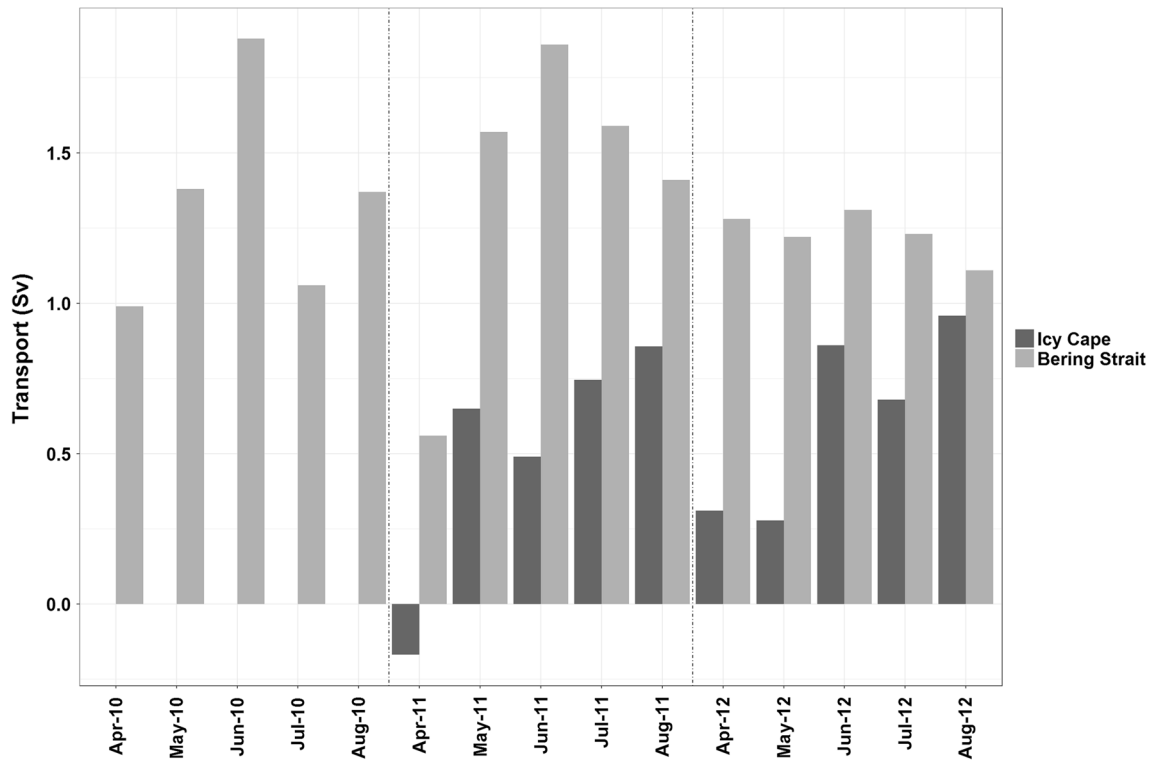


Fig. 4 Monthly volume transport Sverdrups (Sv) through the Bering Strait (light) and Icy Cape (dark) for 2010–2012. Dotted lines indicate the separation of years

Table 3 Yearly mean abundance (No. m⁻³) ± 95% CI for dominant taxa

Taxon	2010 (n = 45)	2011 (n = 42)	2012 (n = 43)
Euphausiids			
Calytopis stage	0.68 ± 0.37	0.03 ± 0.04	0.05 ± 0.09
Furcilia stage	9.94 ± 8.72	6.72 ± 5.52	19.51 ± 22.06
Juvenile and adult stages	0.18 ± 0.11	0.21 ± 0.21	0.68 ± 0.30
Amphipods			
Hyperidea	0.14 ± 0.23	2.65 ± 3.39	2.02 ± 2.84
Gammiridea	0.14 ± 0.23	0.00 ± 0.00	2.02 ± 2.42
Copepods			
<i>Pseudocalanus</i> spp.	934.79 ± 137.86	1049.82 ± 191.72	786.07 ± 299.71
<i>Oithona</i> spp.	689.67 ± 147.27	524.24 ± 156.73	700.58 ± 209.03
<i>Acartia</i> spp.	26.51 ± 6.83	32.45 ± 19.55	130.95 ± 81.03
<i>Calanus glacialis</i>	84.51 ± 32.18	76.00 ± 21.15	315.65 ± 129.23
<i>Calanus hyperboreus</i>	0.00 ± 0.00	0.27 ± 0.22	0.04 ± 0.07
<i>Eucalanus bungii</i>	31.46 ± 15.22	10.77 ± 18.19	5.61 ± 3.69
<i>Metridia pacifica/lucens</i>	26.38 ± 22.95	10.85 ± 8.38	7.07 ± 7.02
<i>Neocalanus cristatus</i>	0.07 ± 0.05	0.18 ± 0.11	0.97 ± 0.74
<i>Neocalanus</i> spp.	1.67 ± 0.81	0.77 ± 0.38	2.62 ± 1.19
Other taxa			
Cnidaria	59.14 ± 20.68	74.97 ± 27.71	0.97 ± 0.72
Larvacea	426.59 ± 163.09	773.57 ± 256.47	48.33 ± 23.36
Pteropods (shelled and non-shelled)	108.95 ± 52.96	10.51 ± 5.33	5.52 ± 4.37
Chaetognatha	42.07 ± 8.85	47.88 ± 10.37	28.96 ± 7.44
Cirripedia cypris	130.55 ± 36.75	135.94 ± 73.08	107.52 ± 53.22

