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Advection and in situ processes as drivers of change for the abundance of large zooplankton taxa in the Chukchi Sea

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ABSTRACT

The Chukchi Sea has recently experienced increased water temperatures, increased advection of water from the Bering Sea, declines in sea-ice concentration, and shorter periods of ice coverage. These physical changes are expected to impact trophic food-webs and ecosystem attributes. In this study, a series of research surveys were conducted in the summers of 2011–2015 to characterize the physical environment and its relation to the abundance of large zooplankton. Large zooplankton are key prey for many higher trophic level organisms including seabirds, marine mammals, and fishes. Yearly advection from the Bering Sea influenced the adult large zooplankton abundance, but this influence was less apparent in the earlier development stages. Known development times of stages of zooplankton, along with their location within the study area, suggested that a fraction of the zooplankton standing stock was the result of local production. Decreased advection and later ice retreat resulted in higher abundances of the lipid-rich copepod *Calanus glacialis*. Warmer conditions with increased advection from the Bering Sea resulted in higher abundances of euphausiids. Warming, sea-ice melting, and increases in transport of Bering Sea water and plankton into the Chukchi Sea are ongoing, and changes in food-web structure are likely to result.

1. Introduction

The zooplankton of the Chukchi Sea shelf consist of taxa that are more similar to the Pacific Ocean community than the Arctic Ocean community (Ashjian et al., 2010, 2017; Hopcroft et al., 2010; Eisner et al., 2013; Questel et al., 2013; Pinchuk and Eisner, 2017), a result of the transport of North Pacific water through the Bering Strait into the Arctic. Northward advection through the Bering Strait combines several water masses that results in the transport of relatively warm, nutrient-rich water, as well as primary and secondary producers into the Arctic (Woodgate et al., 2005; Gong and Pickart, 2015; Danielson et al., 2017; Stabeno et al., 2018). Northward advection through the Bering Strait in the summer, along with sea-ice melting and episodic upwelling from the Beaufort Sea on to the shelf and Barrow Canyon, results in a highly productive and complex shelf ecosystem that responds to local, regional and global forcing (e.g. Bond et al., 2018). Adding to the complexity of the Chukchi Sea shelf ecosystem, recent reports have shown dramatic changes in timing and extent of sea-ice coverage, along with considerable increases in sea surface temperatures (National Snow and Ice Data Center, nsidc.org; Timmermans and Ladd, 2019; Perovich et al., 2019).

In summer, the northern Bering and Chukchi seas experience increased day length and melting sea ice, resulting in a phytoplankton bloom. The bulk of the bloom sinks to the bottom due to the shallow depth (<50 m) and relatively low grazing impact on phytoplankton (Campbell et al., 2009), supporting a robust benthic community. Recent studies, however, have shown a temporal decrease in benthic biomass in the northern Bering Sea, suggesting a possible weakening of benthic-pelagic coupling as the ice retreat now occurs earlier in the season (Grebmeier et al., 2006a; Grebmeier et al., 2006b; Grebmeier, 2012). Concurrently, zooplankton biomass in the Chukchi Sea has increased over the past seven decades (Ershova et al., 2015), which can be explained, in part, by increasing temperatures, reduction in sea ice, and an increase in northward water transport through the Bering Strait (Ershova et al., 2015; Woodgate et al., 2015; Woodgate, 2018). These trends suggest a potential ecosystem regime shift is underway in the Pacific Arctic, with consequences for local food webs. These changes emerge from both direct and indirect effects on both the indigenous biota residing in the ecosystem as well as the introduced species. Changes in the timing and type of production within the pelagic and

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benthic communities, will result in changes in benthic-pelagic coupling that have the potential to effect higher trophic levels such as birds, marine mammals, fish, and the people who live in the region.

One specific taxon of interest for our studies were bowhead whales (*Balaena mysticetus*) that forage as they migrate southwestward in the fall through the Utqiagvik (formerly known as Barrow) region from the Beaufort Sea (Moore et al., 2010; Quakenbush et al., 2010; Citta et al., 2012). Studies have reported improvements in bowhead body condition in association with earlier ice retreat and increase in the area of open water (George et al., 2015). The observed improvements in bowhead body condition may be the result of increased prey populations, specifically euphausiids and copepods that dominate the prey in stomachs of bowhead whales harvested near Utqiagvik, Alaska (Lowry et al., 2004; Ashjian et al., 2010; Moore et al., 2010; George et al., 2015). Previous studies suggested that euphausiids are advected along the bottom from the northern Bering Sea into the Chukchi Sea, and subsequently concentrated into dense aggregations through upwelling onto the Beaufort Sea shelf towards Barrow Canyon (Berline et al., 2008; Ashjian et al., 2010). Zooplankton sampling in the Chukchi Sea has generally underestimated populations of euphausiids because estimates were based on collections from small (0.25–0.6 cm diameter) aperture size plankton bongo nets (Hopcroft et al., 2010; Eisner et al., 2013; Questel et al., 2013; Ashjian et al., 2017; Pinchuk and Eisner, 2017) and because the predominantly daytime vertical or oblique sampling failed to target krill layers near the bottom (Coyle and Pinchuk, 2002).

The main objectives of this study were 1) to understand the transport pathways of euphausiids from the Bering Strait to Barrow Canyon, 2) evaluate the abundance of other large planktonic prey for whales in the region, and 3) provide data on the status and trends of Chukchi Sea zooplankton communities. This study builds on other research based on conceptualized modeling to explain the dynamics of late-summer euphausiid populations in this region (Berline et al., 2008; Ashjian et al., 2010) by providing empirical data collected from epibenthic and plankton tows that should more accurately reflect the abundance of euphausiid and other epibenthic taxa. We compared epibenthic and pelagic zooplankton abundances to assess whether they were significantly different and to explore whether epibenthic tows were a more accurate reflection of near-bottom taxa. We hypothesized that advection of zooplankton from the Bering Sea to be the main driver of zooplankton abundance in the region. To test this, we compared zooplankton abundance across years and locations, and calculated krill development times to see if euphausiids captured in this study could have reached that stage after having been advected from the Bering Sea.

2. Methods

2.1. Study area

The Chukchi Sea has a broad, mostly shallow (<50 m) shelf situated between Alaska and Siberia (Fig. 1). Survey transects varied among years, 2011–2015, depending on the scientific focus for the year, available ship time, and ice distribution. Surveys were conducted in the late summer, lasting approximately 30 days (~August 5th – September 5th), except for 2014, which was September 22nd – October 12th. For analysis and description purposes, the study area was divided into ‘Beaufort’, ‘Southwest,’ ‘Central,’ and ‘Northeast’ regions that are established from statistically different oceanographic conditions (Eisner et al., 2013; Randall et al., 2019).

2.2. Physical data

Hydrographic data, including temperature and salinity, were collected using a SBE 911plus and FastCAT SBE 49 systems (SeaBird Electronics). Sea Surface temperatures (SST) were averaged from 5 – 10 m depth. We quantified broad-scale patterns in sea-ice concentration 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’s (https://nsidc.org; Comiso, 1999). Bering Strait volume transport data were acquired from moored Acoustic Doppler Current Profiler (ADCP)

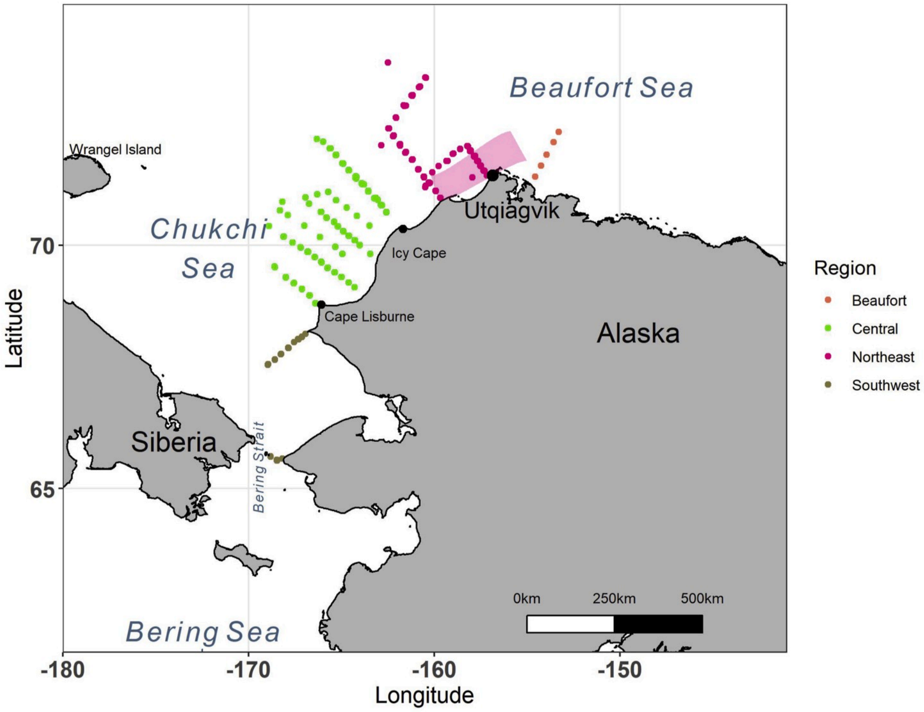


Fig. 1. Study area in the Chukchi Sea. Each region is symbolized by a colored circle. The study area was split up into southwest, central, northeast, and Beaufort regions. The pink shaded region indicates Barrow Canyon.

measurements (Woodgate et al., 2015; Woodgate, 2018). Northeastward water column volume transport, in Sverdrups (Sv), was calculated according to Stabeno et al. (2018) from current data measured at C1, C2, and C3 moorings along the Icy Cape transect. Transport was averaged over 14 and 30 days leading up to the date that the station was sampled.

