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# Long-Term Changes in
# Summer Zooplankton Communities
## of the Western Chukchi Sea, 1945–2012

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**ABSTRACT.** The Chukchi Sea pelagic ecosystem, which is finely tuned to the region's seasonal ice formation and retreat, has been undergoing dramatic oceanographic change related to shifting sea ice cover and increasing temperatures over the last decades. We examine historical data sets on zooplankton communities in the central Chukchi Sea during the time period 1946 to 2012. Analysis is confounded by differences between years in terms of spatial coverage, seasonal variability, and methodology; nonetheless, trends remain detectable when a sufficient number of study years is compiled. In addition to high levels of interannual variability, we demonstrate that there have been significant increases in zooplankton biomass and abundance in recent years compared to historical studies, along with shifting distribution ranges for several key species. This signal is most pronounced for the copepods, particularly *Calanus glacialis*, which appears to be indirectly benefiting from warming of the region. While summer zooplankton communities of the Chukchi Sea have been primarily Bering-Pacific in character for as long as records exist, continuing warming and ice loss are increasing the influence of Bering-Pacific fauna within the Chukchi region.

## INTRODUCTION

The Chukchi Sea is an important transition zone between the Pacific and Arctic Oceans, being a significant source of heat, freshwater, and organic carbon for Arctic waters. The Pacific water entering the Bering Strait is rich in nutrients, phytoplankton, and zooplankton and is responsible for the exceptionally high productivity of the Chukchi Sea compared to other Arctic shelf seas (Kosobokova and Pertsova, 2012; Grebmeier and Maslowski, 2014). This environment is changing rapidly as manifested by sea ice concentrations consistently below the long-term mean for the last decade (Wood et al., 2015), a longer ice-free summer period, and above-average sea surface temperatures during most months. Changing environmental conditions in the region are presumed to propagate to its marine biological communities, although proof of such change is so far elusive.

Planktonic communities in particular may serve as useful "beacons of climate change" (Richardson, 2008) due to their relatively short life cycles, rapid response in growth rates to changing temperatures,

**From left to right:** *Calanus glacialis*, *Eumedusa birulai*, *Metridia longa*, *Rathkea octopunctata*, *Eucalanus bungii*, and *Limacina helicina*.

and dependence on ocean currents for dispersal. These attributes make them two to three times more responsive to climate-related changes than terrestrial communities (Richardson, 2008). A growing body of literature for many regions of the Arctic demonstrates the close relationship of zooplankton community structure to water column properties and water mass distribution (summarized in Wassmann et al., in press). This relationship is particularly pronounced within the Chukchi Sea, where several incoming Pacific water masses of different origin carry distinct planktonic communities (e.g., Hopcroft et al., 2010; Eisner et al., 2012; Ershova et al., 2015) that dilute or displace the resident Arctic shelf communities. With the higher frequency of warmer summer temperatures during recent years and a longer ice-free period, it is expected that Pacific species will be transported farther north into the Arctic and will remain in the plankton for longer time periods, potentially competing for resources with resident Arctic species. A longer summer period and warmer waters may also lead to phenological shifts in plankton life history, as has been reported for many plankton groups in various parts of the world (Richardson, 2008). The life

cycles of many Arctic and sub-Arctic species are finely tuned to ice breakup and seasonal phytoplankton blooms. An earlier ice retreat would potentially be damaging to these species and provide a competitive edge to organisms whose life-history traits are more opportunistic.

Unfortunately, historical time series for Chukchi Sea pelagic communities do not exist. A number of sporadic, spatially isolated and methodologically inconsistent surveys have been conducted over the past century, beginning in the 1940s, but many remain unpublished or buried in national journals and institutional reports. Most of these studies were confined to one of the two sides of a strongly enforced political border, with most early work done in Russian waters and more recent studies restricted to US waters. Sampling efforts have intensified significantly in the past two decades, fueled by interest in both climate change and the development of natural resources, but only recently have coordinated time series begun to emerge (Grebmeier, 2012).

In the current work, we present an outline and analysis of the modern and historical data available on zooplankton communities in the central and western Chukchi Sea region, examine the extent

of variability within the communities, and explore some underlying mechanisms that may be responsible for driving these patterns. A central hypothesis is that during the earlier sampling years (1946–1976), Chukchi Sea plankton communities were overall less "Pacific" in character and more typical of Arctic shelf seas. Secondarily, we expect that phenological shifts have occurred in key species as a direct result of warmer temperatures and earlier ice retreat. There are many challenges involved in confirming these ideas, the greatest being the highly variable spatial coverage and methodology of the historical and contemporary data. Documenting temporal or climatological trends is further complicated by lengthy temporal gaps in the historical data, with several decades lacking any observations. Recent Chukchi Sea work repeatedly shows that planktonic communities exhibit an extremely high level of variability—spatially, seasonally, and interannually (Matsuno et al., 2011; Questel et al., 2013; Ershova et al., 2015). Thus, one of the central challenges when examining a time series, such as the one analyzed in this study, will be discerning natural variability vs. climate-mediated long-term change.

## METHODS

### Description of Data Sets

We accumulated reports and publications on expeditions to the Chukchi Sea undertaken during the 1900s and obtained later data sets directly from colleagues to build an extensive compilation of zooplankton studies conducted in the central and western Chukchi, and also considered matching physical oceanographic data, when available (supplementary Table S1, Figure 1). We have intentionally excluded studies that were confined to the shelf break (i.e., the Shelf Basin Interaction [SBI] program [Grebmeier and Harvey, 2006], the Burton Island expedition, and others) to avoid encompassing the distinct Arctic Basin communities (e.g., Kosobokova and Hopcroft, 2010), as well as studies confined to the most northeastern Chukchi (e.g., Questel et al., 2013) where historical data are generally lacking. Our compilation incorporated 28 expeditions reaching as far back as 1946 (on the Russian icebreaker *Severnyj Poljus*) and as recent as September 2012 (Russian-American Long-term Census of the Arctic, RUSALCA). Most of the recovered data sets were spatially confined to either US or Russian waters,
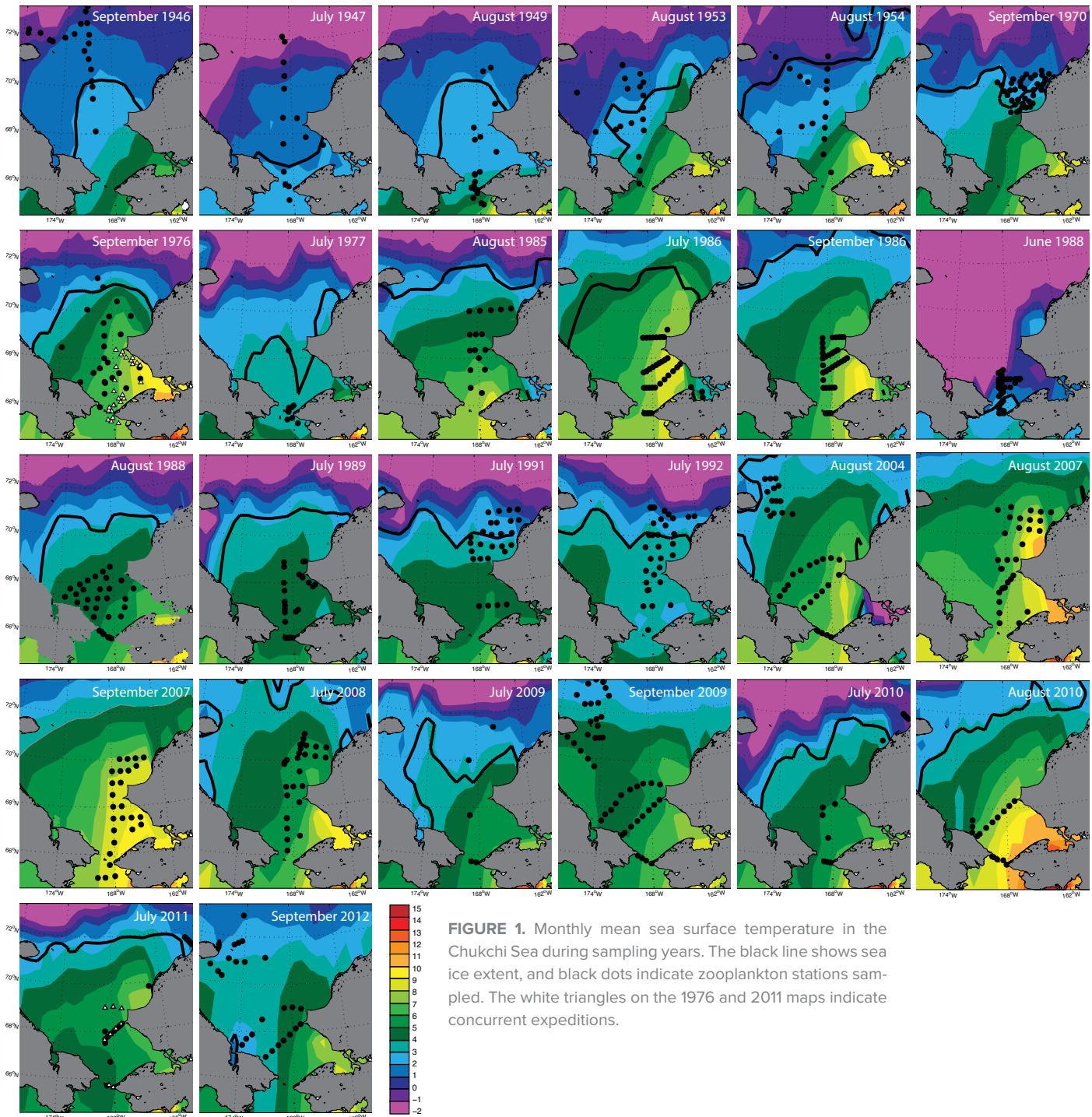