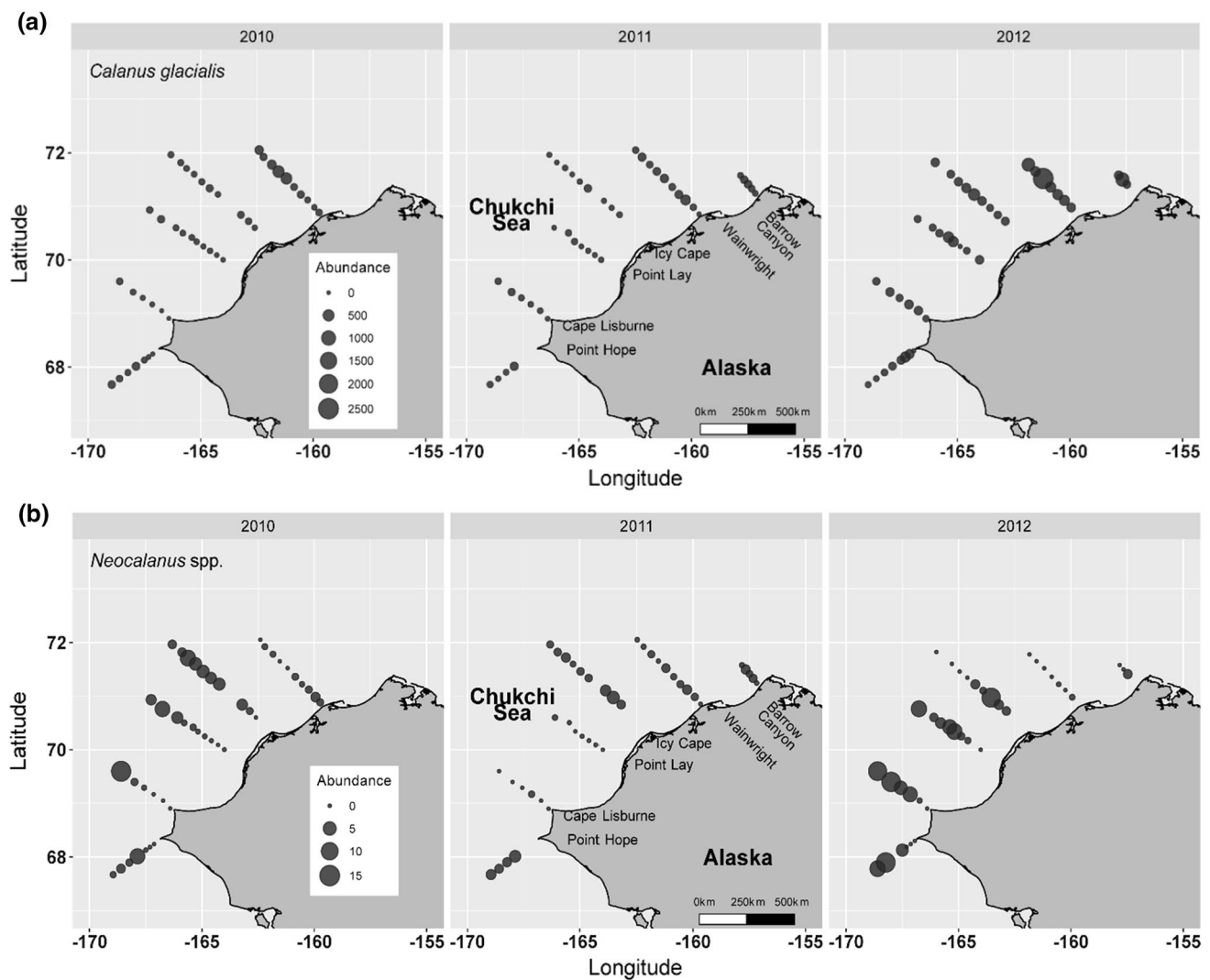


Fig. 5 Spatial distributions of abundance (No. m⁻³) for **(a)** *Calanus glacialis*, and **(b)** *Neocalanus* spp. for 2010–2012

particularly at the outer stations (Fig. 5b). Lowest abundances of *Neocalanus* spp. occurred in 2011, with a spatial separation of the highest abundances along Point Hope, Icy Cape, and Wainwright transects. In 2012, *Neocalanus* spp. were more abundant from Point Hope to the first five stations along the Icy Cape transect. Euphausiid adult and juveniles had similar spatial distributions in 2010 and 2011 (Fig. 6a). In 2012, abundances of euphausiid adult and juveniles were higher across the entire region compared to the previous two years. In 2010, euphausiid furcilia abundance was higher than the latter two years, particularly along the southwestern, Point Hope transect (Fig. 6b). The remaining transects in 2010 had similar abundances of furcilia. Furcilia abundances in 2011 were similar across all transects except for the last three northern-most stations of Icy Cape. Abundances of furcilia in 2012 were the highest among years and relatively confined along the Point Hope, Cape Lisburne, and Point

Lay transects. Euphausiid calyptopis were highest in 2010 among the Icy Cape and Wainwright transects as well as a single station within the Point Hope transect (Fig. 6c). There was no clear spatial pattern for euphausiid calyptopis in 2011 and 2012 because of low abundances of individuals and presence at very few stations.

Zooplankton community assemblages

Cluster analyses (73% similarity) and NMDS mostly agreed in combining three major assemblages in 2010, with a stress value of 0.18 (Fig. 7a.). Group 1 stations in 2010 were located across the every transect line from Bering Strait to Wainwright. Specifically, Group 1 was represented by the first few stations along the Bering Strait, Point Hope, Wainwright and Icy Cape transect lines, while consisting of almost the entire Cape Lisburne and Point lay transect