2.3. Zooplankton net data

Zooplankton were collected primarily during daylight hours using a multiple-opening and closing 1 m^2 Tucker Sled trawl equipped with a FastCAT, and sled-like runners at the bottom so that samples could be taken in close proximity to the bottom. A 505 μm (2013–2015) or a 333 μm (2011–2012) mesh net sampled while the sled was towed at a speed of 1.5–2.0 knots along the bottom for 2 min, then mechanically tripped to close and simultaneously open a second net to sample the entire water column from the bottom to the surface (wire retrieval rate 20 m min^{-1}). For smaller taxa, a 25 cm net with 150 μm mesh was suspended in the larger net that profiled the entire water column. Note that this setup is not ideal in cases where clogging in the 20- cm net occurs, thus the possibility of inaccurate volume filtered readings exist in this study. Samples that appeared questionable (e.g. low flowmeter readings, large jellyfish in the net) were excluded from the analysis. Smaller taxa such as *C. glacialis* and euphausiid furcilia were enumerated in the water column only and not in the epibenthic samples. Both Tucker nets were equipped with a separate calibrated General Oceanics flow meter to estimate volume filtered. Plankton captured by the nets were washed into the cod-ends, sieved through appropriately-sized wire mesh screens and preserved in glass jars with sodium borate-buffered 5% Formalin. Samples were inventoried at the end of the cruise and then sent to the Plankton Sorting and Identification Center in Szczecin, Poland, for processing. Subsampled taxa were enumerated and identified to lowest possible genera and life stage and returned to the Alaska Fisheries Science Center for verification. Ten percent of the returned samples were checked for quality assurance/quality control of species identification and enumeration.

2.4. Zooplankton data analysis

Zooplankton abundance was reported as four general categories in the context of known bowhead whale prey in the region (Lowry et al., 2004; Moore et al., 2010), including: euphausiids (primarily *Thysanoessa raschii*), amphipods (dominant species included *Themisto libellula* and unidentified Gammaridea), mysids (dominant species included *Neomysis rayii* and *Pseudomma truncatum*), and copepods (*Calanus glacialis*). Analysis of variance (ANOVA) was used to examine epibenthic and pelagic variation across years in *T. raschii*, mysid, and amphipod abundance.

Development times of *Thysanoessa* spp. stages were estimated using the formula:

$$R_2 = R_1 * Q_{10}^{\frac{T_2 - T_1}{10}}$$

where R_1 and R_2 are the development rates (d^{-1}) at temperature T_1 and T_2 (°C), respectively (Teglhus et al., 2015). We used the Q_{10} of 2.04 (Pinchuk and Hopcroft, 2006). The calculated temperature (T_2) and development rate (R_2) were normalized to 5 °C and 0.016 d^{-1} (for furcilia; 0.045 d^{-1} for calyptopis), obtained from Teglhus et al. (2015). We chose the measured rates from Teglhus et al. (2015) because of the similar temperature conditions (5–8 °C) and because a mixed population of krill was used as we also have a mixed community. These were also the slowest known development rates for *Thysanoessa* spp. furcilia compared to previous studies (see Table 3 in Teglhus et al., 2015); this prevented an overestimation of development rates of *Thysanoessa* spp. under conditions that may be significantly influenced by availability of food such as phytoplankton (Pinchuk and Hopcroft, 2007). Development times were then compared to satellite-tracked drifter data (Stabeno et al., 2018) to explore the possibility of recent reproduction in the Chukchi Sea.

We used the mgcv package (Wood, 2011) in R (R Core Team, 2019) to fit generalized additive models (GAM) with Gaussian distribution to relate changes in C2 and C5 stages of *C. glacialis, T. raschii* (adult and juvenile), and euphausiid furcilia mean abundance to environmental variables. These two particular stages in each species were chosen to contrast different ages, with C2 representing younger and C5 representing older *C. glacialis*, and furcilia representing younger and adults/juveniles representing older *T. raschii*. For simplicity, we excluded stages C3 and C4 from the analysis as these stage abundances are correlated to the C5 stage (data not shown). We chose to exclusively use epibenthic abundances of *T. raschii* since most of our sampling occurred primarily during the day and when the vast majority of euphausiids would be at or near the bottom. Restricted Maximum Likelihood (REML) method was used as the smoothing parameter estimation. The model selection was done by assessing deviance explained, R^2, and Akaike information criterion (AIC). Residuals were analyzed to ensure there were no obvious deviations from normal distributions, and we examined the response versus. fitted value for patterns. We assessed ten environmental variables for inclusion in the GAMs including: latitude, longitude, bottom temperature, surface temperature, bottom salinity, surface salinity, 14 and 30-day northeastward transport, year, and day of the year (hereinafter referred to as ordinal day).

3. Results

3.1. Environmental conditions

Sea surface temperatures (SST) were warmest in 2011 (mean SST 6.89 ± 1.35 °C) and coldest in 2013 (mean SST 2.64 ± 2.61 °C). Both 2012 (mean SST 5.46 ± 2.41 °C) and 2015 (mean SST 6.13 ± 2.18 °C) had similar warm SSTs towards the central and southwest portion of the survey, and colder SSTs across the northeast portion; however, 2012 was colder in the northeast region (Fig. 2). Sea surface temperatures in 2014 (mean SST 3.09 ± 1.62 °C) were colder over the entire survey area and had substantially less northeast to southwest variability. Randall et al. (2019) using the mean bottom temperatures in the central region, found 2013 (−1.4 °C) to be the coldest year, with 2011–2012 and 2014–2015 having similar warmer bottom temperatures (~2 °C). Similarly, differences between years were evident from initial dates at which ice concentration was less than 10% (Table 1). Sea-ice remained in the northeast region until mid to late August in years 2012–2014, and melted in mid-to late July in 2011 and 2015.

Monthly mean northward transport (Sv) through the Bering Strait tended to peak in the spring and summer (~May–August), with lower transport in the winter (Fig. 3). Higher spring/summer transport occurred in 2011and 2015, peaking at around 1.92 (±0.09) Sv in May and 1.87 (±0.06) Sv in July of 2015 and 1.91 (±0.10) Sv in June of 2011. Spring and summer transport was moderate in 2014 and lower in 2012 and 2013, with mean values as low as 1.14 (±0.18) and 1.18 (±0.14) in August of 2012 and 2013, respectively.

3.2. Zooplankton abundance

Average pelagic amphipod abundances increased from 2011 to 2015; average benthic abundances were generally higher than pelagic abundances but also increased over the same period (Fig. 4a). Overall, 2013, 2011 had the highest and lowest average amphipod abundance respectively. Mysid epibenthic and pelagic abundances were relatively low across all years (Fig. 4b), but epibenthic abundances were relatively higher in all years and there were no increasing or decreasing trends across the years. The euphausiids community consisted of four species of the genus *Thysanoessa*: *T. inermis, T. longipes, T. spinifera, and T. raschii*; the latter, being the most abundant (approximately 70% of total abundance) of the four, was singled out in this study for purposes of

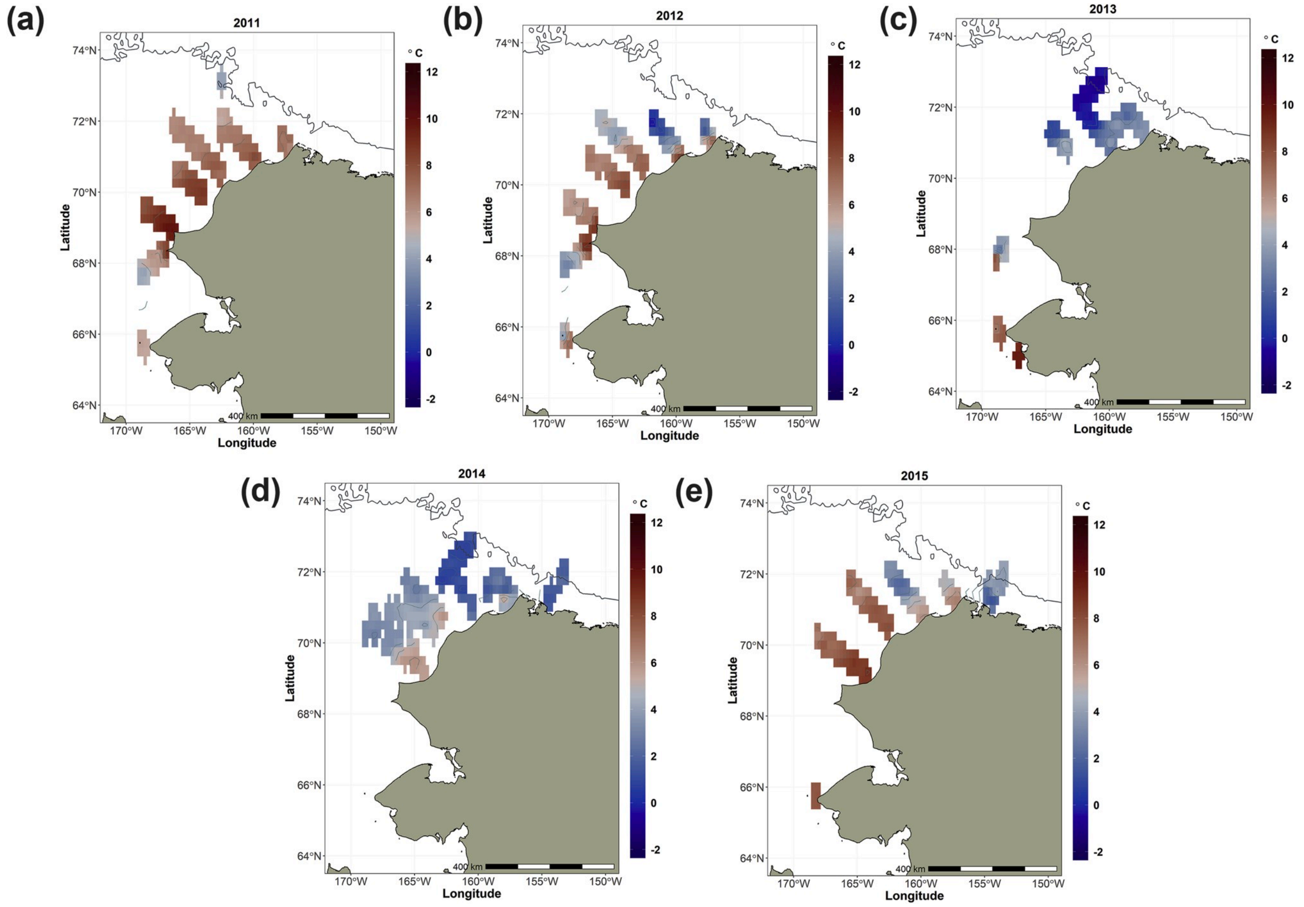


Fig. 2. Sea surface temperature (°C) averaged from 5-10 m for each year.