**FIGURE 1.** Monthly mean sea surface temperature in the Chukchi Sea during sampling years. The black line shows sea ice extent, and black dots indicate zooplankton stations sampled. The white triangles on the 1976 and 2011 maps indicate concurrent expeditions.

with the notable exceptions of the 1976 expedition on R/V *Mayak* (Pavshtiks, 1984), the 1988 BERPAC (Joint US-USSR Bering-Pacific Expedition; Kulikov, 1992) survey, and four RUSALCA expeditions (2004–2012; Ershova et al., 2015). Overall, spatial coverage was highly variable between cruises, with several expeditions covering the entire Chukchi domain from the Bering Strait to 72°N and beyond, while others worked only in the southern Chukchi region or in a small localized sampling region (i.e., a 1970 US Coast Guard ecological survey in the eastern Chukchi Sea known as WEBSEC 70 and R/V *Thomas Thompson* cruise TT221 in 1988). Most of the sampling efforts took place in the mid-summer months (July–August), although several expeditions occurred in September, and one (TT221) was conducted in June, which is oceanographically early spring in the Chukchi Sea region. With the exception of September 1946, most sampling occurred when ice cover was less than 50%, allowing accessibility by non-icebreaking vessels.

## Environmental Data

Physical data (temperature and salinity) were compiled for most data sets (see Table 1) from cruise reports, the US National Oceanographic Data Center (NODC), or directly supplied by colleagues. Historical sea surface temperature (SST) and sea ice data were obtained from the Met Office Hadley Centre (http://www.metoffice.gov.uk/hadobs/hadisst), and modern SST data were obtained from the National Oceanic and Atmospheric Administration (NOAA) at http://www.esrl.noaa.gov/psd. The ice edge was defined as the 15% ice concentration contour. Due to the frequent two-layer nature of water masses within this region, average surface (0–10 m water depth) and bottom (up to 10 m above bottom) temperature and salinity were calculated for each station. Bottom and surface waters at each station were then categorized into water mass types using cluster analysis as well as subjective interpretation

using literature values. Cluster analysis was performed using Euclidean distances of normalized values using the R library vegan. This method of water mass identification is approximate and may be somewhat inaccurate (particularly for surface waters), but it provides a useful broad-scale approximation of the water masses present in the area historically.

## Climatic Indices

Variations in atmospheric indices such as the Pacific Decadal Oscillation (PDO) and the Arctic Oscillation (AO) influence the Pacific Ocean marine environment as well as the biological communities that inhabit it (Mantua et al., 1997; Hare and Mantua, 2000). To examine the potential relationship of these indices to plankton variability in the Chukchi Sea, we obtained a six-month average of each index for the winter months (November to April) prior to each sampling year. Mean monthly values were obtained from the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) (http://research.jisao.washington.edu/pdo) and the NOAA National Centers for Environmental Information (https://www.ncdc.noaa.gov/teleconnections/ao).

## Standardization and Subsetting of Biological Data

The zooplankton data were highly variable in quality, with taxonomic resolution being vastly different (see supplementary Table S1). Many studies identified only the copepods to species or genus level and grouped all remaining

organisms into broad taxonomic categories (i.e., "Amphipods," "Cnidaria"). High-resolution data (with 50+ taxonomic categories identified) were only available for the 2004–2012 RUSALCA, the 2007 *Oscar Dyson*, the 2009–2011 *Laurier*, and the 1946 *Severnyj Poljus* expeditions. Taxonomy was aligned using the Arctic Register of Marine Species (Sirenko et al., 2015) and the World Register of Marine Species (WoRMS Editorial Board, 2015) to establish synonyms and remove suspicious identifications. The species complex *Calanus glacialis*/*Calanus marshallae*, which is often indistinguishable morphologically, was considered to be primarily *C. glacialis* based on results from molecular analysis (e.g., Nelson et al., 2009; author Nelson, unpublished data) and therefore simply referred to as *C. glacialis* within this analysis. The group "large copepods" included *Calanus glacialis*, *Metridia* spp., *Neocalanus* spp., and *Eucalanus bungii*; the other copepod species were grouped into "small copepods." While our data span nearly seven decades, they inherently represent a patchy time series, with large decadal gaps in the sampling years (1955–1970, 1992–2004).

The most complex problem in comparing zooplankton data sets was accounting for differences in the sampling gear used, with the mesh pore sizes and the mouth openings of the nets being of greatest concern. The type of gear used to collect plankton samples is known to greatly influence the biomass, abundance, and composition of the resulting data due to extrusion or avoidance (Skjoldal et al.,

TABLE 1. Summary of Chukchi Sea water mass characteristics concurrent with zooplankton sampling.

| WATER MASS | TEMPERATURE °C | SALINITY |
|---|---|---|
| Alaska Coastal Water (ACW) | >5 | 26–32 |
| Bering Sea/Anadyr Water (BSAW) | 0–5 | 31–33 |
| Melt Water (MW) | <2.5 | 26–30 |
| Siberian Coastal Water (SCW) | 0–5 | 20–27 |
| Winter Water (WW) | <0 | 31–33 |
| MW/SCW | 2.5–6 | 26–29 |
| ACW/BSAW | 2.5–10 | 29–32.5 |

2013). Most American studies historically employed coarse 500 μm nets (0.5–1 m mouth diameter), while Russian studies used Juday nets (~170 μm, 0.37 m mouth diameter) or Nansen nets (333 μm, 0.7 m mouth diameter). The 500 μm nets undersample the small organisms, such as small copepods and meroplankton, that generally constitute >90% of total abundance in this region, while the 170 μm Juday nets may under-

these species is substantial; only those large enough to be sampled adequately by the more commonly used coarser mesh nets (333 μm and 500 μm) were included in the creation of distribution maps for this community type.

While biomass estimates within this habitat are reported to be similar (i.e., within a factor of 1.5–2) across the range of the mesh sizes (150–500 μm) considered in this study (Questel et al.,

(temperature, salinity, water mass type, bottom depth, atmospheric indices) were also explored using mixed modeling. Fixed factors in the models included year, month, water temperature, salinity, bottom depth, water mass type present at each station, and mean AO and PDO signals for each year (six month winter average); the random factors included station location (averaged to a 1° × 1° grid). We also included the gear used (net type) as a blocking factor. Abundance and biomass values were log-transformed to account for unequal variance. Mixed modeling was performed in R using the lme4 (Bates et al., 2015) and nlme (Pinheiro et al., 2015) libraries. Significance was defined as $p < 0.05$. The data were examined for spatial correlation using R package geoR (Ribeiro and Diggle, 2015) and autocorrelation between years and was found to meet the assumptions of independence over space and time. The best model was selected using AIC (Akaike Information Criterion) employing the R package bbmle (Bolker and R Development Core Team, 2014). Multiple comparisons were estimated using the R library lmerTest (Kuznetsova et al., 2015). The relationships between zooplankton community structure and physical data for each data set were explored using the BIOENV routine (Clarke and Ainsworth, 1993) from the R library vegan (Oksanen et al., 2015). This method establishes the best subset of environmental variables, so that the Euclidean distances of scaled environmental variables have the maximum correlation with the Bray-Curtis dissimilarity index of the community abundance data for each station (Oksanen et al., 2015). Community matrices contained log-transformed abundances of all species that contributed at least 3% to transformed abundance. Ambiguous species and broad taxonomic categories were excluded from the analysis. The environmental matrix included normalized temperature and salinity for the bottom and surface 10 m layers. The significance of these correlations was established using Mantel's test of associations (Mantel, 1967).

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represent the larger, rarer, and faster-swimming species (see Questel et al., 2013). Abundance values were always converted to ind m⁻³. It is notable that average abundances reported for each expedition highlight the fact that the coarse-mesh nets report an abundance of ~100–400 ind m⁻³, while the fine mesh nets provide a value closer to ~1,500–9,000 m⁻³ (supplementary Table S1). For this reason, we only directly compare abundances of the large, widespread copepods, which are generally common enough to be well represented by fine-mesh net collections but large enough for most developmental stages to be captured by coarser nets. These large copepods are also the least likely to be misidentified. The species that we define as indicators of the Alaska Coastal Water (ACW) communities are those neritic species that are shared with the Alaska Coastal Current in the Gulf of Alaska and absent or rarely observed outside of this water type (e.g., Cooney, 1981; Coyle et al., 1996; Hopcroft et al., 2010; Ershova et al., 2015). The list of

2013), the methods for calculating zooplankton biomass varied during each expedition: most studies measured wet weight of the total sample (displacement volume), but some measured wet weight of individual groups, and others used linear measurements of body length to predict dry weight (DW) or wet weight from length-weight regressions. We converted all available biomass values to mg DW m⁻³ using existing equations converting wet weight to dry weight for different groups of organisms (Kiørboe, 2013). When biomass data were not available, we used averaged biomass for each taxonomic category from published data (Ershova et al., 2015), which was then multiplied by the abundance values. Average cruise biomass was calculated for the sampling region south of 71°N and east of 180°W to maximize comparability between cruises.