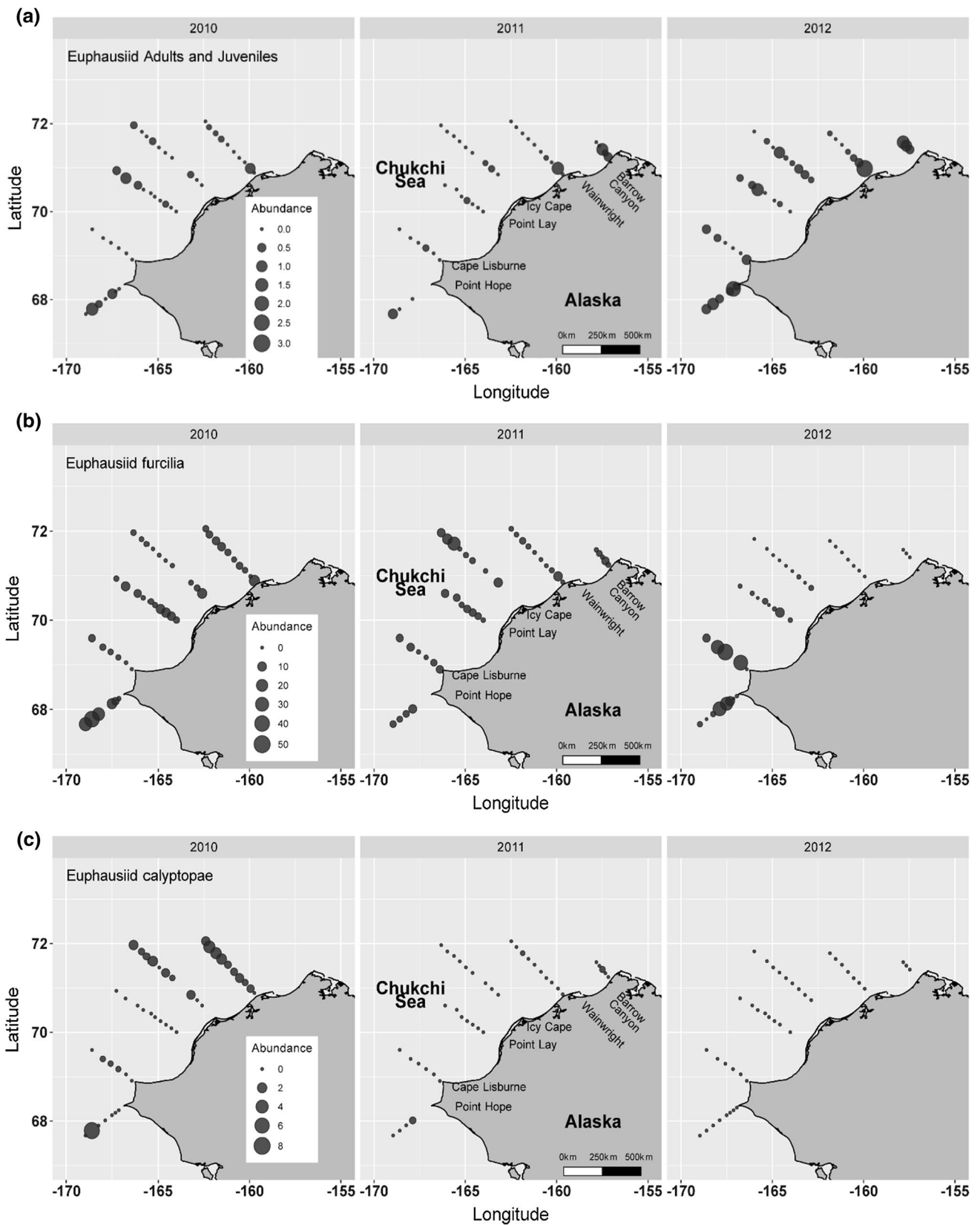


Fig. 6 Spatial distributions of abundance (No. m^{-3}) for euphausiid (a) adults and juveniles (b) furcilia, and (c) calyptopae for 2010–2012. Note the scales differ for the three life stages