Table 1

Estimate of the initial date at which ice concentration was less than 10% within the southwest and northeast region of the sampling area.

	Southwest	Northeast
2011	3 June	15 July
2012	22 June	19 August
2013	29 June	31 August
2014	16 June	16 August
2015	14 June	18 July

simplicity. Epibenthic *T. raschii* abundances were lowest in 2013 and highest in 2014 (Fig. 4c). Pelagic *T. raschii* abundance was lowest in 2011 and highest in 2015.

There were no consistent differences in the abundance of *T. raschii*, mysid, and amphipods between the bottom layer and water column when we took into account year and a depth-year interaction in our analyses. ANOVA results did not show significant differences between epibenthic and pelagic *T. raschii* abundances independent of year. However, *T. raschii* abundance did show significant differences between years ($F = 3.20$, $p = 0.01$), independent of depth and depth/year interactions ($F = 5.56$, $p < 0.001$). Similarly, ANOVA results did not show significant differences between epibenthic and pelagic amphipods independent of year ($F = 2.16$, $p = 0.14$). However, amphipod abundances did show significant differences among years independent of depth ($F = 4.467$, $p = 0.001$) and depth/year interactions ($F = 3.294$, $p = 0.01$). ANOVA results showed significant differences between epibenthic and pelagic mysids independent of year ($F = 9.59$, $p = 0.002$), years independent of depth ($F = 4.80$, $p = 0.0008$), and depth/year interactions ($F = 0.84$, $p = 0.50$). Time of day was hypothesized to influence euphausiid

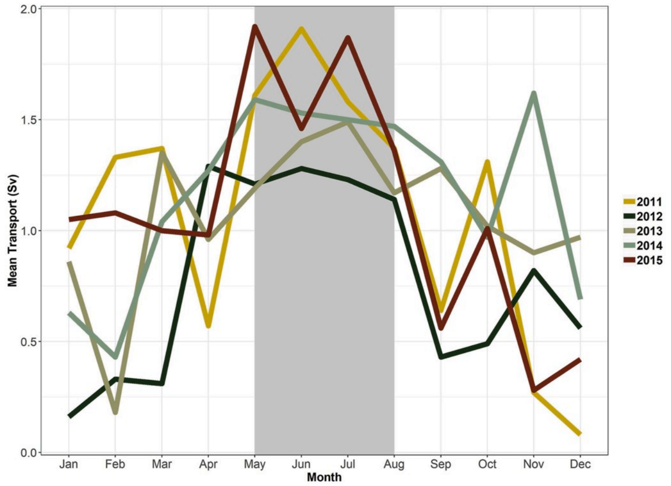


Fig. 3. Mean transport (Sv) of water by month for each year through the Bering Strait. The grey underlay highlights the approximate peak transport months.

abundance, however, ANOVA results did not find differences in day/night sampling abundances of *T. raschii* at the $p < 0.05$ significance level.

A post-hoc Tukey's 'Honest Significant Difference' test of depth-year interactions of *T. raschii*, mysids, and amphipods showed 2014 and 2015 were significantly ($p < 0.05$) different from most previous years (Table 3). Within years 2014 and 2015, *T. raschii* showed significant ($p < 0.05$) differences between epibenthic and pelagic depths. Similarly, both mysids and amphipods showed significant ($p < 0.05$) differences

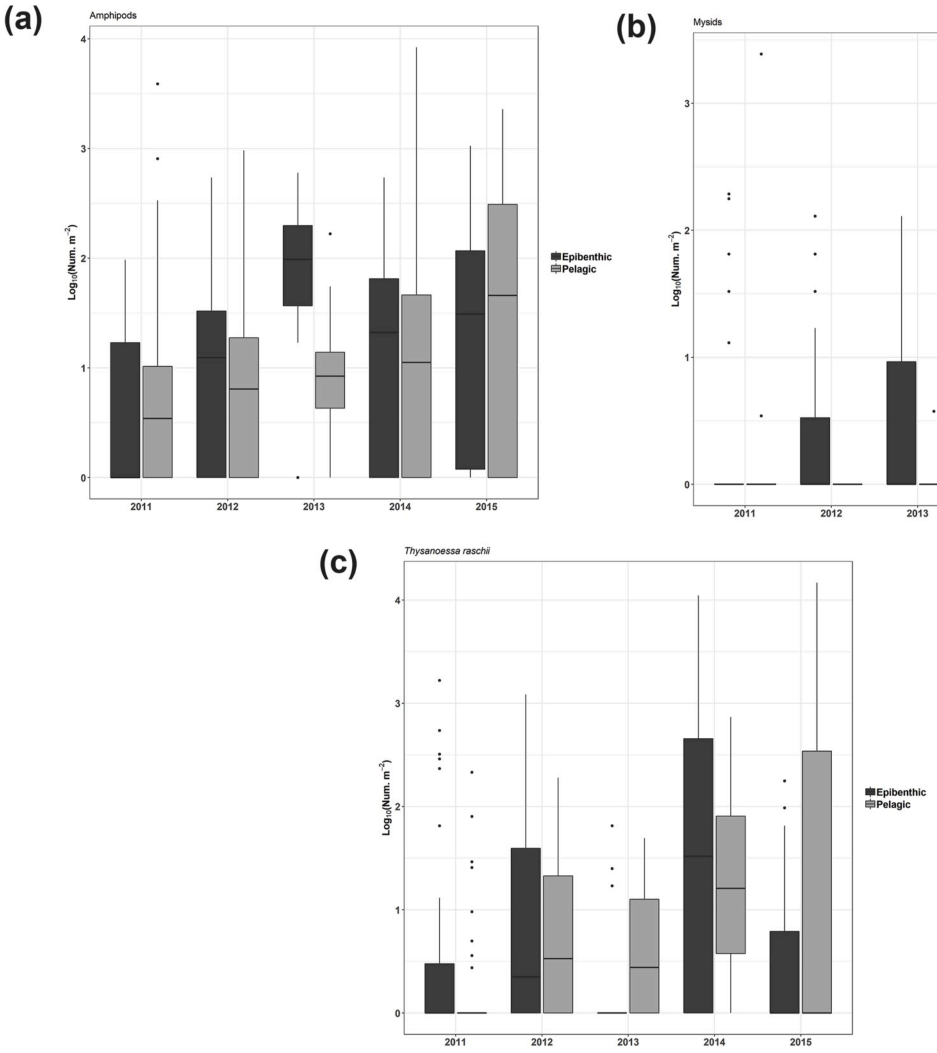


Fig. 4. Yearly epibenthic and pelagic total abundance (Log$_{10}$(Num m^{-2})) for amphipods (a), mysids (b), and *Thysanoessa raschii* (c).

between epibenthic and pelagic depths within 2014. Overall, we cannot independently assess year without noting whether *T. raschii*, mysids, or amphipods samples were caught in the water column or just above the bottom.

There was a lack of spatial differences among years for amphipods, with positive catches across all regions (Fig. 5a). The highest amphipod frequency of occurrence was in 2013, with complete absence in only one station (epibenthic and pelagic combined). Mysid abundance was low for each year across all regions (Fig. 5b); within years, more mysids were captured in the northeast than other regions. Mysid had the highest frequency of occurrence in 2014 with animals captured at stations in 3 of the 4 regions (epibenthic and pelagic combined). A lack of spatial differences of *T. raschii* among years was evident (Fig. 5c), with positive catches appearing across most regions. The highest *T. raschii* frequency of occurrence was in 2014, with presence detected from at least one station in three of the four areas (epibenthic and pelagic combined). There were no obvious trends in presence/absence or abundance as a function of distance from land.

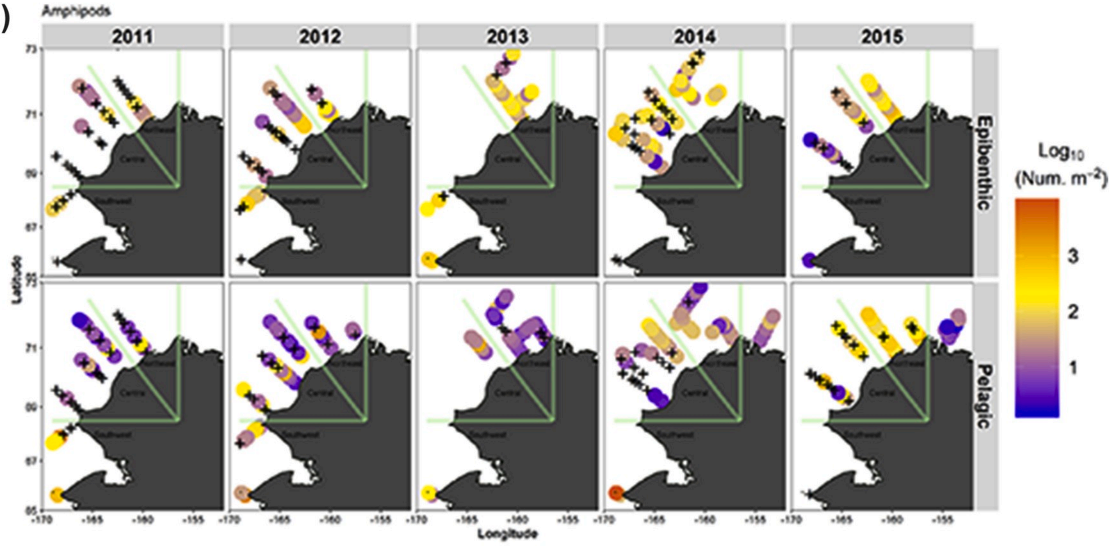
Abundances of *C. glacialis* were lower in warmer years (2011, 2014, and 2015) and higher in colder years (2012, 2013; Fig. 6). *Calanus glacialis* were ubiquitous across all regions, with presence detected at most stations (Fig. 7).