We established temporal trends of overall biomass and abundance of key species using linear mixed effects models. Relationships of biomass and abundance to variations in the physical environment

## RESULTS

### Physical Environment

Overall, temperature and ice conditions during the sampling periods were variable, with colder conditions observed during the earlier sampling years (Figure 1). The ice edge during the period of sampling extended to at least 70°N during all years prior to 1992. SST also averaged less than 0°–2°C at these latitudes. September 1986 was the warmest year of the pre-2000 sampling time period, with surface water temperatures in the sampling region averaging 7°C and the sea ice edge being north of 72°N in the eastern Chukchi. June 1988 was the coldest sampling period, with near-freezing temperatures and most of the Chukchi Sea still completely ice covered. This data set reflects oceanographic spring, rather than summer, conditions in the Chukchi Sea. The climatic indices (PDO and AO) for the examined time span show periods of predominately positive or negative, with the largest PDO switch occurring ~1976/77 and the AO switching sign more chaotically (supplementary Figure S1).

The strong east-to-west gradient in SST across the Chukchi Sea shelf, which is associated with the Alaska Coastal Current, is visible during some of the sampling periods, while in others the warm surface water is smeared across the entire Chukchi domain (2004, 2007), or weakly pronounced (2009, July 1986, 1991).

The data sets collected since the year 2000 are variable in terms of SSTs, but the sea ice extent was always observed much farther north (north of the plotted sampling region in 2004, 2007, 2009, and 2010). The summers of 2004, 2007, and 2010 stand out as particularly warm years, with SST in the southern Chukchi region exceeding 10°–12°C.

### Description of Water Masses

Five broad water mass types were identified as previously described in the literature: Alaska Coastal Water (ACW), Bering Sea/Anadyr Water (BSAW), Winter Water (WW), Melt Water (MW), and Siberian Coastal Water (SCW) (i.e., Pickart et al., 2010; Eisner et al., 2012; Pisareva et al., 2015), as well as two water types with intermediate properties (BSAW/ACW, MW/SCW) (Figure 2, Table 1). It is notable that our characterization of BSAW is based on its typical summer properties, such that the seasonal timing of warming in the Bering Sea will strongly influence our ability to recognize this water type in the Chukchi Sea.

Overall, water mass distribution follows similar patterns from the oldest to the most recent study years (Figure 3). The warm and fresh ACW is the spatially most variable water mass among expeditions. During some years, ACW is found across almost the entire southern Chukchi domain (as observed in RUSALCA 2009); in others, it is completely absent, or limited to one to two coastal stations. During some years, the ACW reached as far north as 71°–72°N (e.g., during RUSALCA). Several Russian data sets fail to capture the ACW completely, because the sampling was too far from the Alaskan coast. The colder and salty BSAW was present during every sampling year within the southern and central Chukchi Sea, and was found as far north as 70°–71°N during most study years. BSAW was frequently found underlying the warmer and fresher ACW.

The very cold and salty WW, which forms in the fall and winter months as brine and is expelled during sea ice formation, was found in the bottom waters north of 70°N during colder years and north of 72°N during the warmer years. WW was generally overlaid by MW or advected Pacific water (ACW or BSAW). Fresh and cold SCW was only visible in data sets collected close to the Russian coast, and only during some expeditions (*Severnyj Poljus*, 1946; *Lomonosov*, 1953; BERPAC, 1988; RUSALCA, 2009–2012). In September 2012, this water type was found in the central Chukchi, well away from the Siberian coast; it is possible that this water is partially ice meltwater, rather than belonging to the SCW.

### Physics Shaping Planktonic Communities

Within each individual year, bottom temperature was most commonly the strongest factor shaping community structure,
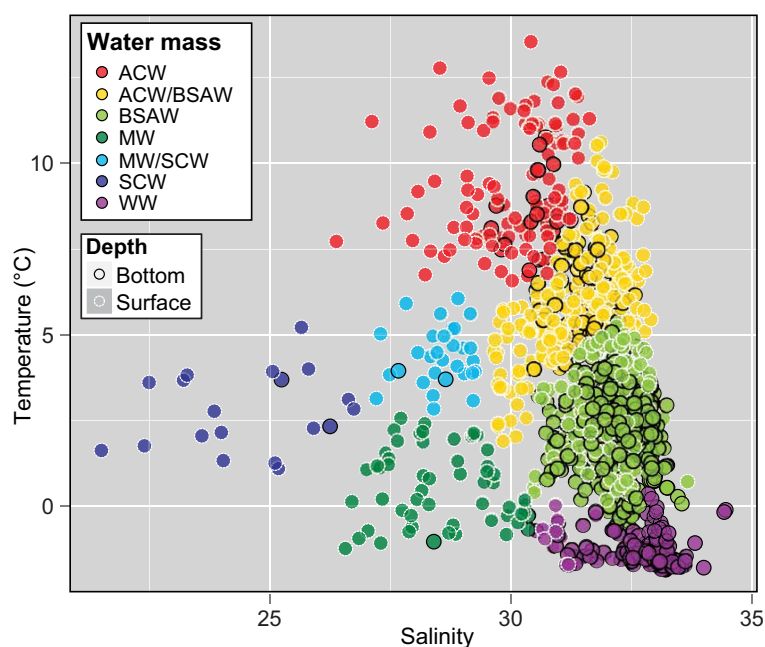


**FIGURE 2.** Temperature-salinity plot of water masses sampled concurrent with zooplankton collections in the Chukchi Sea, 1946–2012 (top/bottom 10 m properties). ACW = Alaska Coastal Water. BSAW = Bering Sea/Anadyr Water. MW = Melt Water. SCW = Siberian Coastal Water. WW = Winter Water.

although in some years it was surface temperature (Table 2). Including salinity improved the correlation in several instances. Salinity was the most important factor during 1949, both cruises in 1986, and June 1988. The relationship between physical properties of the water column and community structure was generally very pronounced, with Spearman's correlations being 0.4–0.7.

## Annual Biomass

Average yearly biomass in the southern Chukchi domain (south of 71°N and east of 180°W) ranged from 10–140 mg DW m$^{-3}$ (average for all years ~65 mg DW m$^{-3}$), with variability between stations during some cruises spanning four orders of magnitude (0.5–700 mg DW m$^{-3}$; supplementary Table S1). Substantially lower biomass (<50 mg DW m$^{-3}$) was observed during most of the earlier study years (pre-1980), with the notable exception of 1954, when the biomass, driven by large copepods, was significantly above average at several stations (overall mean 85 mg DW m$^{-3}$). Notably, summer temperatures were also warmer in 1954 and ice extent was reduced compared to other years of that time period (Figure 1). During the later
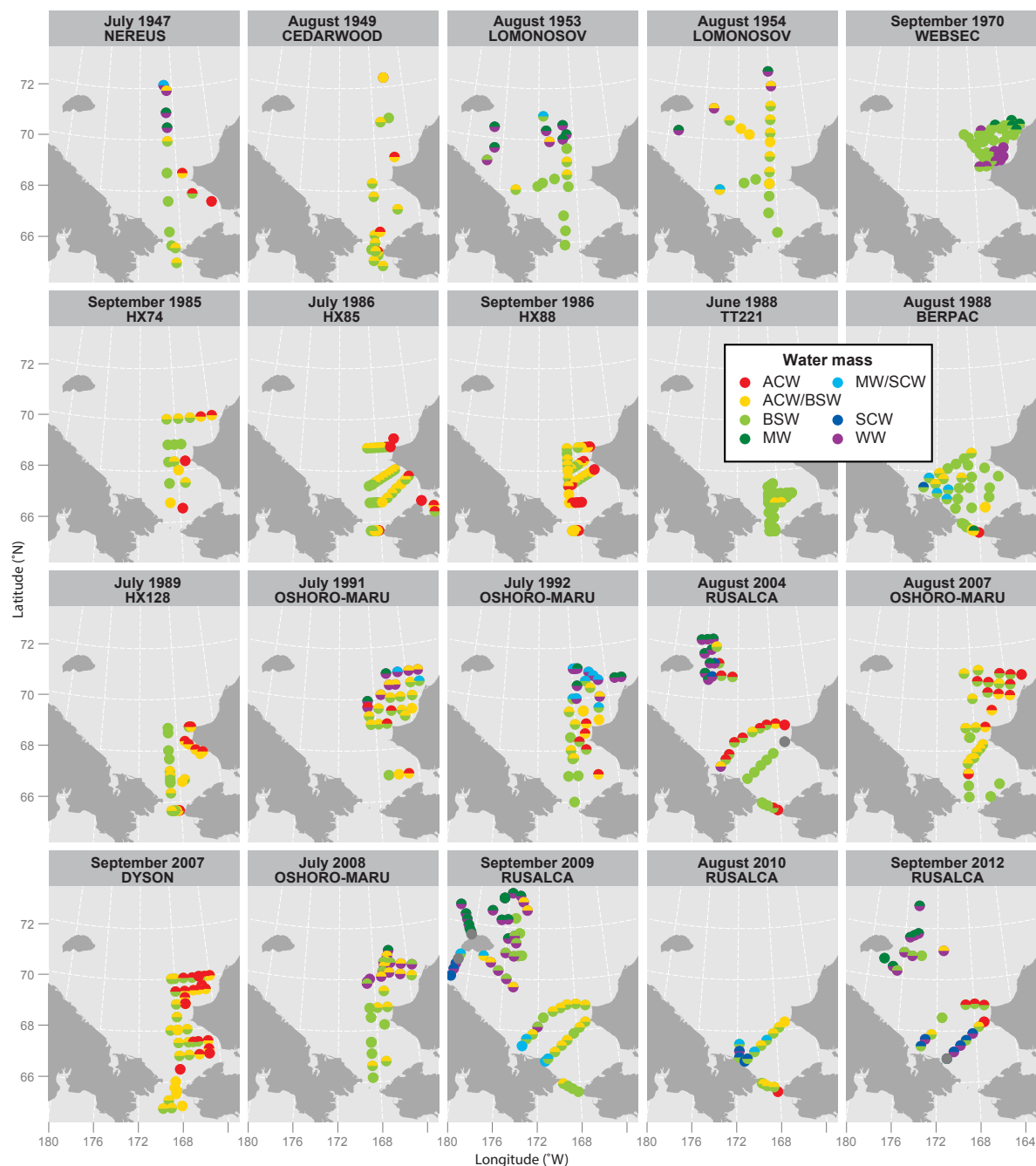