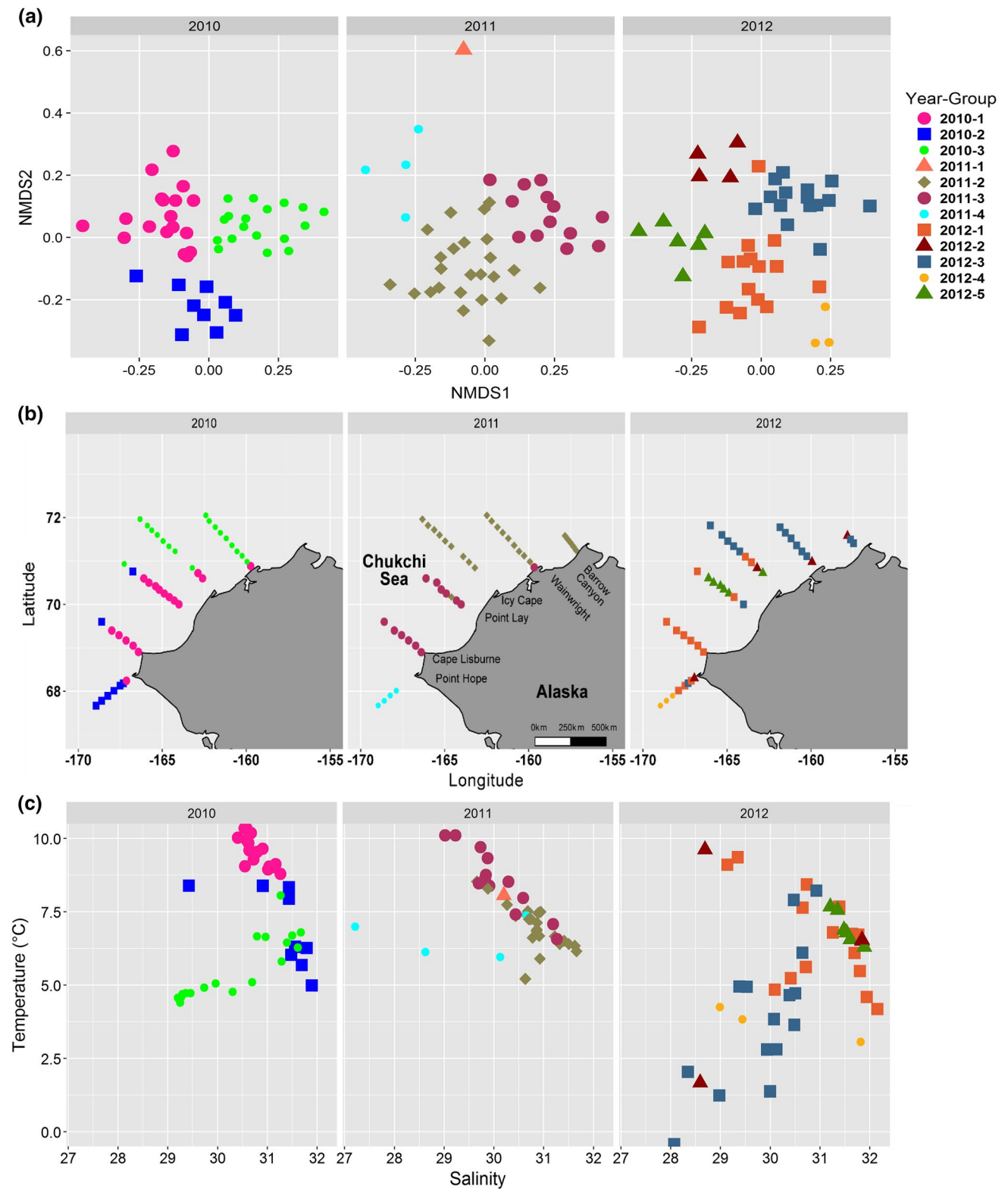


Fig. 7 Non-metric multidimensional scaling plot (a) with groups from the cluster analysis for each separate year. Each group from the cluster analysis is represented by different colors and shapes. Maps

(b) for each year with the cluster analysis station grouping marked as colored symbols. Station cluster groups (symbol) plotted (c) in relation to surface (5–10 m) temperature °C and salinity for 2010–2012

Table 4 Percent contribution of each taxa to cluster analysis groups

Zooplankton	2010			2011			2012				
	G1	G2	G3	G2	G3	G4	G1	G2	G3	G5	
<i>Oithona</i> spp.	16.1	12.0	10.5	11.5	18.4	7.0	15.9	21.5	15.6	27.5	
<i>Pseudocalanus</i> spp.	14.8	13.3	16.2	16.1	17.1	15.9	15.8	18.2	19.8	16.7	
<i>C. glacialis</i>	5.4	7.1	8.3	8.1	7.6	6.7	12.2	14.9	15.4	12.6	
<i>Metridia pacifica/lucens</i>		5.0		1.8		5.8					
Metriididae				2.6							
<i>Eucalanus bungii</i>	5.1	6.4				4.8	3.9				
<i>Acartia</i> spp.	4.4	3.8	6.0	1.8	5.7	3.1	9.8	7.6	9.7	5.5	
<i>Neocalanus</i> spp.				2.3		3.0				4.6	
<i>Neocalanus cristatus</i>										3.1	
Other copepoda	3.9	6.8		4.0		8.4		5.5	4.3	7.4	
Unidentified calanids			4.1								
Euphausiid furcilia		4.2	3.4	3.4	4.0	3.6	5.3			4.2	
<i>Thysanoessa raschii</i>								4.8			
Larvacea	4.9	5.8	14.0	14.4	14.5	8.5	7.5	7.8	7.0		
<i>Cirripedia cypris</i>	6.0	7.4	9.4	7.6		8.3	7.0		7.0	3.3	
Cnidaria	8.2	5.3	4.6	8.2	4.4					2.9	
Ctenophora				1.8							
Chaetognatha	6.0	6.1	7.1	7.2	8.7	4.1	7.3	13.1	7.5	10.7	
Thecosomata	7.6		4.5		4.7						
Cladocera	5.0										
<i>Cirripedia nauplius</i>	4.4	8.2	2.4		6.8	12.6			6.8		
Total %	91.8	91.4	90.5	90.8	91.9	91.8	90.2	92.2	96.2	91.1	

lines except the last 1 to 2 stations, respectively. The top five zooplankton contributors (in order) from Group 1 included *Oithona* spp., *Pseudocalanus* spp., Cnidaria, Thecosomata, *Cirripedia cypris* (Table 4). Group 2 consisted of the second Bering Strait station, most of the Pt. Hope transect and a single outer station along the Cape Lisburne and Point Lay transects (Fig. 7b). The major contributors from Group 2 included *Pseudocalanus* spp., *Oithona* spp., *Cirripedia nauplius* and *cypris*, and *C. glacialis*. Group 3 represented most of the Wainwright and Icy Cape transects except for the first one or two stations respectively. The top contributors from Group 3 included *Pseudocalanus* spp., Larvacea, *Oithona* spp., *Cirripedia cypris*, and *C. glacialis*.

Similar to 2010, the 2011 zooplankton data showed three major groupings at 72% similarity. NMDS results, with a stress value of 0.16, generally agreed with the cluster analysis' three major groups (Fig. 7a). Spatially, the transects and stations allocated within groups in 2011 was similar to 2010 (Fig. 7b). Specifically, Group 2 consisted of the entire Wainwright (except for the first station), Icy Cape, and Barrow (not sampled in 2010) transects. The top five zooplankton contributors the Group 2 assemblage included *Pseudocalanus* spp., Larvacea, *Oithona* spp., Cnidaria, and *C. glacialis* (Table 4). Group 3 comprised of the entire Cape Lisburne and Point Lay (except for the third station) transects, as well as the first station along the Wainwright transect. The major

contributors to the Group 3 assemblage included *Oithona* spp., *Pseudocalanus* spp., Larvacea, Chaetognatha, and *C. glacialis*. The entire Group 4 assemblage consisted of all Point Hope stations. The top contributors from Group 4 included *Pseudocalanus* spp., *Cirripedia nauplius*, Larvacea, other Copepoda, and *Cirripedia cypris*.