3.3. Early life stages

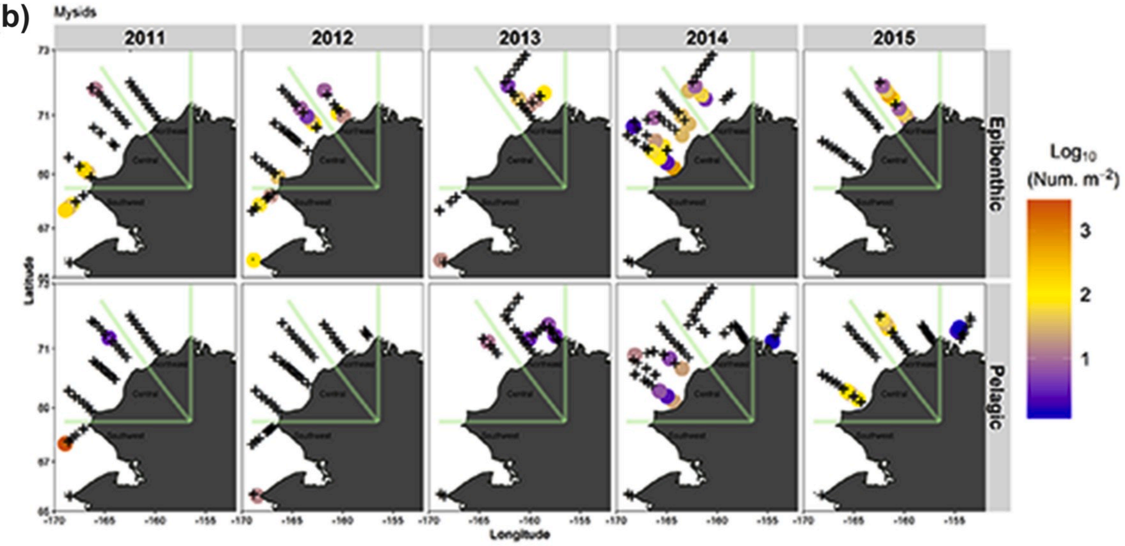
Development time calculations suggest that it takes approximately 51 and 78 days at 8 and 2 °C water temperature, respectively, for *Thysanoessa* spp. stages to develop from eggs to furcilia (Table 2). Note that the furcilia counted in this study were not identified to species. Euphausiid furcilia stages were most abundant in the central and southwestern regions of each year (Fig. 8). Euphausiid furcilia were completely absent from the northeastern region in 2012 and 2013. Both 2011, 2014 had similar abundances along the central and southeastern regions, with 2011 having slightly higher abundances in the northeast. In 2015, highest abundances were located in the central region, with lower abundances extending into the northeast. Euphausiid calyptopis, a developmental stage of much shorter duration (~40 days shorter; Teglhus et al., 2015), were only caught in very low abundances (~1.0 log$_{10}$ (Num. m^{-2})) in 2011 at 3 stations (map not shown) from the northeast and southwest regions.

Spear et al. (2019) estimated *C. glacialis* egg to C2 stages have approximate development times of 8 to 12 days at temperatures ranging between 12 and -1.5 °C respectively. *Calanus glacialis* C2 stages were almost exclusively caught in the northeast region, including Icy Cape (Fig. 9). Higher total abundances appeared in both 2012 (4.92 log$_{10}$ (Num. m^{-2})) and 2013 (5.19 log$_{10}$ (Num. m^{-2})), while the lowest total abundances were in 2011 (3.38 log$_{10}$ (Num. m^{-2})).

(a) Amphipods



(b) Mysids



(c) *Thysanoessa raschii*

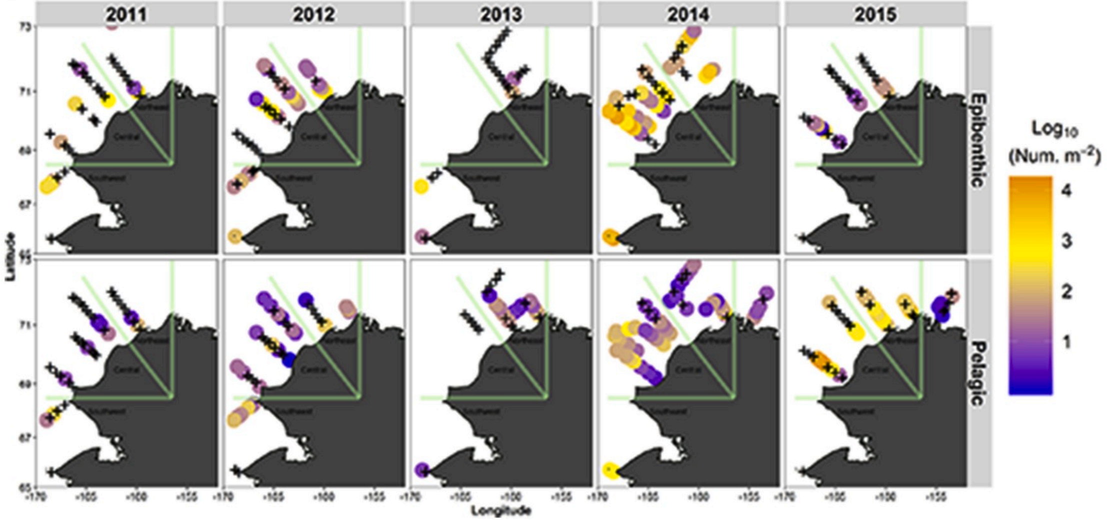


Fig. 5. Yearly maps of epibenthic and pelagic total abundance (Log$_{10}$(Num m^{-2}))for amphipods (a), mysids (b), and *Thysanoessa raschii* (c). The letter "X" denotes tows where the taxon was absent. Note that the scale differs among taxa.

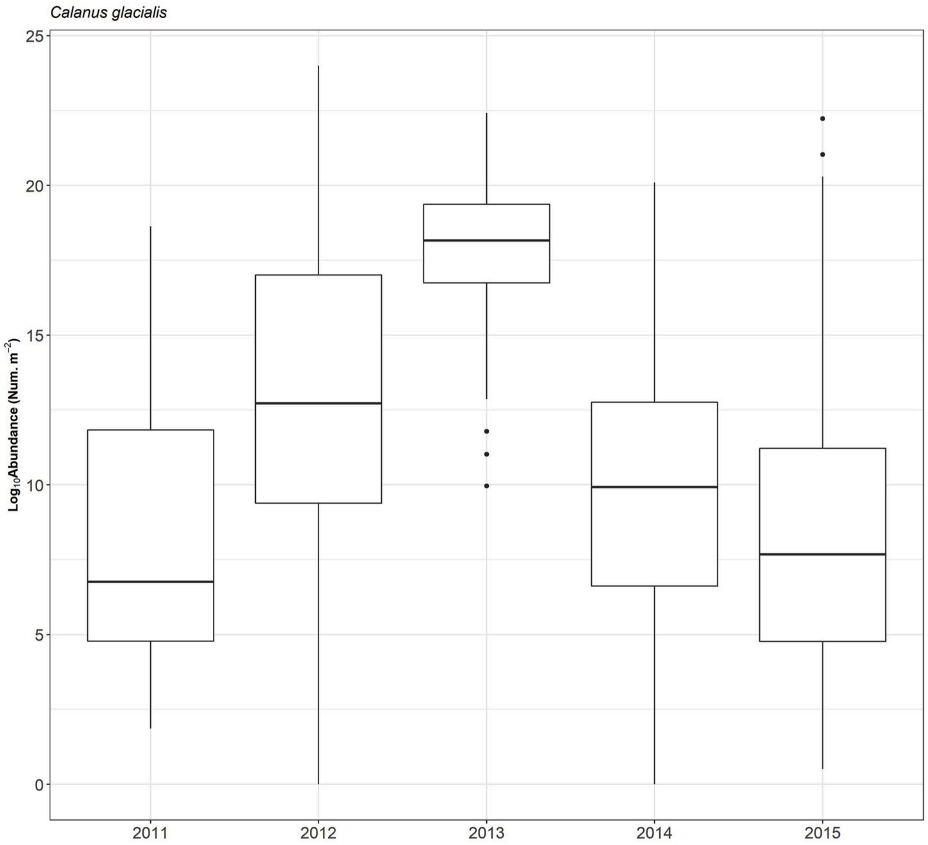


Fig. 6. Yearly pelagic total abundance ($\text{Log}_{10}(\text{Num m}^{-2})$) of *Calanus glacialis*.

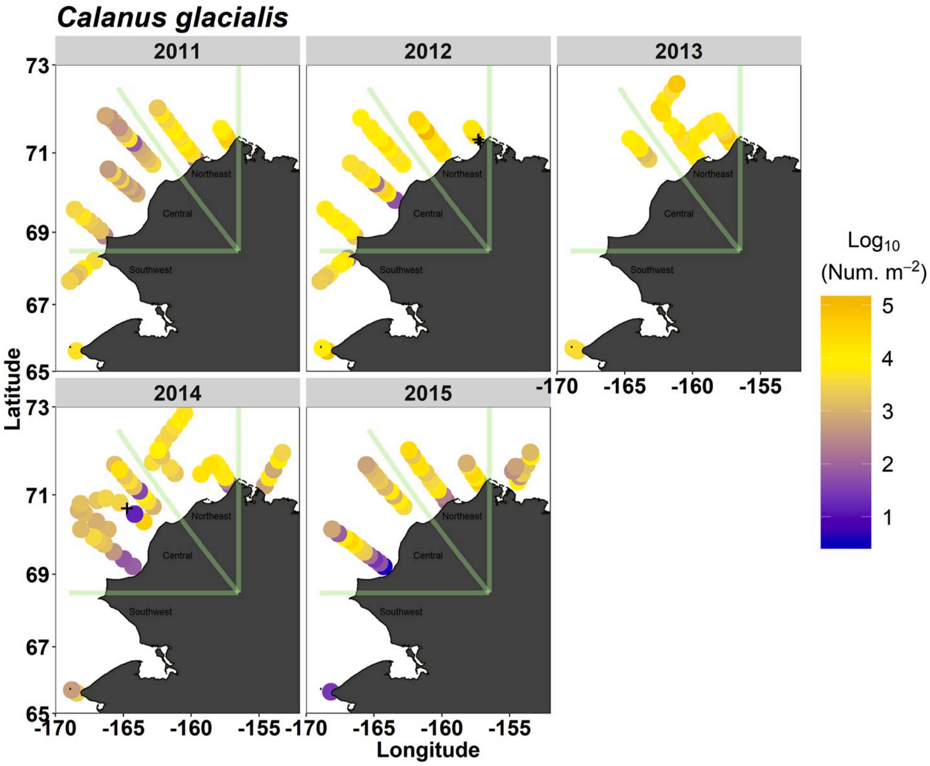


Fig. 7. Yearly maps of pelagic total abundance ($\text{Log}_{10}(\text{Num m}^{-2})$) of *Calanus glacialis*. The letter “X” denotes tows where the taxon was absent.