**FIGURE 3.** Distribution of water masses sampled in the Chukchi Sea, 1946–2012. Upper color on each symbol represents surface water type (top 10 m average), and lower color represents bottom water type (bottom 10 m average). ACW = Alaska Coastal Water. BSAW = Bering Sea/Anadyr Water. MW = Melt Water. SCW = Siberian Coastal Water. WW = Winter Water.

sampling years (1991–2012), the observed biomass was relatively similar, averaging 50–100 mg DW m$^{-3}$. The best fitting mixed model as determined by AIC included year, month, water mass, and PDO/AO index. When examined over the entire southern sampling region, the increase in biomass observed over the seven decades was highly significant ($p < 0.01$) (Figure 4), with an average increase of 10 mg DW m$^{-3}$ per decade. Stations containing BSAW or BSAW/ACW had significantly higher biomass (by an average of 20–30 mg DW m$^{-3}$) than stations containing other water mass types. Stations containing SCW had the lowest biomass of all water masses (supplementary Table S2). Mean PDO signal accounted significantly ($p <0.05$) for some additional variability in biomass, with higher biomass observed during the cold phase PDO years. The years sampled earlier in the summer (July) had significantly higher biomass than those sampled in the period from August to October; the only spring sampling (on cruise TT221 in 1988) showed substantially lower biomass than sampling in August the same year by the same investigators (supplementary Table S2).

Given the strong association between water masses and planktonic communities, as well as the substantial differences in biomass between them, we will structure subsequent biological characterization around the water mass types.

## Alaska Coastal Water Communities

Alaska Coastal Water stations were defined as those that contained ACW at least in the surface layer. While this definition introduces a certain degree of noise due to the nature of depth-integrated plankton data in a vertically layered physical environment, it allows us to compare these communities broadly between years. Typically, communities inhabiting ACW were dominated by small copepods (*Pseudocalanus* spp., *Acartia* spp., *Oithona* spp.), meroplankton (mostly barnacle and bivalve larvae), and cladocerans, which were common during some years and nearly absent in others (Figure 5). Large, heavy Pacific copepods were absent or scarce within these communities; as a result, total biomass was generally lower than that observed in Bering Sea waters (supplementary Table S2). Other taxa (chaetognaths, larvaceans) were present variably. The communities identified in ACW waters for the study year 2012 (RUSALCA) exhibited an unusually high biomass of large copepods and near absence of meroplankton. The elevated biomass of large copepods is likely a consequence of the presence of significant volumes of BSAW very close to the Alaskan coast and the layering of ACW and BSAW. The absence of meroplankton, on the other hand, could be due to the late timing of the cruise and the abnormally cold temperatures observed during that year.

Overall, the distribution of species characteristic of ACW (Table 3, supplementary Figure S2) corresponds closely to

**TABLE 2.** Pearson correlations ($\rho$) of variables determined via BIOENV analysis relating species abundance and physical parameters. T.surf/S.surf = surface temperature/salinity. T.btm/S.btm = bottom temperature/salinity.

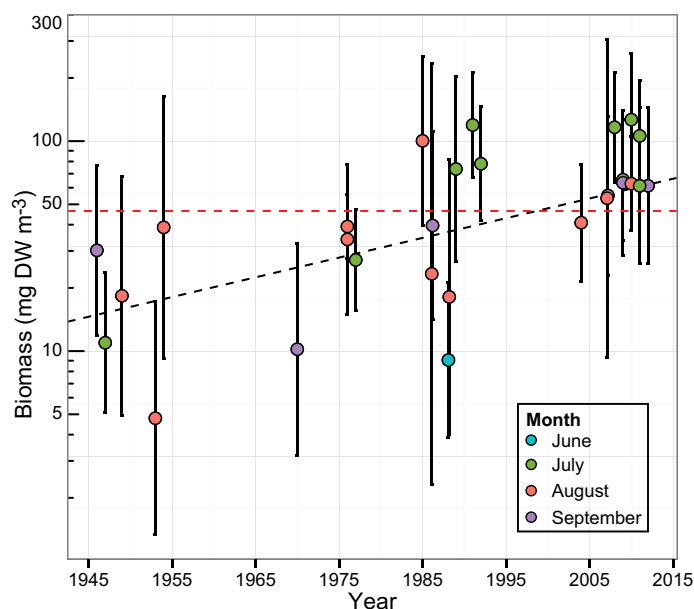| CRUISE/Ship | YEAR | MONTH | ENV. PARAMETERS ($\rho$) |
|---|---|---|---|
| *Nereus* | 1947 | July | T.btm, 0.56 |
| *Cedarwood* | 1949 | August | S.surf, 0.498 |
| *Lomonosov* | 1953 | August | T.surf, 0.2 |
| *Lomonosov* | 1954 | August | T.btm, 0.25 |
| HX74 | 1985 | Aug–Sep | T.btm, S.btm, 0.41 |
| HX85 | 1986 | July | S.surf, S.btm, 0.66 |
| HX88 | 1986 | Aug–Sep | S.btm, 0.45 |
| BERPAC | 1988 | August | T.btm, 0.45 |
| TT221 | 1988 | June | S.surf, 0.43 |
| HX128 | 1989 | July | T.btm, 0.38 |
| *Oshoro-Maru* | 1991 | July | T.btm, 0.34 |
| *Oshoro-Maru* | 1992 | July | T.btm, 0.39 |
| RUSALCA | 2004 | August | T.btm, S.btm, 0.65 |
| *Oshoro-Maru* | 2007 | August | T.surf, S.btm, 0.48 |
| *Oshoro-Maru* | 2008 | July | T.surf, S.surf, 0.28 |
| RUSALCA | 2009 | September | T.btm, S.btm, 0.6 |
| RUSALCA | 2010 | August | T.btm, 0.7 |
| RUSALCA | 2012 | September | T.surf, 0.55 |



**FIGURE 4.** Mean log-transformed biomass vs. year sampled in the Chukchi Sea. Each symbol represents one cruise; bars represent 95% confidence interval. Black dashed line indicates fitted linear trend over averaged data. Red dashed line indicates long-term mean.

the stations where ACW was present, although one of the species (*Centropages abdominalis*), while most common in ACW, was also present in smaller numbers in other water masses. Similar to water mass distribution, the distribution of ACW-specific taxa is highly variable year to year; during some years, these organisms are localized to a few stations near the Alaskan coast while in others they are found throughout the entire Chukchi domain.

Some species, such as the hydrozoan medusae *Aglantha digitale* were largely confined to the ACW during most years, although in some years they occurred across the entire Chukchi domain (supplementary Figure S3). September 1970 (WEBSEC) stood out among all the sampling years because *A. digitale* dominated the plankton communities in both absolute numbers and biomass, exceeding even the copepods. Data from others years contain very few cases of this species or no records at all (which could be due to sampling or identification bias—in some data sets, all medusoids were grouped into a broad "Cnidaria" category).

## Bering Sea (BSAW) Communities

BSAW and BSAW/ACW, the most common water masses observed during each sampling year, contained the highest zooplankton biomass (supplementary Table S2). These waters were dominated by large Pacific copepods (Figure 5), which typically comprised 50–80% of the total biomass. Of the four most important large copepod taxa, *Calanus glacialis* and *Metridia pacifica* are shelf species, while *Neocalanus* spp. and *Eucalanus bungii* are more characteristic of oceanic Anadyr Waters. The abundance of *M. pacifica*, *E. bungii*, and *Neocalanus* spp. in BSAW was extremely variable, spanning up to three orders of magnitude during a single expedition, as well as from year to year (Figure 6). Generally, the distribution of these species follows the pathway of the BSAW, with decreasing abundances to the north and to the west (Figure 7). The timing of each expedition played a critical role in the abundances observed because the advection of these species is closely linked to their life cycles in the Bering Sea. For example, in 1986 and 1988, *Metridia pacifica* was nearly absent in the plankton in the earlier months (July and June), but was highly abundant just two months later (September and August). The best-fitting mixed model describing all three species as determined by AIC included year, month, and bottom temperature (supplementary Tables S3–S6). There is a slight but significant ($p < 0.01$) trend toward increasing abundance of all three species in Bering Sea waters over the study period. Abundances of these copepods, especially *Eucalanus bungii*, also correlated positively ($p < 0.01$) to water temperature observed during each cruise (Figure 8). Both surface and bottom water temperatures were significant factors, with the best model containing bottom temperature. There was no correlation of abundance to salinity or station depth, and the inclusion of the AO or
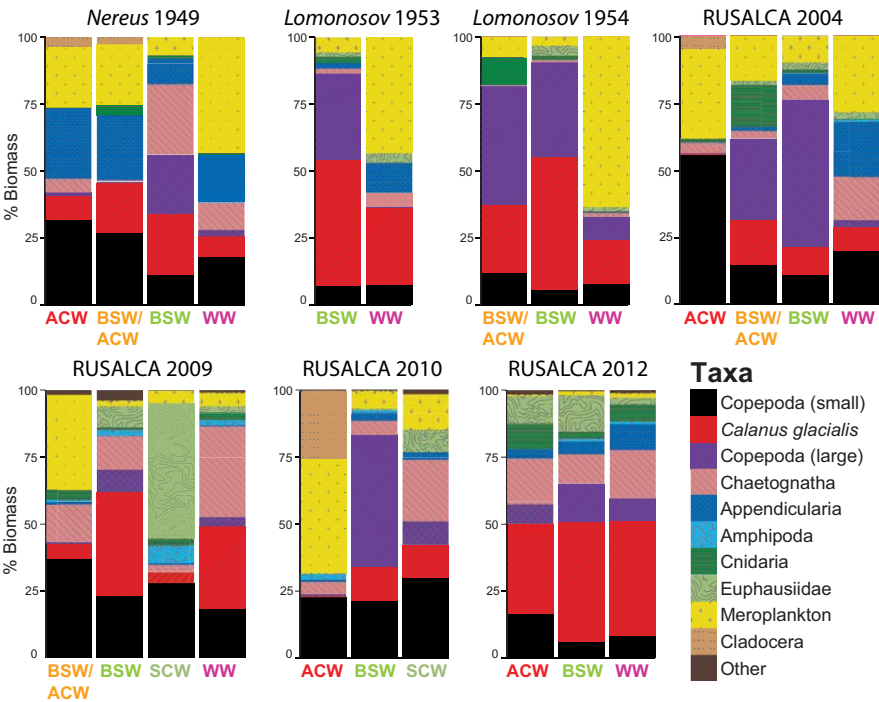