Five station groups, with 70% similarity, were identified through cluster analysis in 2012. The NMDS ordination generally reinforced the results from the cluster analysis (Fig. 7a), with stress levels of 0.22 improving to 0.14 when increasing from two to three dimensions. This year showed greater spatial diversity in community assemblages compared to previous years in this study (Fig. 7b). Group 1 assemblage encompassed stations from the Bering Strait through Icy Cape. The Cape Lisburne transect consisted entirely of Group 1 assemblage. Other transects had Group 1 designated among the first one to four stations except the outer-most station of Point Lay. The top five contributors that made up the Group 1 assemblage included *Oithona* spp., *Pseudocalanus* spp., *C. glacialis*, *Acartia* spp., and Larvacea (Table 4). Group 2 zooplankton assemblage contained just four stations, mostly located along the first or second station, scattered across Point Hope, Icy Cape, Wainwright, and Barrow transects. The major contributors from the Group 2 assemblage included *Oithona* spp., *Pseudocalanus* spp., and *C. glacialis*. Chaetognatha, and Larvacea. Group

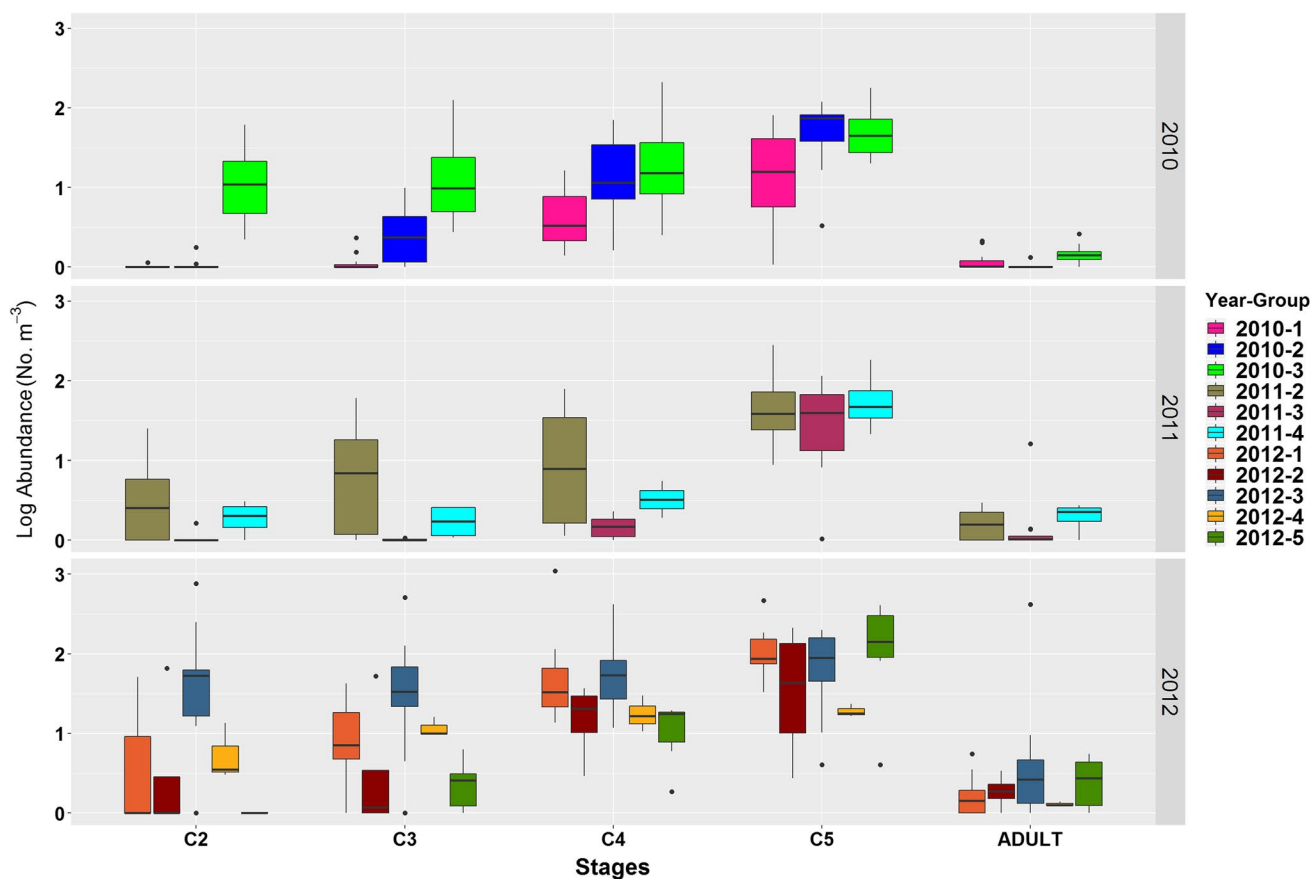


Fig. 8 Box-whisker plot of log abundance (No. m^{-3}) for each stage (C2–C5 in numeric order from least to most developed) of *Calanus glacialis* separated by each cluster analysis grouping

3 assemblage encompassed the last five stations along the Icy Cape transect, and most of the stations along Wainwright and Barrow transects. The highest percentage zooplankton taxa that contributed to Group 3 included *Pseudocalanus* spp., *Oithona* spp., *C. glacialis*, *Acartia* spp., and Chaetognatha. Group 5 consisted of five stations along the center of the Point Lay transect and the 1st station on the Icy Cape transect. The highest percentage zooplankton taxa that contributed to Group 5 included *Oithona* spp., *Pseudocalanus* spp., *C. glacialis*, Chaetognatha, and *Acartia* spp. Note the substantial increase in percent contribution from *C. glacialis* in each group in 2012 compared to previous years.

There was some separation of zooplankton groups when assemblage clusters were plotted in relation to temperature and salinity (Fig. 7c), confirming previous research on the influence of water masses in the Chukchi Sea (e.g. Ershova et al. 2015a). There was less variation in surface temperature and salinity in 2011 than 2010. In 2012, there was much greater variability in temperature and salinity than in the previous two years; however, there was much more overlap in the salinity and temperature signatures among the assemblages identified by the cluster analysis.

Calanus glacialis were found in high abundances across all stages within northeastern-most groups over all 3 years (Fig. 8; Group 3 in 2010; Group 2 in 2011; Group 3 in 2012). Most of the remaining groups in 2010 and 2011 (except for the Point Hope transect in 2011), which contained the majority of the remaining sampling area, did not contain C2 stages. Only one group (Group 5) out of five, which was located in the central portion of the study area, did not contain C2 stages in 2012.