Table 2
Amount of days at different temperatures for *Thysanoessa* spp. stages to develop from eggs.

Stage	12 °C	8 °C	2 °C	−1.5 °C
Calyptopis	13.4	17.8	27.3	35
Furcilia	38.2	50.9	78	100

3.4. *Relationships between plankton abundance and physical variables*

Bottom temperature, 30-day northeastward transport, longitude, and ordinal day were the most significant variables associated with mean *T. raschii* abundance (Table 4). The model helped explain 42.3% of the deviance with an r^2 of 0.38. Extreme lower and higher bottom temperature conditions were associated with lower *T. raschii* abundance (Fig. 10). There was a positive relationship between 30-day northeastward transport and *T. raschii* abundance. The longitude parameter also showed that *T. raschii* abundance was positively associated with the northeastern and southwestern portions of the study area. The strong positive relationship with ordinal day showed that higher abundances showed up later in the year in 2014. This is because the only year in which we sampled past day of year 260 was 2014. Furcilia abundance had significant relationships with bottom temperature, 14-day northeastward transport, year, ordinal day, and longitude. The model explained 56.8% deviance in abundance for euphausiid furcilia with an r^2 of 0.53 (Table 4). There was not a clear abundance pattern in relation to the bottom temperature (Fig. 11). In contrast to the relationship between transport and *T. raschii* adults, there was a negative relationship with furcilia abundance and 14-day northeastward transport.

The model helped explain 43% of the deviance with an r^2 of 0.39 of the *C. glacialis* C5 stage (Table 4). The most significant parameters included surface salinity, surface temperature, bottom temperature, 14-day transport, ordinal day, and year. Higher surface temperatures had a positive association, while lower surface had a slightly negative association, with C5 abundances (Fig. 12). Conversely, lower bottom temperatures had a positive relationship and higher bottom temperatures had a negative relationship with C5 abundance. Stage C5 abundance was also negatively associated with lower salinity seawater. There was a slight negative association with strong northeastward transport and C5 abundance. Interestingly, there was not a significant association with northeastward transport and *C. glacialis* C2 stages. The C2 stage was similar to C5 stages in the relationship with bottom temperatures, as there was a negative relationship with higher bottom temperatures and a positive relationship lower bottom temperatures (Fig. 13). There was positive association of C2 stages with higher longitudes. Overall, C2 stages had the strongest GAM model, which explained 57% of the deviance and a r^2 of 0.55 (Table 4).

4. Discussion

4.1. *Euphausiid transport*

T. raschii is an amphiboreal species whose distribution also extends to the Arctic Ocean and associated continental shelves. We observed the presence of *T. raschii* in all years near Utqiagvik, with relatively high abundances in 2014 and 2015. The annual presence of euphausiids there is important as they are a dominant component of the diet for bowhead whales in the region (Lowry et al., 2004; Moore et al., 2010). A positive association with northeastward transport and a positive association with higher longitudes, implies that *T. raschii* were advected from the south. The positive association with lower longitudes may be the result of krill being advected into the Chukchi Shelf from the Beaufort Sea as described by Ashjian et al. (2010); other explanations include lack of sampling in the central region in 2013, sampling later in the 2014, or because of the current patterns that tend to extend farther offshore in the central region (Stabeno et al., 2018), resulting in animal presence just outside of the sampled transect. Overall, these findings support the hypothesis of Berline et al. (2008) and Ashjian et al. (2010) that the

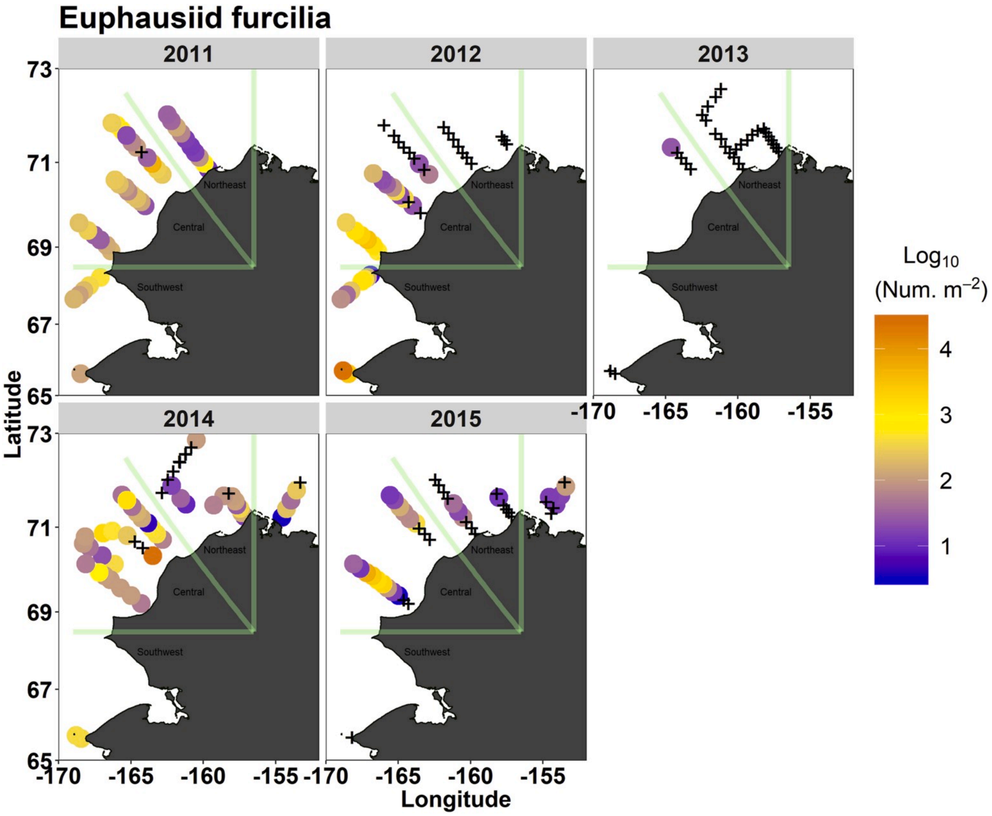


Fig. 8. Yearly maps of pelagic total abundance ($\text{Log}_{10}(\text{Num m}^{-2})$) of euphausiid furcilia. The letter "X" denotes tows where the taxon was absent.

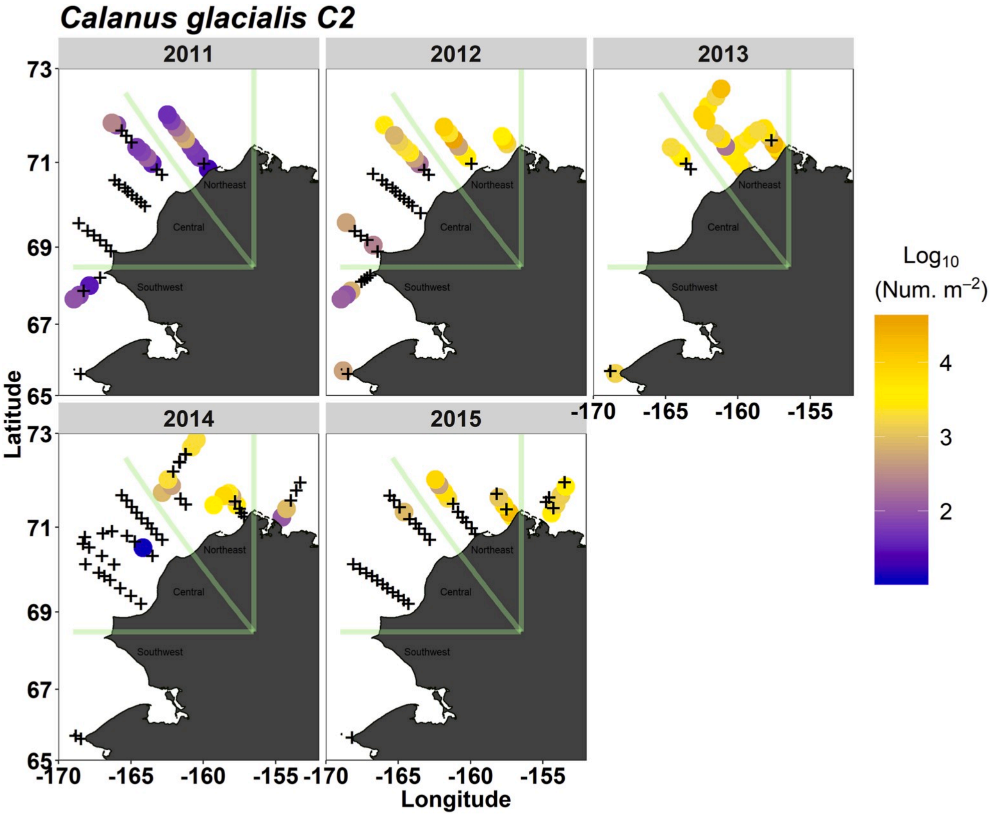


Fig. 9. Yearly maps of pelagic total abundance ($\text{Log}_{10}(\text{Num m}^{-2})$) of *Calanus glacialis* C2 stage. The letter "X" denotes tows where the taxon was absent.