**FIGURE 5.** Relative contribution to biomass of different taxonomic groups in the Chukchi Sea during several of the study years (only years sampled by 100–200 μm mesh nets reported due to under sampling of smaller taxa by coarser nets).

**TABLE 3.** List of mesozooplankton species characteristic of Alaska Coastal Waters.

| SPECIES | TYPICAL BODY LENGTH (μM) (ALL STAGES) | INCLUDED IN DISTRIBUTION MAP (SUPPLEMENTARY FIGURE S2) |
|---|---|---|
| *Evadne nordmanni* | 500–1,200 | yes |
| *Podon leuckarti* | 150–1,200 | yes |
| *Acartia hudsonica* | 250–1,000 | no |
| *Eurytemora* spp. | 300–1,000 | no |
| *Centropages abdominalis* | 400–1,400 | yes |
| *Pseudocalanus newmani* | 300–1,000 | no |
| *Epilabidocera longipedata* | 2,000–4,000 | yes |
| *Tortanus discaudatus* | 1,000–3,000 | yes |

PDO index for each year did not improve the model for any of the species.

*Calanus glacialis* was the most important contributor to biomass during every cruise (Figure 5) with the exception of September 1970, when biomass was dominated by the hydrozoan *Aglantha digitale*. Abundance of *Calanus glacialis* was typically less variable than it was for the Pacific oceanic species, with the standard deviation for each cruise generally spanning only a single order of magnitude (Figure 6). The factors for the best-fitting mixed model describing *C. glacialis* abundance included year, month, and PDO/AO. There is a significant (p <0.01) trend of increasing average abundance of this species in the Chukchi Sea within Bering Sea waters (~10 ind m$^{-3}$ per decade). The inclusion of temperature or salinity as a factor in the model did not account for any additional variability between years; however, a significant relationship (p <0.01) between *C. glacialis* abundance and PDO/AO signal (six-month winter average; Figure 9) was observed in BSAW waters, with higher abundances during the lower PDO years and the higher AO years.

### Resident Chukchi (WW) Communities

Winter Water communities were defined as those sampled at stations containing WW in at least the bottom layer. These waters are typified by "resident" Chukchi communities composed of species that can overwinter and/or reproduce beneath the winter sea ice. These species are shared with other Arctic shelf seas, but are not generally found in Bering Sea waters (Ershova et al., 2015). Copepods contribute only about 50% of the biomass of these assemblages, and there is a high biomass of gelatinous taxa, such as chaetognaths and larvaceans (Figure 5). During the summer months, a very high percentage of meroplankton (mainly barnacle larvae) was observed; in contrast, during the two September cruises, meroplankton were nearly absent. Some of the organisms common in these communities

include a number of shelf "Arctic" species (e.g., *Microcalanus pygmaeus*, *Metridia longa, Aeginopsis laurentii*); ice-associated taxa, such as the copepod *Jaschnovia brevis* and the amphipod *Apherusa glacialis*; and a number of hydrozoan jellyfish that have a benthic polyp stage and are therefore limited in spatial distribution (e.g., *Halitholis cirratus*, *Catablema visicarium*, *Plotocnide borealis*).

Large Bering Sea copepods were scarce within these communities, although they were present in small numbers, particularly during the recent sampling years. Average abundance north of 70°N and east of 175°W of *Eucalanus bungii*, *Neocalanus* spp., and *M. pacifica* suggests a small trend toward increasing abundance during the later years (Figure 10) (significant for *Neocalanus* spp., p <0.001 and nonsignificant [p = 0.2] for *M. pacifica* and *E. bungii*). While there was a significant presence of *Calanus glacialis* in Chukchi Winter Water (Figure 5), their developmental stage distribution (Figure 11) suggests that they belong to

a different population than the one carried into the Chukchi with Bering Sea waters (see below).

### *Calanus glacialis* Stage Distribution and Shifting Phenology

The stage distribution of *C. glacialis* is a good indicator of the overall seasonal state of the zooplankton community. Fall communities were mainly dominated by fifth stage copepodites (C5), while earlier in the summer the community was typically composed of C3–C4 stages. There is a strong significant relationship between mean developmental stage and surface temperature (p <0.01, R$^2$ = 0.4), and the communities sampled during the "warm" summers of 1954, 1992, and 2004 (July/August) are as far along in their development as those sampled over a month later during the "cold" years 2009 and 2012. This observation implies that yearly variability in seasonal succession can be quite pronounced, which further confounds year-to-year comparisons of
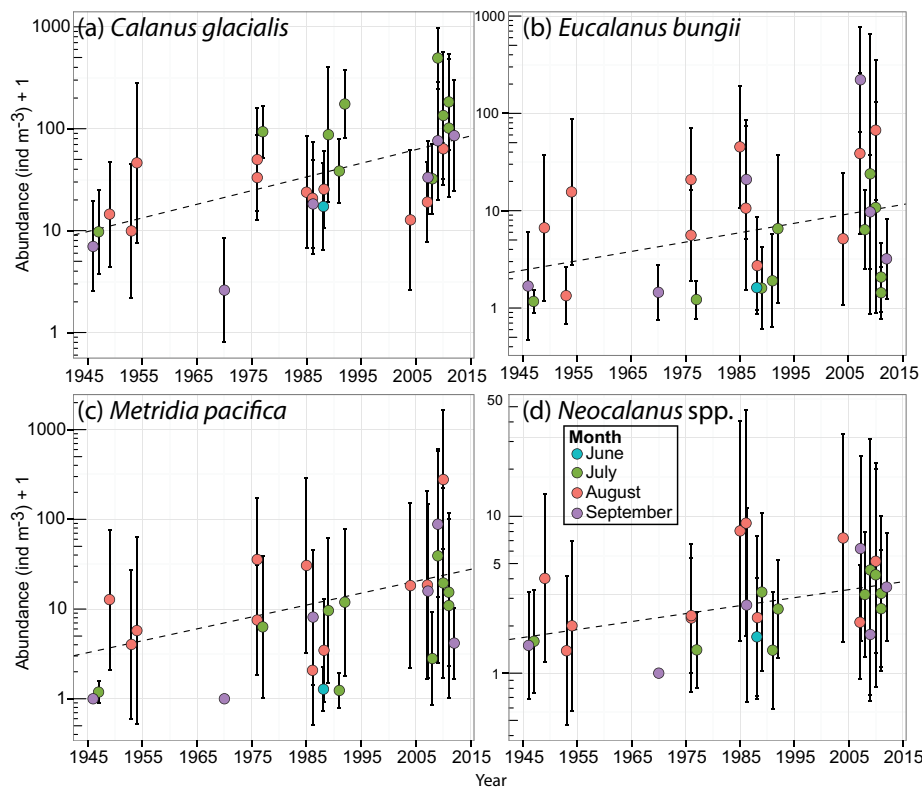


**FIGURE 6.** Interannual variability of Pacific copepod species abundance in the Chukchi Sea during 1946–2012. Each symbol represents one cruise; bars indicate 95% confidence interval. Dashed line shows fitted linear trend over averaged data.