Biological and physical interactions

The strongest correlations between zooplankton assemblages and the physical environment occurred along the transects that were southwest of Icy Cape in all years, with the exception of Group 5 in 2012 (Table 5). Across all years, Icy Cape stations more often correlated with temperature and salinity whereas Wainwright stations did not (Table 6). Additionally in 2010 and 2011, outer stations had the weakest correlations; in 2012, the outer stations correlated with bottom temperature. Inner stations among all years exhibited strong correlations.

Table 5. 2010–2012 Correlation coefficients of surface and bottom temperature (S.T. and B.T respectively) and salinity (S.S. and B.S.) vs. both canonical analysis values (C1 and C2) of each cluster groups

Year	2010			2011			2012				
	1	2	3	2	3	4	1	2	3	4	5
S.T. C1	-0.08	-0.53	-0.38	0.13	0.53	0.91*	0.39	-0.23	0.33	-0.97*	0.52
S.T. C2	0.71***	0.68*	0.12	0.27	0.03	0.21	0.07	-0.22	-0.61*	0.07	-0.23
S.S. C1	0.38	0.33	-0.22	-0.41*	0.46	0.05	-0.23	0.92*	0.20	0.90	-0.54
S.S. C2	0.53*	-0.45	0.32	-0.11	0.12	-0.99***	-0.50*	-0.03	-0.50	0.13	0.32
B.T. C1	-0.35	-0.21	-0.57*	0.45*	0.59*	0.37	0.39	-0.24	0.20	0.08	0.28
B.T. C2	0.67**	0.32	-0.30	-0.39	0.08	0.29	-0.04	-0.17	-0.60*	-0.97*	-0.55
B.S. C1	0.35	0.19	0.44	-0.38	-0.65*	-0.25	-0.49	0.68	0.21	0.35	-0.26
B.S. C2	-0.53*	-0.43	-0.03	0.34	-0.08	0.26	-0.13	0.15	0.55*	0.78	0.59

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 6. 2010–2012 Correlation coefficients of surface and bottom (S.T. and B.T respectively) and salinity (S.S. and B.S.) versus both canonical analysis values (C1 and C2) of each cluster groups

Year	Station	Icy Cape	Wainwright	Inner stations	Outer stations
2010	S.T. C1	-0.31	0.30	-0.80*	0.31
	S.T. C2	-0.72*	0.52	-0.04	0.31
	S.S. C1	0.30	0.31	-0.72*	0.26
	S.S. C2	-0.54	0.57	0.15	0.45
	B.T.C1	-0.66	-0.04	-0.91**	-0.15
	B.T.C2	-0.69*	0.51	-0.25	-0.45
	B.S.C1	0.36	0.08	0.75*	0.30
	B.S.C2	0.47	-0.61	-0.10	0.28
2011	S.T. C1	0.75*	-0.41	0.09	-0.36
	S.T. C2	0.70*	0.60	0.11	0.38
	S.S. C1	-0.74*	-0.33	-0.33	-0.47
	S.S. C2	-0.64*	-0.05	0.003	0.06
	B.T.C1	0.56	0.28	0.80***	-0.38
	B.T.C2	0.09	0.04	-0.13	-0.42
	B.S.C1	-0.52	-0.11	-0.78**	0.53
	B.S.C2	-0.09	-0.20	0.09	0.42
2012	S.T. C1	0.92*	0.60	0.66	0.08
	S.T. C2	1.00***	0.64	-0.50	-0.61
	S.S. C1	-0.75	0.15	0.74*	-0.55
	S.S. C2	-0.57	0.22	-0.47	-0.26
	B.T.C1	0.56	0.23	0.44	0.21
	B.T.C2	0.61	0.27	-0.59	-0.79*
	B.S.C1	-0.12	-0.43	-0.78*	0.20
	B.S.C2	-0.89*	-0.57	0.45	0.53

Inner stations were located > 7 km and < 130 km from land

Outer stations were located > 130 km and < 233 km from land. Inner and outer station designations were determined from inner and outer current patterns (see Fig. 3 and Stabeno et al. 2018)

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 7 Amount of days at different temperatures for *Calanus glacialis* stages to develop from eggs

Stage	12 °C	8 °C	2 °C	-1.5 °C
C2	8.38	9.28	10.82	11.83
C3	15.05	16.67	19.43	21.25
C4	31.57	34.97	40.77	44.58
C5	76.12	84.31	98.29	107.48
Adult	77.93	86.32	100.63	110.04

We calculated development times of *C. glacialis* based on temperatures between 12 and -1.5 °C. These development times were then compared to transport times (from drifter speeds) and dominant current directions to investigate spawning locations. *C. glacialis* egg to C2 stages have approximate development times of 8 to 12 days at temperatures between 12 and -1.5 °C respectively (Table 7); C3 stages were 15 to 21 days; C4 were 31 to 44 days; C5 stages were 76 to 107 days; Adult stages were 78 to 110 days. Average transport times were approximately 100 days from Bering Strait to the Beaufort slope over the summer months (Fig. 3; Stabeno et al. 2018). Transport from Bering Strait to Icy Cape would take 90 days; Bering Strait to Point Lay would take 65 days; Bering Strait to Cape Lisburne would take approximately 32 days; Bering Strait to Point Hope would take 16 days. Development times of C2, C3, C4 stages suggests that most that were caught northeast of Point Lay were likely spawned in the Chukchi Sea.

Discussion

Similar to recent studies in the Chukchi Sea (Hopcroft et al. 2010; Eisner et al. 2013; Questel et al. 2013; Ershova et al. 2015a, b; Pinchuk and Eisner 2017), we found that

zooplankton communities are influenced by currents that flow into polar regions from southern latitudes that contain Bering Sea fauna, with little contribution from Arctic species. However, this study found evidence suggesting that yearly advection from the Bering Sea and resulting influence on zooplankton communities is limited when current patterns and speeds allow for a decrease in off-shelf transport along the northeastern Chukchi Sea (east of Icy Cape). In addition, although we did not find clear differences in correlations between zooplankton groups and temperature/salinity in warm vs. cold years, we did find that zooplankton communities were slightly decoupled from water masses, exhibited more diversity, and were more influenced by *C. glacialis* in the colder year. All of these findings suggest more localized processes are influencing zooplankton community structure.