Table 3
Post-hoc Tukey's test significant *p* values for the depth-year interactions of each taxon.

	Depth:Year	*p* value
T. raschii	Epibenthic:2014 – Pelagic:2011	0.0200
	Pelagic:2015 – Pelagic:2011	0.0252
	Epibenthic:2014 – Epibenthic:2011	0.0462
	Epibenthic:2014 – Pelagic:2012	0.0179
	Pelagic:2015 – Pelagic:2012	0.0234
	Epibenthic:2014 – Epibenthic:2012	0.0417
	Pelagic:2015 – Epibenthic:2011	0.0494
	Epibenthic:2014 – Pelagic:2014	0.0235
	Pelagic:2015 – Pelagic:2014	0.0307
	Epibenthic:2015 – Epibenthic:2014	0.0342
	Epibenthic:2015 – Pelagic:2015	0.0390
Mysids	Epibenthic:2014 – Pelagic:2011	0.0000
	Epibenthic:2014 – Epibenthic:2011	0.0001
	Epibenthic:2014 – Pelagic:2012	0.0000
	Epibenthic:2014 – Epibenthic:2012	0.0001
	Epibenthic:2014 – Pelagic:2013	0.0008
	Epibenthic:2014 – Epibenthic:2013	0.0009
	Epibenthic:2014 – Pelagic:2014	0.0000
	Epibenthic:2014 – Epibenthic:2015	0.0001
	Epibenthic:2014 – Pelagic:2015	0.0001
Amphipods		
	Epibenthic:2014 – Pelagic:2011	0.0060
	Epibenthic:2014 – Epibenthic:2011	0.0017
	Epibenthic:2014 – Pelagic:2012	0.0010
	Epibenthic:2014 – Epibenthic:2012	0.0014
	Epibenthic:2014 – Pelagic:2013	0.0101
	Epibenthic:2014 – Epibenthic:2013	0.0087
	Epibenthic:2014 – Pelagic:2014	0.0063
	Epibenthic:2014 – Pelagic:2015	0.0312
	Epibenthic:2014 – Epibenthic:2015	0.0010

Table 4
GAM model significant terms for each taxon with R^2 and the percentage of deviance explained. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

	Significant terms	R^2	Deviance explained
***Calanus glacialis* C5**	Surface Salinity*** Surface Temperature* 14-day Transport* Bottom Temperature*** Ordinal Day*** Year***	0.394	43%
***Calanus glacialis* C2**	Mean Bottom Temperature*** Mean Surface Temperature** Longitude* Julian Day* Year*	0.551	57%
Thysanoesssa raschii	Mean Bottom Temperature** 30-day Transport* Longitude*** Ordinal Day ***	0.375	42.3%
Euphausiid furcilia	Mean Bottom Temperature *** 14-day Transport*** Longitude*** Ordinal Day*** Year***	0.53	55.8%

euphausiids concentrated by physical processes near Barrow Canyon likely originated from the northern Bering Sea.

Conversely, temperature-dependent euphausiid furcilia development times suggest their extent into the central and northeast regions in warmer conditions was a result of spawning in the Chukchi Sea. Transport of water takes ~90 days to reach Icy Cape from the Bering

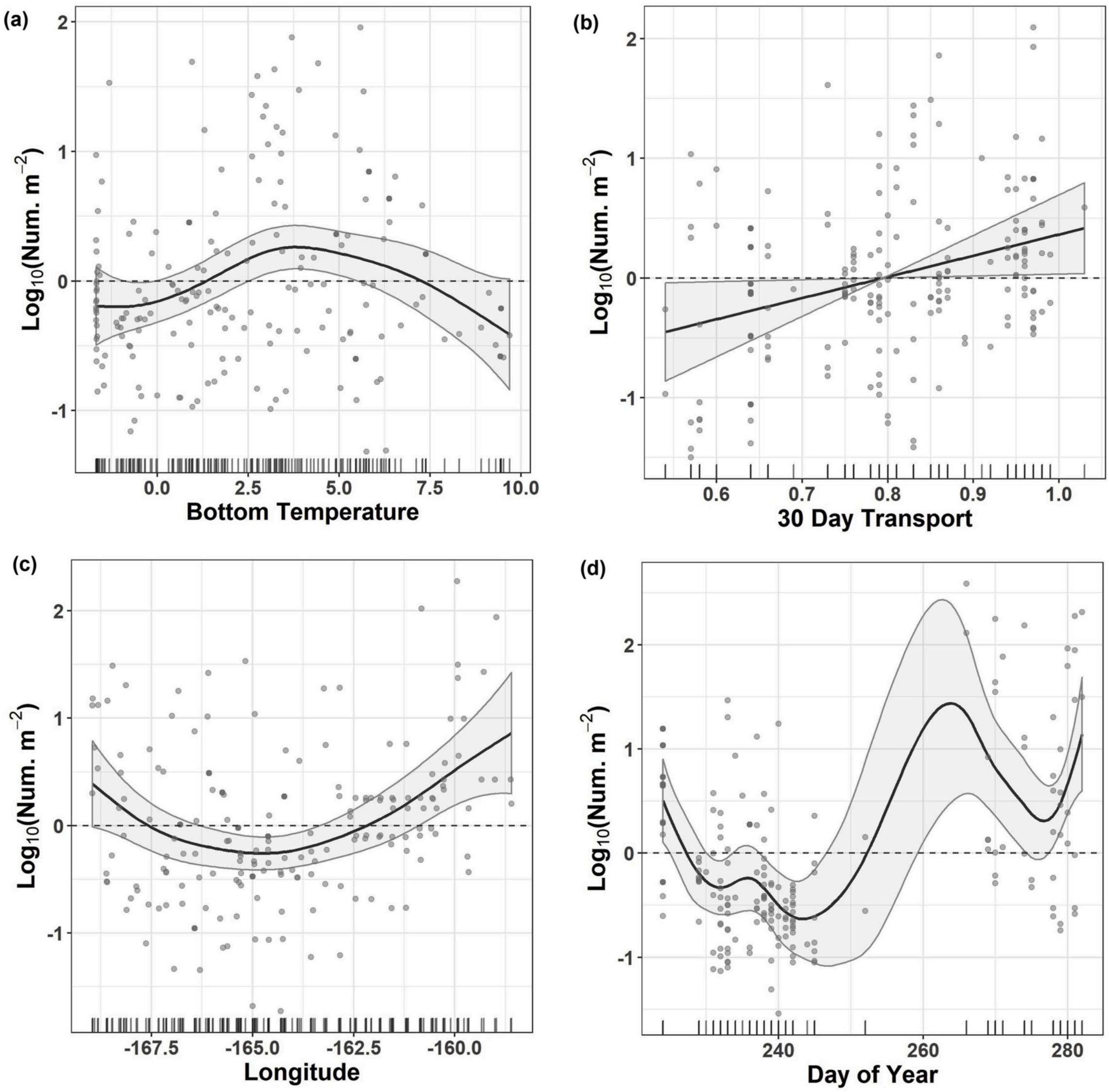


Fig. 10. GAM smooth for the distribution of *Thysanoessa raschii* epibenthic abundance (Log$_{10}$(Num m^{-2})), 2011–2015. Variables included mean bottom temperature (a), 30-day transport (b), longitude (c), and day of year (ordinal day) (d).

Strait (Stabeno et al., 2018). This is roughly 12 to 40 days longer than the development time from egg to furcilia at comparable temperatures. The hypothesis of local production is also supported by the negative relationship with 14-day transport or lack of clear relationship with bottom temperatures. In particular, the negative relationship with 14-day transport (in addition to a lack of association with 30-day transport) showed that the greater and more recent transport resulted in reduced abundances, suggesting they were likely recently spawned nearby and subsequently transported away.

Adult euphausiids were present in the northeast region in 2012 and 2013, even though overall transport during those years was low. The absence of younger stages could have resulted from a change in the timing of reproduction relative to our sampling, failed spawning, or very high mortality of the larvae because of cold temperatures or high predation. Euphausiid eggs were present in the northeast region in 2014 and 2015, but were absent in 2012 and 2013 (egg data not collected in 2011), suggesting reproduction only occurred when this region was not occupied by colder water masses.

The higher pelagic abundances of euphausiids in 2013 and 2015 were not due to a day/night effect as a comparison of day/night abundances found no significant differences (not shown). The significant increase in abundance of *T. raschii* in 2014, compared to remaining years, suggests that sampling later in the season likely had considerable impact. This is evidenced by the relationship between ordinal day and euphausiid abundance in 2014. Other environmental and physical results did not suggest any other anomalous features that may have caused this significant jump in abundance. Thus, it suggests that because we sampled later in 2014 we observed more euphausiids compared to other years. This is most likely the result of advection timing (as explained in Berline et al., 2008), but may also reflect local recruitment. Alternative explanations for increased abundance include local production or retained for a longer period of time. Most historical surveys have not sampled later than mid-September to avoid disturbing subsistence hunting by Iñupiat whalers as the whales migrate westward from the Beaufort. Thus previous surveys (Grebmeier and Harvey, 2005; Lane et al., 2008) reporting low numbers of euphausiids could be due to the mismatch between euphausiid transport from the south and survey timing.