communities. It is notable that our stage data also suggest there are likely two or more distinct populations present in the area (Figure 11). Bering Sea waters during late summer generally contain mostly late-stage (C4–C5) copepodites, while the *C. glacialis* population within resident Chukchi waters (WW) is composed of young C1–C3 stages. Since these populations likely respond differently to environmental factors, more elaborate patterns are probably obscured in regions
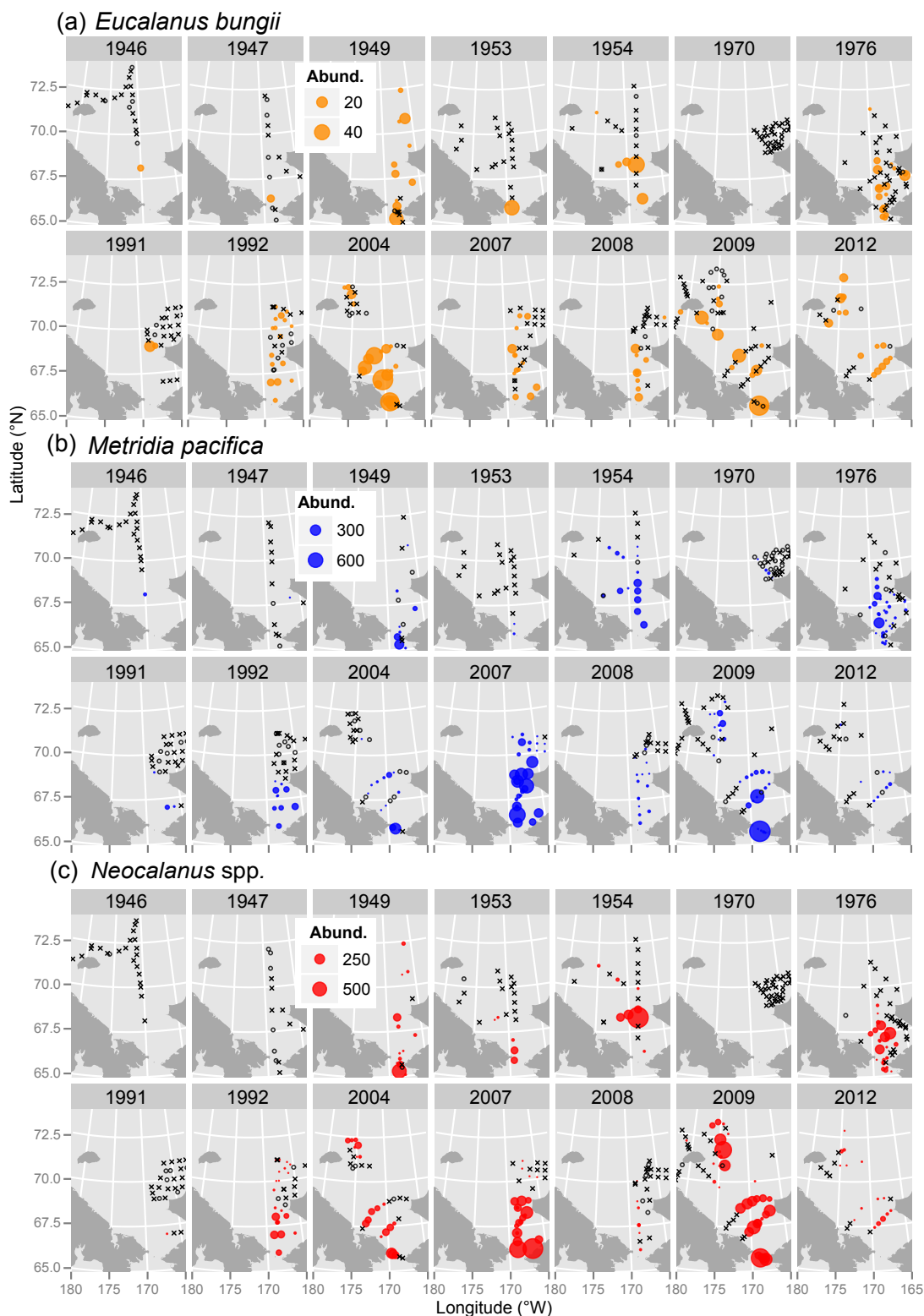


**FIGURE 7.** Abundance (ind m$^{-3}$) of (a) *Eucalanus bungii*, (b) *Metridia pacifica*, and (c) *Neocalanus* spp. in the Chukchi Sea during 1946–2012. o = stations where taxon was present (<1 ind m$^{-3}$). x = stations where taxon was not found.
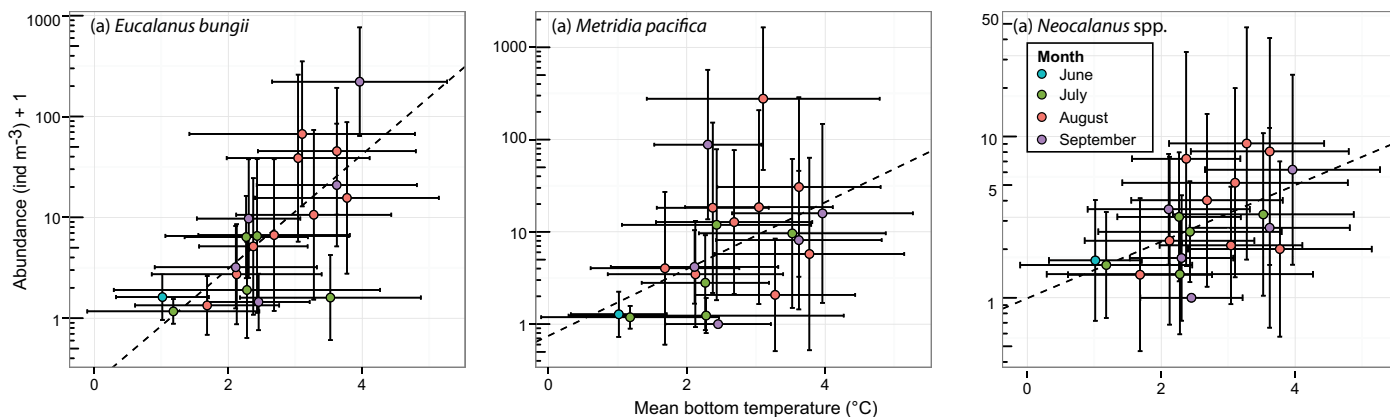
**FIGURE 8.** Relationship of mean abundance of (a) *Eucalanus bungii*, (b) *Metridia pacifica*, and (c) *Neocalanus* spp. to mean temperature in BSAW (each symbol represents one cruise) in the Chukchi Sea during 1946–2012. Bars indicate standard deviation (not on log scale). Dashed line indicates fitted linear trend over averaged data.

where these populations overlap. The "young" state of the Chukchi *C. glacialis* community found around Wrangel Island in September 1946 (mean stage 1.6) compared to 2004, 2009, and 2012 during the same time of year (mean stage 2.2–2.7) suggests a shift in phenology; however, data from one early year are insufficient for drawing any definite conclusions.

## DISCUSSION
## Community Structure and Interannual Variability

Our results represent the first quantitative examination of the changes that have occurred in pelagic communities in the Chukchi Sea over a 70-year period. While overall water mass distribution patterns were similar over the study years, the degree of penetration of these water masses may have changed, with either higher volumes of Bering Sea waters entering the Chukchi Sea during the summer months (Woodgate et al., 2012), or summer BSAW becoming identifiable sooner within the year, and therefore appearing to penetrate further. Despite strong interannual variability, overall community structure (i.e., the proportional contribution of taxa) within each respective water mass also remained relatively similar over the period examined (Figure 5), with strong correlations observed between biological communities and the physical environment (Table 2). Although only temperature and

salinity were available as environmental factors for the historical data sets, recent studies find strongest correlations only to these two variables even when a larger suite of data (e.g., chlorophyll, nutrients, oxygen) is available (Questel et al., 2013). Our data demonstrate that during some years, the patterns and differences between communities in different water masses are highly pronounced (i.e., 1949, 2004), while in others they are weaker or much more subtle (i.e., 2012; Figure 5).

Differences between communities are often shaped by the presence or absence of rarer "indicator" species, while the most common and numerous groups are generally found across the entire sampling domain. The differences in taxonomic resolution as well as in sampling methodologies among the assembled data sets makes it difficult to establish these subtle differences, although they are apparent on a year-to-year basis. Trends are further complicated by the fact that some of the most abundant and ecologically important species (e.g., *Calanus glacialis*, *Aglantha digitale*) may have more than one population present in the area, as suggested by both developmental stage distribution and genetic analysis (Nelson et al., 2009). The obvious trends that we observe here, even when most taxonomic detail is removed from the data, suggest that patterns would be even stronger if consistent higher-resolution taxonomy were available. While some

patterns remain visible throughout most years, the system exhibits extremely high variability in biomass, abundance, and community composition. This inherent variability can easily lead one to confuse interannual differences with long-term change in zooplankton communities when based on only a few study years (i.e., Matsuno et al., 2011). Variable timing of the cruises also contributes to the variability in zooplankton data, since the seasonal progression of the planktonic communities in this region can take place extremely rapidly (Questel et al., 2013). Our data suggest that highest biomass was present in July and then declined toward the fall season, perhaps reflecting changing transport volumes of Pacific water through the Bering Strait.
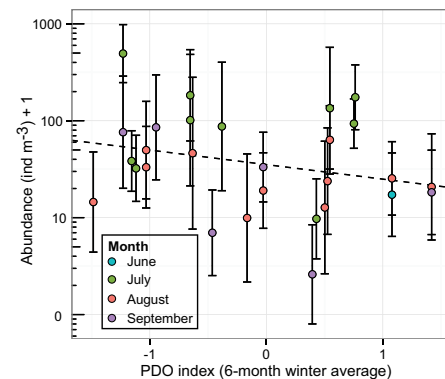


**FIGURE 9.** Relationship of mean abundance of *Calanus glacialis* to the Pacific Decadal Oscillation (PDO) signal (six-month winter average) in the Chukchi Sea during 1946–2012. Bars indicate 95% confidence interval.