In 2012, we observed lower temperatures, later ice retreat, and reduced transport of water through Bering Strait, which fostered conditions that favored cold water-associated zooplankton assemblages across most of the shelf. Conversely, 2010 and 2011 had warmer conditions, earlier ice retreat in late summer, and increased transport into the Chukchi Sea; conditions that favored advection of warmer water taxa northward from the Bering Sea across most of the Chukchi shelf. These physical differences manifested as differences in zooplankton communities, with 2012 being somewhat different from those in 2010 and 2011, years with similar physical environments and zooplankton communities.

Changes in spatial distributions of several different taxa were highlighted between warm and cold years. *Neocalanus* spp., a high quality, lipid-rich prey for fish (Heintz et al. 2013) are found in high concentrations on the outer Bering Sea shelf, slope, basin, and in the Anadyr Current (a lower salinity current that flows northward through the Bering Strait along the coast of Siberia) (Springer et al. 1989; Hunt and Harrison 1990; Hunt 1997), and therefore likely reflect advection of outer BSW into the Arctic (Pinchuk and Eisner 2017). Consequently, the spatial distributions of *Neocalanus* spp. in 2010 and 2011, years that had greater volume transport through the Bering Strait, were further offshore. When transport volume was lower, in 2012, *Neocalanus* spp. were more prevalent inshore and were found less frequently in the northeastern Chukchi Sea than in previous years, although the mean abundance was just as high. This pattern corroborates the observation that assemblages are influenced by warm and cold climate shifts within the region, and increased northward transport of water resulting in increased advection of Pacific species into the Chukchi Sea during SST “warm states” (Pinchuk and Eisner 2017).

Euphausiid adults and juveniles were present in higher concentrations with a widespread distribution in 2012

compared to other years, which may be due to colder temperatures (Ressler et al. 2014) and the utilization of the spring ice algae bloom during colder years (Lessard et al. 2010). Euphausiid furcilia were generally present throughout all stations in 2010 and 2011, but were only present at southwestern transects at inshore stations in 2012. This change in spatial distribution between years suggests that furcilia may be impacted by the strength of volume transport and advection (greater in 2010 and 2011) through the Bering Strait, or possibly nearby spawning because of warmer water temperatures and preferred habitat.

The presence of euphausiid calyptopae in 2010 supports the hypothesis that spawning occurred within the Chukchi that year. The calytopis stage is an early larval stage that has development times from 10–41 days depending on temperature (standardized to 5 °C; Tegllhus et al. 2015). Thus, the presence of calyptopae in 2010 along the Icy Cape and Wainwright transects suggests that they were likely spawned in the Chukchi Sea considering the average transport times to reach those locations from the Bering Sea (77 and 85 days, respectively). Successful reproduction may be due to a northward habitat shift associated with temperature increases (Timofeev 2000; Buchholz et al. 2010; Huenerlage and Buchholz 2015; Dalpadado et al. 2016). We did not see evidence of spawning of euphausiids in 2011 or 2012, which may have been the result of unfavorable conditions such as timing of the ice associated algae bloom.

Euphausiids have been historically considered expatriate species that are unable to successfully reproduce in the Arctic (Dalpadado and Skjoldal 1996). In the Chukchi Sea, it was hypothesized that a significant fraction of euphausiids, commonly found in the stomachs of bowhead whales (*Balaena mysticetus*) near Utqiagvik, Alaska, were the result of a conveyor belt of individuals from the northern Bering Sea through the Central Channel and Herald Valleys and then concentrated by local physical processes (Berline et al. 2008; Ashjian et al. 2010). The abundance of adult and juvenile euphausiids sampled in the Central Channel during this study were very low and did not support the conveyor belt hypothesis. However, lower abundances in the Tucker trawl may be attributed to net avoidance (Sameoto et al. 1993; Wiebe et al. 2013).

Calanus glacialis was abundant in nearly every transect across all years, however the highest abundances occurred within the Icy Cape, Wainwright, and Barrow Canyon regions. In addition, all life stages from early C2 to adult stages were found in the highest abundance in this region, suggesting that *C. glacialis* may be reproducing. *Calanus glacialis* are often associated with ice algae that are a source of long-chain omega-3 fatty acids, and a high-quality dietary requirement that contributes to successful reproduction for females (Søreide et al. 2010; Durbin and Casas 2013). We found evidence of increasing concentrations of chl-*a* from

southwest to northeast within the study area, with the highest concentrations along the Wainwright transect. Thus, the healthy population and high abundance of *C. glacialis* east of Icy Cape may be a result of recent ice cover and associated algae, as well as a post-ice retreat phytoplankton bloom that likely helped to sustain the population (Søreide et al. 2010; Coupel et al. 2012). In contrast to these northeastern regions, assemblages associated with warmer water temperatures corresponding to a strong influence from the BSW and ACW did not include the full range of life stages of *C. glacialis*, instead having more abundant C4 and C5 stages. Accordingly, we hypothesize that these older individuals were derived from a population spawning in the Bering Sea and transported northward into the region.