Our estimates of adult euphausiid abundance may be somewhat improved over prior estimates derived from small mouth plankton nets towed only in the water column (e.g. Eisner et al., 2013). However, euphausiids are difficult to accurately estimate even with larger nets

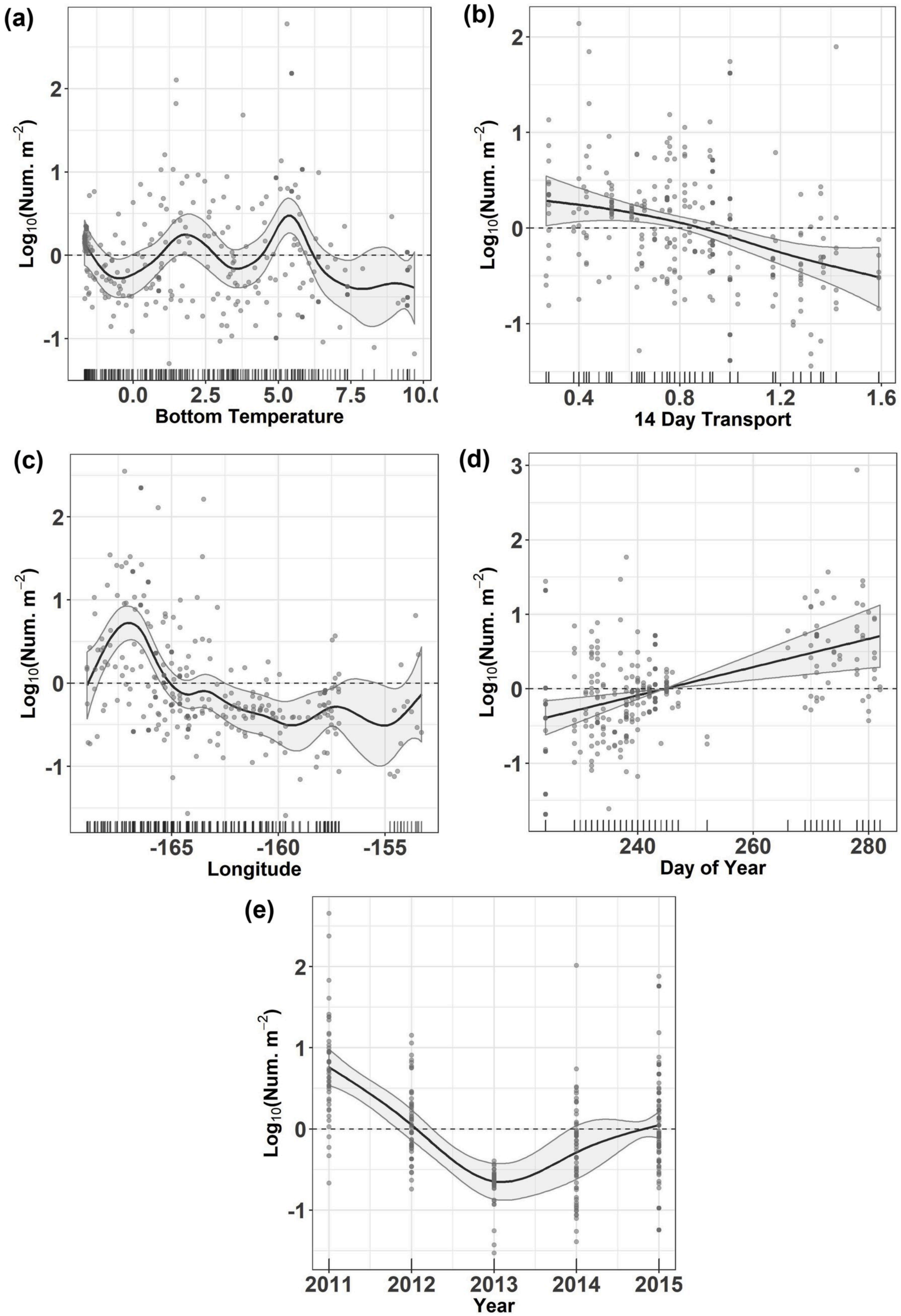


Fig. 11. GAM smooth for the distribution of euphausiid furcilia pelagic abundance ($\text{Log}_{10}(\text{Num m}^{-2})$), 2011–2015. Variables included mean bottom temperature (a), 14- day transport (b), longitude (c), day of year (ordinal day) (d), and year (e).

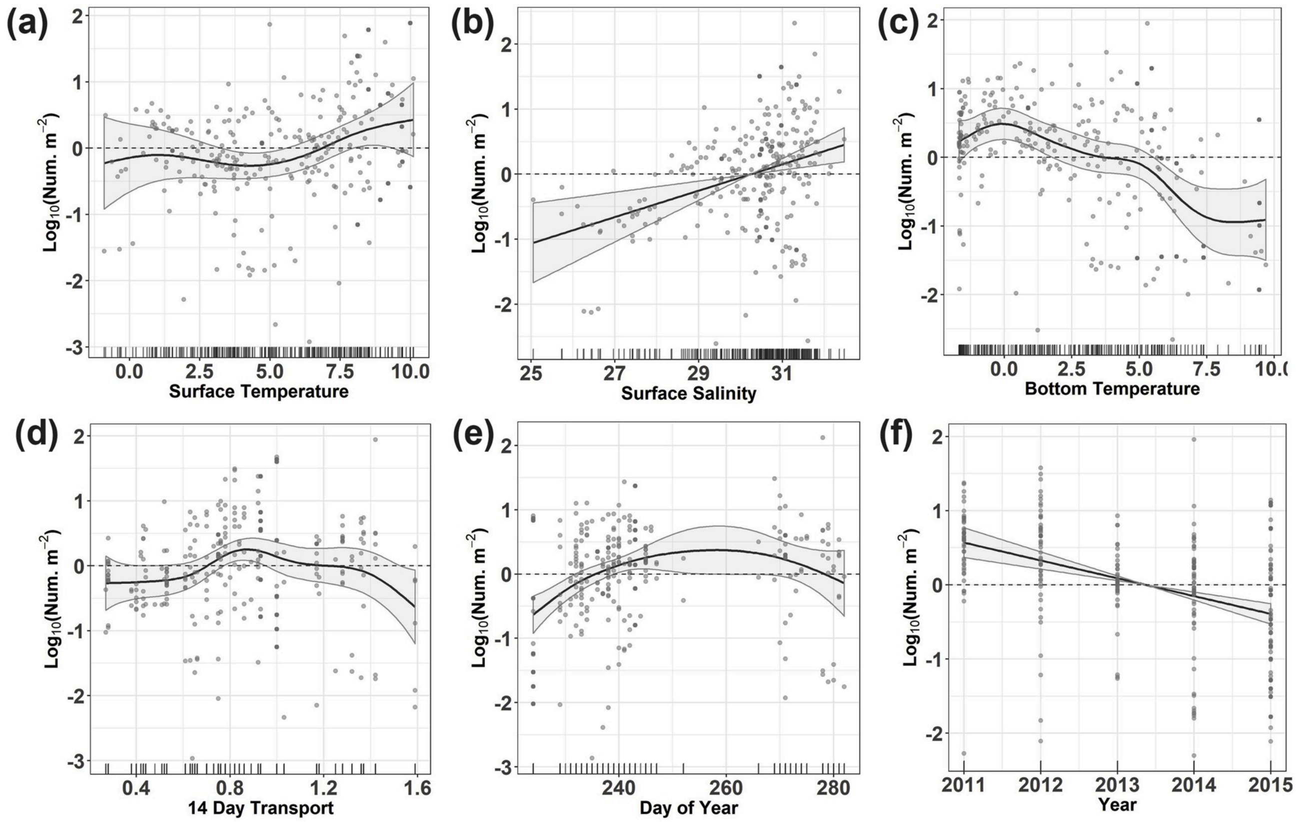


Fig. 12. GAM smooth for the distribution of *Calanus glacialis* C5 stage pelagic abundance ($\text{Log}_{10}(\text{Num m}^{-2})$), 2011–2015. Variables included mean surface temperature (a), surface bottom salinity (b), bottom temperature (c), 14-day transport (d), day of year (ordinal day) (e), and year (f).

that sample at faster tow speeds. (e.g. Hunt et al., 2016). Net avoidance by euphausiids has long been recognized as chronic problem in oceanographic studies (e.g. Brinton, 1967; Sameoto et al., 2011; Wiebe et al., 2013). Net avoidance abilities may even extend to the young stages (e.g. Smith, 1991). Future work using acoustical or optical techniques may be able to provide better estimates of euphausiid abundance, although as this study demonstrated there is a need to sample very close to the seafloor.

4.2. Other large zooplankton

We found that *C. glacialis* were most abundant in colder conditions, with the abundance increase being driven by earlier development stages. This finding is supported by research showing that *C. glacialis* were strongly tied to the ice edge algae production, which is increased in colder years (Søreide et al., 2010). Both C2 and C5 stages showed a significant positive association with colder bottom temperatures. The C5 stage, as opposed to the C2 stage, also had a positive association with warmer surface temperatures and significant relationship with northeastward transport, suggesting that C5 stages were more likely to be influenced by advection. The C2 stage had significantly higher abundances in the northeast region, a negative relationship with higher surface temperatures, and lack of a significant relationship with transport, suggesting local production rather than transported from the south. This is supported by previous research showing *C. glacialis* having approximate development times of 8 to 12 days at temperatures between 12 and -1.5 °C, respectively, from egg to C2 stage (Hirst and Lampitt, 1998; Kiørboe and Hirst, 2008; Spear et al., 2019). As described earlier, transport times from the Bering Sea to the northeast region were much longer than development times from egg to C2 Stage. C2 copepodites were also more abundant in 2012 and 2013, when temperatures were coldest in the northeast. This suggests that the overall abundance increases in *C. glacialis* in 2012 and 2013, when temperatures were colder, sea ice melted later in the northeast region, and advection was lower, was primarily due to local reproduction. Abundance increases in the northeast region could also be due to upwelling onto the Chukchi Shelf from the Beaufort Sea (Ashjian et al., 2010). Conversely, the lower abundances of C2 stages in warmer conditions may be a result of faster and earlier development into later stages. Thus the various stages of *C. glacialis* region likely have multiple sources (in situ reproduction and transport from the south and east), and the absolute abundance is a function of local and regional processes. This is a notable result; later stages of *C. glacialis* are known to be the primary prey of bowhead whales around West Greenland (Heide-Jørgensen et al., 2013), and a significant contribution to their diet in the Chukchi and Beaufort seas (Lowry et al., 2004; Moore et al., 2010). In addition, if *C. glacialis* are developing faster, they may enter into diapause earlier creating a mismatch with migrating whales.