## Climatic Oscillations and Regime Shifts

Responses of ecosystems to climate change are often not linear but rather characterized by "tipping points" that occur once a certain threshold is reached (Duarte et al., 2012). When such a point occurs, the system shifts into a new stable state, which may remain even if the physical changes are reversed. However, due to the scarcity of time series of sufficiently long duration, it is very difficult for researchers to discern between permanent systematic change and climate-related oscillations. Abrupt changes in climatological indexes such as the PDO, the NAO, and the AO are often associated with regime shifts in the pelagic environment, which may or may not be reversible. In the North Pacific, such abrupt shifts, characterized by marked changes within all levels of the marine ecosystem, occurred in 1977, 1989, and 2000 (Hare and Mantua, 2000; Brodeur et al., 2008). One of the most prominent changes within the plankton was the steep increase in jellyfish biomass, primarily *Chrysaora melanaster*, in the Bering Sea during 1990, and then its rapid decline after 2000 (Brodeur et al., 2008). These events coincided with climatic oscillations in the Bering Sea from warmer (pre-1989) to cooler, and back to warmer (post-2000) conditions. In some sections of the North Atlantic, the pelagic community also experienced a shift from a sub-Arctic to a more temperate type

in the 1990s; it remains unclear whether these patterns represent a permanent shift (Beaugrand et al., 2009) driven by globally warming temperatures or are associated with shifts in the region's climatic indexes (Greene et al., 2013).

Our results indicate a clear shift toward both higher biomass and higher abundance of zooplankton over the timeframe of 1946–2012; however, the low resolution of our data makes it unclear whether these changes are gradual (linear trend), or if there was a shift toward higher biomass sometime in the 1970s to the 1980s. The high correlation of zooplankton biomass and abundance, particularly *Calanus glacialis*, to AO and PDO indices indicates that the system responds quickly to changes in the environment. The relationship between *C. glacialis* and climate variability has been documented for the Bering Sea shelf, where sequential colder (negative PDO) years generally have much higher biomass of *C. glacialis* (Eisner et al., 2014). The patterns that we observe for this species in the Chukchi Sea, including a negative correlation of zooplankton biomass to PDO signal, likely reflect a diluted signal of these processes in the Bering Sea. The long-term shifts in plankton biomass are also clearly reflected in the higher trophic levels—for example, the significant increase in planktivorous birds that has been observed in the northeastern Chukchi since the 1970s (Gall et al., 2013).

## Shifting Biogeographical Boundaries

In many regions of the world ocean, the geographical ranges of species have been shifting as the climate warms and ocean currents change. One of the most pronounced examples of such a range shift in the plankton has been observed in the Northeast Atlantic using the Continuous Plankton Recorder, which has been collecting data since the 1930s. In this region, the warm-water copepod assemblage containing *Calanus helgolandicus* has shifted northward by more than 10 degrees latitude over the past 50 years and continues to move poleward at a rate of ~22 km yr$^{-1}$ (Beaugrand et al., 2009). In the Arctic Ocean, similar reports include the northward shift of the Atlantic amphipod *Themisto compressa*, which was not previously found in Arctic waters but is now observed successfully reproducing there (Kraft et al., 2013). The ranges of a large number of Bering Sea fish species have also shifted northward over the last two decades (Wassmann et al., in press).

The differences in coverage and the spatial and temporal scarcity of our data make it difficult to estimate conclusively the degree to which biogeographical shifts are occurring for the Chukchi zooplankton. The transit time of water flowing from the Bering Strait to the northwestern Chukchi Sea (Herald Canyon) is estimated to be four to six months (Woodgate et al., 2005; Berline et al., 2008), but it can vary
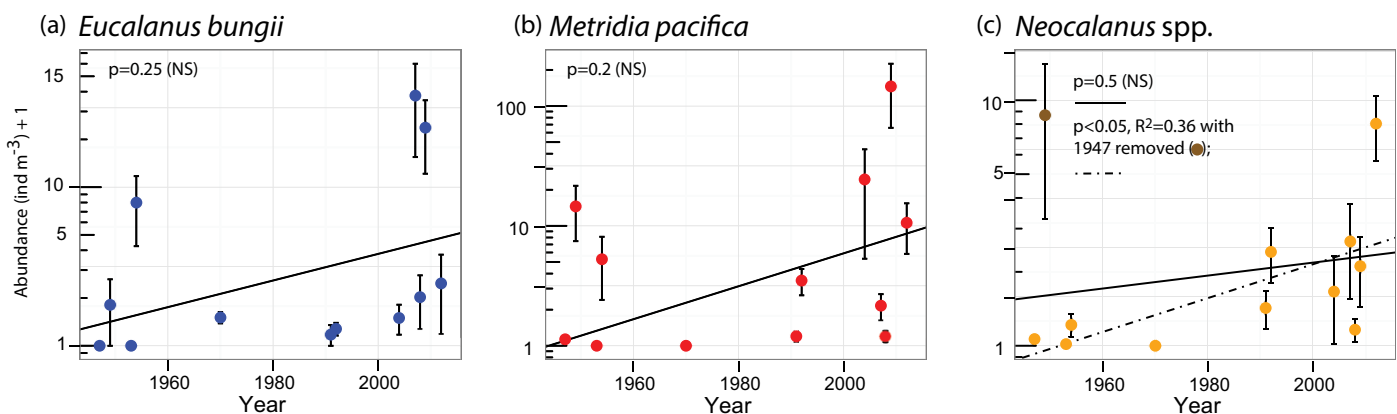


**FIGURE 10.** Mean abundances of (a) *Eucalanus bungii*, (b) *Metridia pacifica*, and (c) *Neocalanus* spp. in the Chukchi Sea north of 70°N and east of 175°W. Bars indicate 95% confidence interval. Solid lines indicate fitted linear trend. Dotted line in (c) indicates fitted trend with one outlier removed.

significantly depending on wind conditions (Winsor and Chapman, 2004), position in the water column, and bathymetry (Berline et al., 2008). Variability in flow time influences the composition and quantity of Pacific zooplankton reaching the shelf break of the Chukchi Sea by the end of the summer, with shorter-lived species having a chance to travel farther north in favorable conditions. Additionally, an earlier onset of "summer" conditions in the Bering Sea and increased inflow of warm Pacific water (Woodgate et al., 2012) together with a longer summer ice-free period should result in advected species developing earlier in the season and being carried farther north, thus playing a role in the local communities for a longer period of time. Currently, the limited stage distribution data available are too scant to determine conclusively whether any phenological shifts are taking place in the resident Chukchi Sea communities or the advected Bering Sea communities. However, the distribution maps for the Pacific copepods *M. pacifica* and *Neocalanus* spp. are certainly suggestive of their displacement northward. While

these species were observed at a few individual stations above 70°N during the early sampling years, they were generally present at more or less every station during the 1990–2000 period (Figure 7), with a trend of increasing abundance at higher latitudes during the later years. Plankton surveys in the central Arctic Basin have reported occurrence of these species in the high Arctic plankton communities, although they are usually found in very small numbers (e.g., Kosobokova and Hopcroft, 2010). While it is unlikely that these Pacific organisms are able to survive and reproduce in the cold and nutrient-poor waters of the Arctic, an increasing inflow of these species could have significant local impact for the plankton-feeding predators within the region.

## The Fate of Chukchi Sea Zooplankton

The Chukchi Sea is an advection-dominated system, with the majority of its water masses arriving directly from the North Pacific via the Bering Strait. Therefore, a significant proportion of the zooplankton communities within this region are

"in transit," as opposed to being produced locally. Most of the Pacific plankton transported through the Bering Strait do not make it to the deep Arctic Ocean (Wassmann et al., in press) due to a generally shorter life span of these species and failure to reproduce in the near-freezing Arctic waters. The shock of sub-zero temperatures and scarcity of available food together with their reduced ability to store lipids are likely to contribute to mortality and make many expatriated species unlikely to survive the Arctic winter.

One of the large knowledge gaps remaining for the Chukchi region is the lack of understanding of the processes that take place in the biological communities during the winter months, when the sea is completely covered with ice and water temperatures are below zero from surface to bottom. To date, no sampling efforts exist for examining the system during the peak of winter (January–March). While summer communities are largely affected by warming temperatures and a longer ice-free period, we assume that during winter the system "resets" itself and communities revert from being
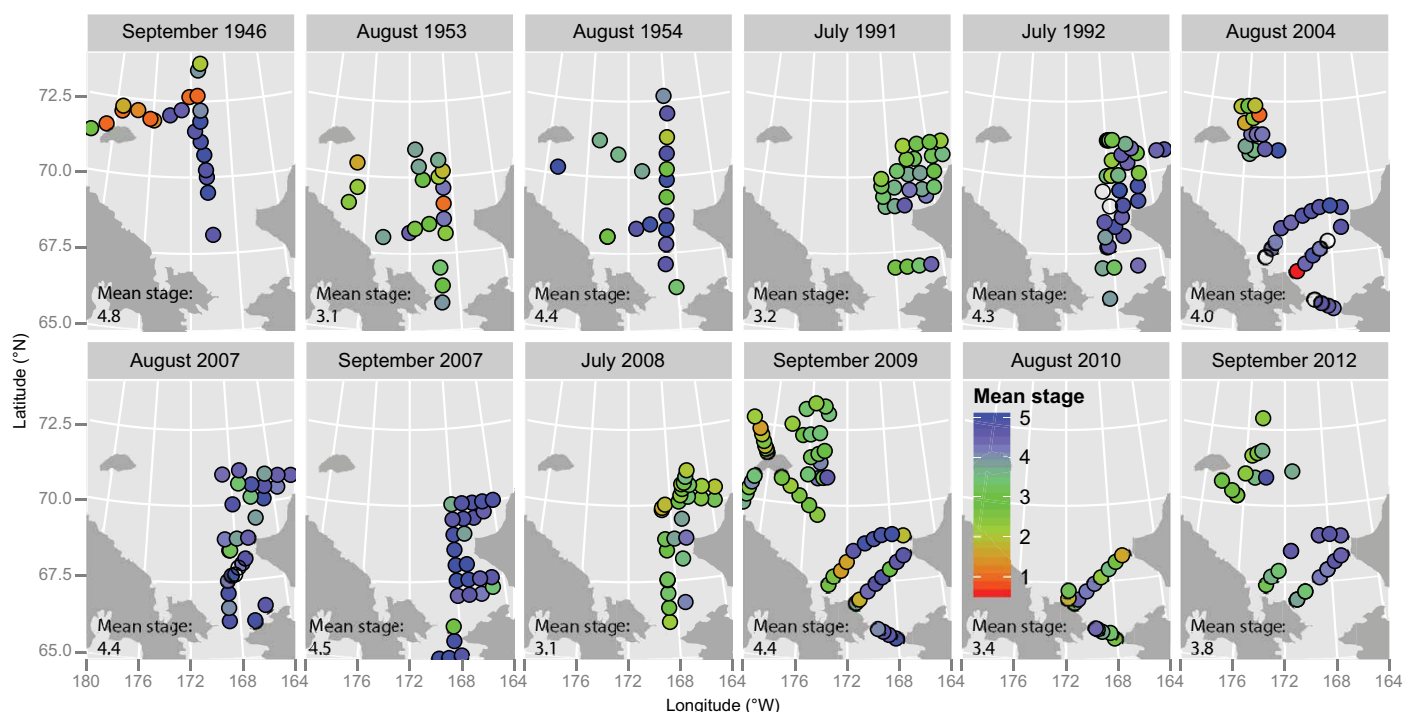