Cluster analyses revealed a mixed community pattern in 2012, while 2010 and 2011 had three spatially similar clusters. A similar northeastern cluster emerged over all three years, suggesting that the influence of transport through Bering Strait on plankton assemblages and dynamics declines with distance from the Bering Strait. Overall, these results align with previous studies showing substantial differences in zooplankton communities between years with different physical characteristics (Questel et al. 2013; Ershova et al. 2015a; Pinchuk and Eisner 2017). Zooplankton community assemblages were correlated with broader physical properties; however, in addition to the local physical environment, there were also underlying temporal and spatial patterns in zooplankton communities that deserve mention. In 2010 and 2011, cluster analysis stations overlapped with surface temperature and salinity suggesting that zooplankton assemblage structure was likely influenced by physical conditions. In contrast, there was no obvious relationship between surface temperature, salinity, and assemblage groupings during 2012. We looked further into these relationships through correlating CAP values from the cluster groups with temperature and salinities. We found that 2010 and 2011 the strength of the correlations decreased moving from southwest to northeast, which also coincides with a decrease in the strength of transport/current speeds (offshore and outside the ACW). There were significant correlations in 2012, however there was not a clear pattern of correlation from the southwest to northeast; instead the study area was split by the lowest correlations in the central (Point Lay) transect. Similarly, Pinchuk and Eisner (2017) showed significant correlations of species biomass with physical properties over the entire study area for 2012 and 2013 (Bering Strait to Pt. Barrow) with an Arctic species group present in the northeastern portion of their study area. However, this study adds to these findings by showing that the correlations between biological and physical variables fluctuate between years when there is a strong difference in warming, advection and timing of ice melt.

Comparison of development times of *C. glacialis* stages with drifter speeds confirms that C2–C4 stages caught northeast of Point Lay were likely spawned in the Chukchi Sea. These findings support the possibility that northeastern Chukchi Sea may be more influenced by local production as opposed to the dominant influence of advection in other areas. Observations such as recent sea-ice melt, decrease in current speed further offshore, and a higher chl-*a* concentration to support reproduction in the region strengthens the local production argument. Increases in abundances of *C. glacialis* C2 and C3 stages across the entire study area in 2012, a year with more preferential conditions such as the least amount of advection and most recent ice melt, supports this hypothesis further. High chl-*a* in the northeast and southwest regions in the present study reflects historical chl-*a* and benthic production patterns within the region (Point Hope and south, and east of Icy Cape; Grebmeier 2012). This consistent high biomass in the northeastern Chukchi Sea is likely the result of long daylight hours and ice presence through late July that supports ice algae production and a strong post-ice algae bloom. Such increased primary production likely supports and sustains high productivity and reproduction of local zooplankton populations. The important role of ice algae and the advantages of high productivity and food availability around the marginal ice zone for mesozooplankton reproduction is well documented (Daly and Macaulay 1988; Søreide et al. 2010; Durbin and Casas 2013). At times, the ingestion rates of copepods on ice algae can be much higher than predicted by ingestion rate-food concentration relationships (Campbell et al. 2016). Additionally, recent research in the Barents Sea, another Arctic marginal sea zone that is highly influenced by advection, also suggests that local production has a greater yearly (in the past 30 years) influence, than previously suspected, in shaping zooplankton communities (Dalpadado et al. 2012; Skaret et al. 2014; Kvile et al. 2017).

Recent advection of *C. glacialis* from the Beaufort Sea could also be an explanation rather than local production in the northeastern Chukchi Sea. Separate southern (Bering Sea) and northern (Arctic) populations of *C. glacialis* that converge in the Chukchi Sea have been identified in previous work (Nelson et al. 2009; Dunton et al. 2016; Pinchuk and Eisner 2017) with conflicting evidence for geographic boundaries and the degree of mixing in the northeastern Chukchi Sea. Age and distribution studies suggest that the northeastern region primarily contains *C. glacialis* of Arctic origin (Pinchuk and Eisner 2017) in contrast to genomic work that suggests that two *C. glacialis* haplotypes were present in the northeastern region in 2012 and 2013, but that the region was dominated by the southern haplotype (Dunton et al. 2016). The prevalence of the northern *C. glacialis* haplotype and the discrepancy in southern and northern haplotype composition is likely related to episodic transport from

the adjacent eastern slope through upwelling events (Ashjian et al. 2010; Pickart et al. 2013). Evidence of episodic transport in this study was confirmed through the presence of *C. hyperboreus* in 2011 and 2012 along the northeastern Chukchi Sea. Overall, dominant speeds and northeastward directions of currents (Stabeno et al. 2018) rules out consistent seeding of *C. glacialis* from the Beaufort Sea.

Conclusions

Arctic zooplankton communities differed among study years resulting from differences in timing of sea ice retreat and the volume of the Pacific water transported through the Bering Strait into the Arctic. Broad-scale advection and transport were the dominant structuring processes during 2010 and 2011, but to a lesser extent in 2012 that had relatively colder conditions, less advection, and later sea ice retreat. These conditions in 2012 may have permitted local biological processes to exert stronger influence over community dynamics than during the previous two warm years. Finally, the northeastern Chukchi Sea may have exhibited local production in all three study years due to the timing of sea ice melt and reduced current speeds, resulting in ideal conditions such as increased primary production and less transport off the shelf.

The findings of this study are relevant to the potential response of lower trophic communities to climate change and warming, including potential shifts in trophic linkages that may alter Arctic food webs. As the climate warms and sea-ice continues to melt or retreat earlier in the year, potential cascading effects within the northeastern Chukchi Sea include: an increase in open-water primary production (Tremblay et al. 2012; Arrigo and Van Dijken 2015), a decrease in the contribution of ice edge algae to annual primary production, a subsequent increase in zooplankton biomass (Grebmeier 2006a, b; Grebmeier 2012; Moore and Stabeno 2015), and, as shown in this study, a possible decrease in *C. glacialis* due to a lack of local production resulting from insufficient conditions such as decreased ice algae production (Søreide et al. 2010; Durbin and Casas 2013). Benthic biomass may also decrease as the flux of ice algal production to the benthos declines and a higher proportion of the annual production is recycled in the water column by increasing micro- and mesozooplankton biomass (Grebmeier 2006a, b; Grebmeier 2012). In contrast, continued warming and increased advection in the southwestern Chukchi Sea could lead to increased zooplankton biomass (including *C. glacialis*) exported from the Bering Sea to the Arctic (Ershova et al. 2015b; Woodgate et al. 2015; Woodgate 2018).

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Compliance with ethical standards

Conflict of interest The authors declare that there is no conflict of interest in presenting this information.

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