The significant differences in pelagic and epibenthic abundance in both mysids and amphipod highlights the importance of sampling near the bottom. Mysids and some amphipod species may spend time in the water column; therefore, sampling the water column and epibenthic layer will yield improved estimates of their abundance. Epibenthic amphipod abundance was significantly higher in 2013 than any other year sampled in this study. This is a notable observation in the context of a changing climate, given that 2013 was also the coldest year and certain species of amphipods, in particular, have known ice-associated and bottom dwelling habits (Vinogradov, 1999; Gradinger and Bluhm, 2004). Both amphipods and mysids are prey for multiple marine mammals, including bearded seals (*Erignathus barbatus*; Cameron et al., 2010), Pacific walrus (*Odobenus rosmarus divergens*; Sheffield and Grebmeier, 2009), beluga whales (*Delphinapterus leucas*; Quakenbush et al., 2015), grey whales (*Eschrichtius robustus*; Nerini, 1984; Darling et al., 1998), and bowhead whales (Lowry et al., 2004). Given the

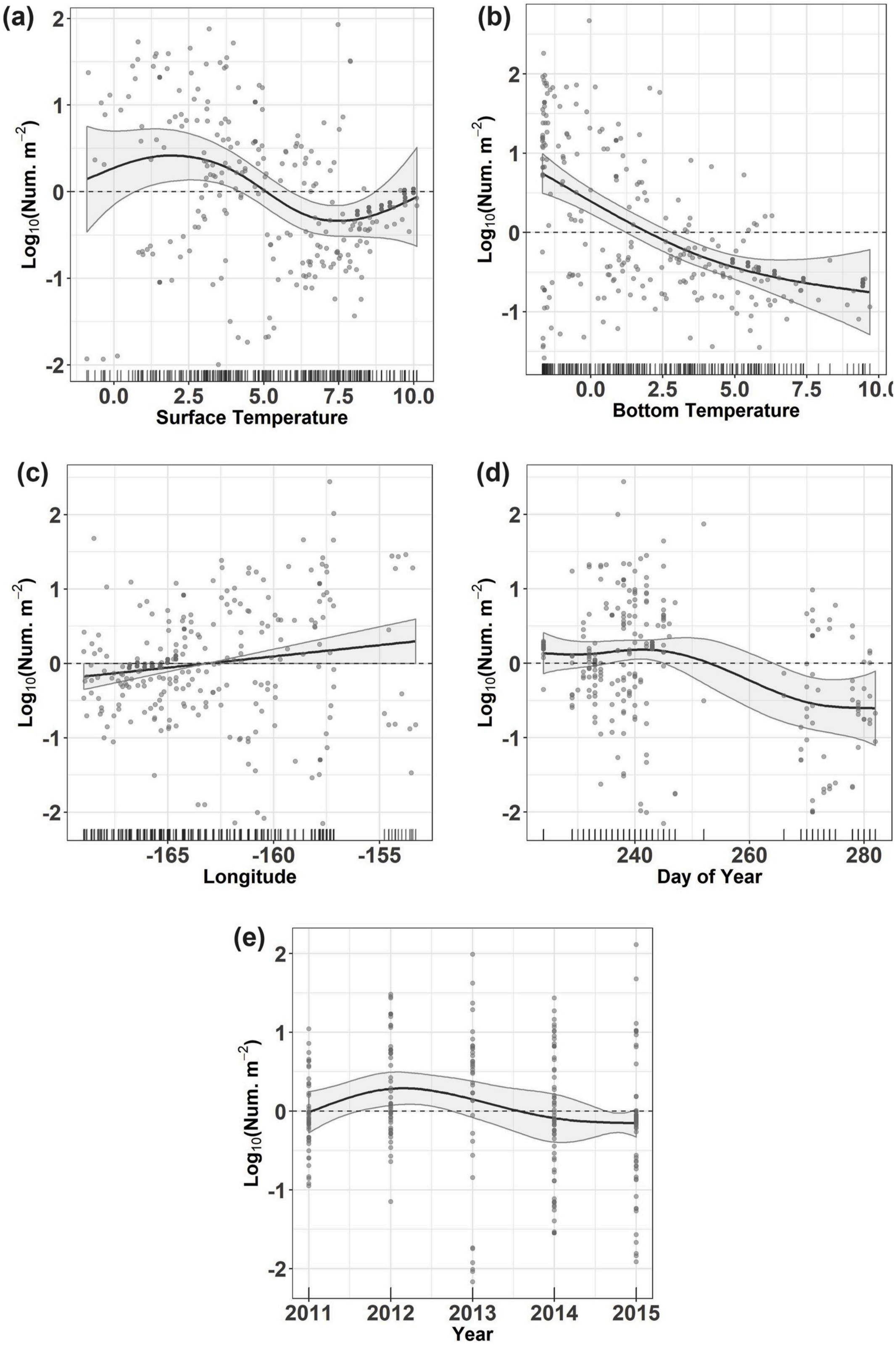


Fig. 13. GAM smooth for the distribution of *Calanus glacialis* C2 stage pelagic abundance (Log$_{10}$(Num m^{-2})), 2011–2015. Variables included mean surface temperature (a), bottom temperature (b), longitude (c), day of year (ordinal day) (d), and year (e).

importance of mysids and amphipods to Arctic food webs, it is important to monitor their response to changes in ice cover and water temperatures.

4.3. *Chukchi Sea large zooplankton status and trends*

The findings of this study are relevant to the potential response of lower trophic levels to climate warming, including changes in Arctic food webs. Recent studies have found a 50% increase in water volume transport through the Bering Strait to the Chukchi Sea from 2001-2014; the immediate impact to the physical environment is an increase in heat flux that is a potential trigger for Arctic sea-ice melt and retreat (Woodgate et al., 2010; 2015; Woodgate, 2018). As the climate warms, increases in primary and secondary production will result in changes in abundance of lipid-rich zooplankton, but it remains to be seen what the overall lipid availability will be (Renaud et al., 2018). Two of the species targeted in this study, *C. glacialis* and *T. raschii*, have an average percent lipid content of approximately 11–15% and 3–5%, respectively, both having a higher average percent lipid content in colder years (Heintz et al., 2013). There is a general consensus that densities of sea ice-associated, lipid-rich *C. glacialis* are expected to decline due to loss of ice in the region. (Tremblay et al., 2012; Grebmeier et al., 2006a; Grebmeier, 2012; Moore and Stabeno, 2015; Renaud et al., 2018). In addition, this study provides evidence that increases in large zooplankton abundance such as euphausiids (which also contain depot lipids) is likely to occur, either via advection from lower latitudes or changes in local production. This is supported by previous studies which found an increase in zooplankton biomass over several decades in the Chukchi Sea (Ershova et al., 2015). An increase in abundance of prey such as euphausiids will likely benefit higher trophic level predators such as planktivorous fish, seabirds and marine mammals. Recently, studies have suggested that the abundance of other planktivores in the northern Bering Sea and Chukchi appear to be changing. For example, in the Bering Sea, there has been a decrease in the lipid-rich nodal species Arctic cod (*Boreogadus saida*) and an increase in the commercial species walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*; Stevenson and Lauth, 2019). Walleye pollock have been observed in the Chukchi and Beaufort seas (e.g. Logerwell et al., 2015) and is an important planktivore in the southeastern Bering Sea ecosystem consuming both euphausiids and large copepods (Dwyer et al., 1987; https://access.afsc.noaa.gov/REEM/WebDietData/DietDataIntro.php). Walleye pollock could become an effective competitor for large zooplankton with other fishes, seabirds, and marine mammals if its abundance continues to increase in the northern Bering, Chukchi and Beaufort seas. At present, however, there is evidence of improved body condition of bowhead whales returning from the Beaufort (George et al., 2015). This suggests that the plankton community in their summer feeding grounds has changed in either biomass, species composition or both.

The strong interaction between top-predators (whales, seabirds, and Arctic cod) and copepods/krill in the northern Chukchi appeared to be mediated by both advection and local production related to sea-ice dynamics. What remains to be seen is whether arctic shelf ecosystems will continue to be bottom-up forced by sea-ice dynamics or whether climate-mediated impacts on intermediate trophic levels (e.g. large zooplankton and small fishes) could become the predominant controlling mechanism, e.g. wasp-waist control (Gaichas et al., 2015; Griffiths et al., 2013; Fauchald et al., 2011). If warming continues, the bottom-up dynamics in this location would likely be disrupted by increased advection over longer time-periods as well as a lack of localized, lipid-rich, ice-associated production. Such a shift would greatly impact the trophic dynamics in the region.

5. Conclusions

This study analyzed five successive years of zooplankton abundance over a wide range of physical oceanographic characteristics in the Chukchi Sea to better understand the status and trends in prey availability for baleen whales, seabirds, and planktivorous fish. The coldest year (2013) was highlighted by later summer sea-ice melt, colder sea surface and bottom temperatures, and lower northward transport through the Bering Strait during the spring and summer months. Generally, the warmest years accompanied with earlier summer sea-ice melt, warmer sea surface and bottom temperatures, and higher Bering Strait transport during the spring and summer months. Adult euphausiid abundances differed across warm and cold conditions. These differences appeared most pronounced regionally (NE-SW gradient) and were related to transport, which suggests that most of these euphausiids are transported to the Chukchi Sea from the Bering Sea. The lack of furcilia in 2012 and 2013, (except in the SW), and the presence of furcilia in 2011 and 2014–15, suggests that only in these warmer years with higher advection were earlier stages transported to the northeast region of the Chukchi Sea. We also found that some euphausiids might be locally produced based on the development times. In contrast, the *C. glacialis* C5 stages were found across all years, but C2 stages were found primarily in the northeast and were more abundant under colder conditions which suggests local production of copepods. Thus, the large numbers of euphausiids and copepods that dominate the prey in stomachs of bowhead whales harvested near Utqiagvik, Alaska (Lowry et al., 2004; Ashjian et al., 2010; Moore et al., 2010; George et al., 2015) are likely the result of transport of euphausiids to this location and the contribution of locally produced *C. glacialis,* although *Calanus* found in the region potentially come from several sources or origins.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Adam Spear: Investigation, Conceptualization, Methodology, Data curation, Formal analysis, Writing - original draft, Visualization. **Jeff Napp:** Investigation, Conceptualization, Methodology, Writing - review & editing, Supervision. **Nissa Ferm:** Data curation, Visualization, Formal analysis. **David Kimmel:** Conceptualization, Methodology, Writing - review & editing.

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