**FIGURE 11.** Distribution of mean copepodite stages of *Calanus glacialis* in the Chukchi Sea during 1946–2012 (copepodite data is only available for this subset of cruises).

mainly Pacific to mainly Arctic in character. This is partially confirmed by the scarcity of Pacific species within the WW communities. The vast majority of the planktonic biomass transported into the Arctic from the North Pacific remains within the Chukchi Sea and becomes food for the local fish, bird, marine mammal, and benthic communities. Bowhead whales alone are estimated to consume one-third of the zooplankton biomass advected through the Bering Strait (Wassmann et al., in press). The presence of advected Pacific euphausiids on the Chukchi and Beaufort shelves (Ashjian et al., 2010; Moore et al., 2010), as well as in the Siberian Coastal Current (Moore et al., 1995), can drive the seasonal migrations of whales in this area, as they have been found to comprise 60–90% percent of the stomach contents in bowhead whales (Moore et al., 2010). Nonetheless, the Chukchi's euphausiids are considered primarily an expatriate population (Berline et al., 2008).

The majority of Bering Sea *Calanus glacialis*, which represents the bulk of biomass transported through the Bering Strait, most likely does reach far past the Chukchi shelf break. The younger *C. glacialis* found in resident Chukchi waters likely represent a distinct "local" population shared with adjacent Arctic shelf seas; alternately, they may be produced by overwintering females that were advected during the previous summer. However, the sharp boundary between the Pacific/Bering and Arctic haplotypes (Nelson et al., 2009), the absence of the Pacific haplotype within the Canada Basin, and the strong pattern observed in distribution of developmental stages (Figure 11) together suggest that the majority of the advected Pacific population of *C. glacialis* are unable to survive the Arctic winter and reproduce in the Arctic Ocean. Preliminary results of population genetics of this species suggest that there is a single population of this species within the Arctic Basin (Agata Weydmann, Polish Academy of Sciences, *pers. comm.*, 2015).

## SUMMARY AND FUTURE DIRECTIONS

While our results are far from a robust time series, they present the first evidence of change within planktonic communities of the western Chukchi Sea over the last 70 years. A significant increase in zooplankton biomass, mostly driven by an advected population of the copepod *Calanus glacialis*, was observed within the southern Chukchi Sea, which likely reflects increasing inflow of biomass-rich Pacific water during the extended summer months. A trend is also observed that suggests a northward shift of Pacific species into the Chukchi Sea, which may be driven by a longer ice-free period and extended warmer summer temperatures combined with a shifting phenology favoring earlier development of species. While summer zooplankton communities of the Chukchi Sea have been primarily Pacific in character for as long as our records report, continuing warming and ice loss may further increase the influence of Pacific fauna within the Chukchi region. Our data show that the success of the key advected species is largely correlated with water temperature, so increases in abundance of these species with future warming are expected. Our findings are consistent with numerous other studies reporting climate-related changes propagating from the environment to the biological communities, both within the Pacific Arctic region and in other parts of the Arctic. To become robust, future sampling efforts need to be directed toward creating a continuous time series, with consistent methods and sampling periods, in order to better understand and predict the distribution of communities in a changing Chukchi Sea. ⓒ

### SUPPLEMENTARY MATERIALS

Supplemental Figures S1–S3 and Tables S1–S6 are available online at http://dx.doi.org/10.5670/oceanog.2015.60.

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## ARTICLE CITATION

## Supplemental Materials for

## Long-Term Changes in Summer Zooplankton Communities of the Western Chukchi Sea, 1945–2012

**FIGURE S1.** Mean six-month winter index values for the Pacific Decadal Oscillation (PDO) and the Arctic Oscillation (AO). Black dots indicate zooplankton biomass anomaly.



**FIGURE S2.** Distribution of Alaska Coastal Water (ACW) indicator species (listed in Table 2) in the Chukchi Sea during 1946–2012. o = stations where taxon was present (<10 ind m$^{-3}$). x = stations where taxon was not found.

**FIGURE S3.** Distribution of *Aglantha digitale* in the Chukchi Sea during 1946–2012. o = stations where taxon was present (<1 ind m⁻³). x = stations where taxon was not found.

**TABLE S1.** Summary of data sets. Taxonomic resolution: Low: <30 species. Medium: 30–50 species. High >50 species. Methods of calculating biomass: (1) biomass from abundance data using mean weights from literature; (2) length-weight regressions; (3) wet weight converted to dry weight; and (4) preserved wet weight with correction for weight loss. SST = sea surface temperature. DW = dry weight.

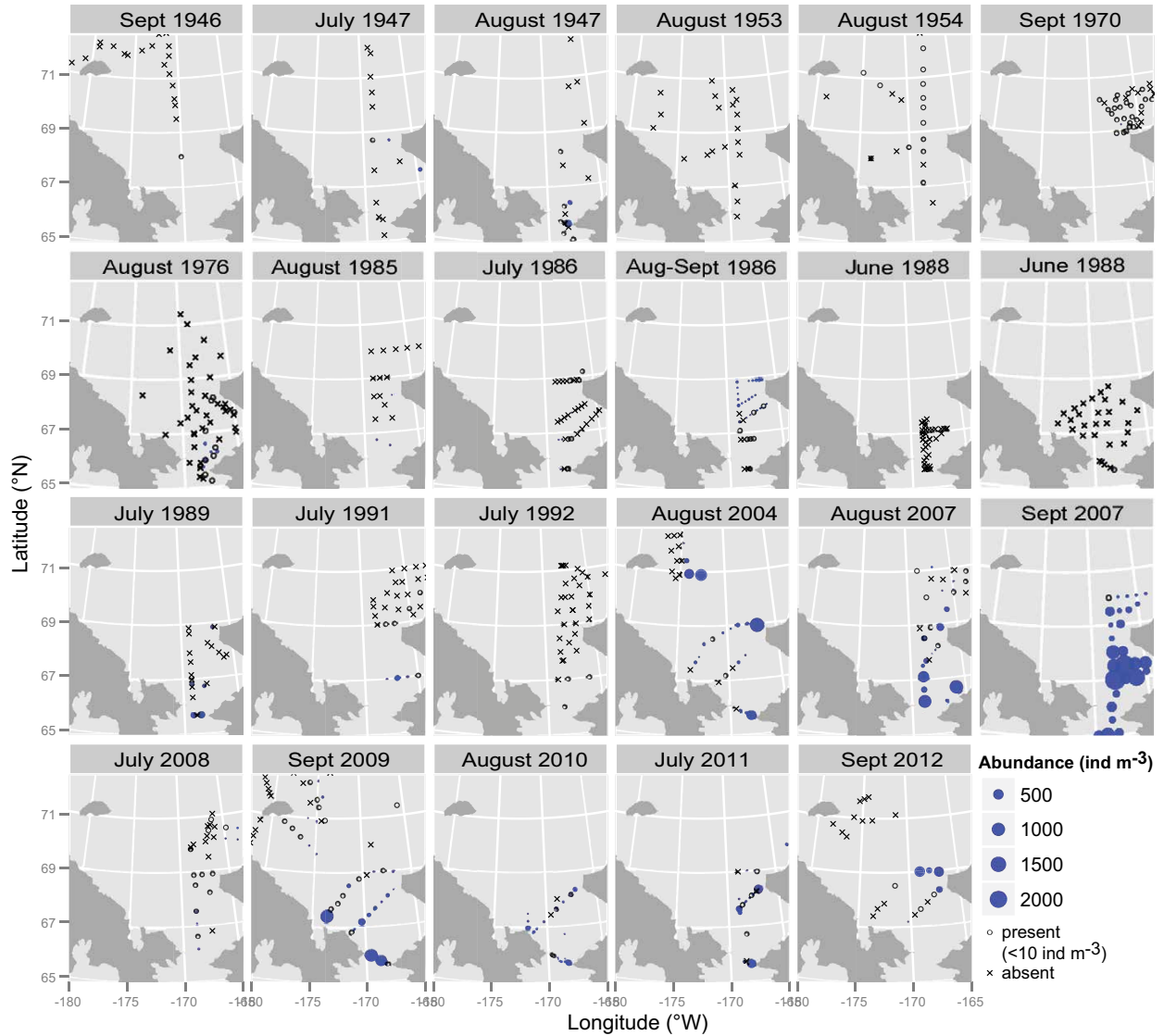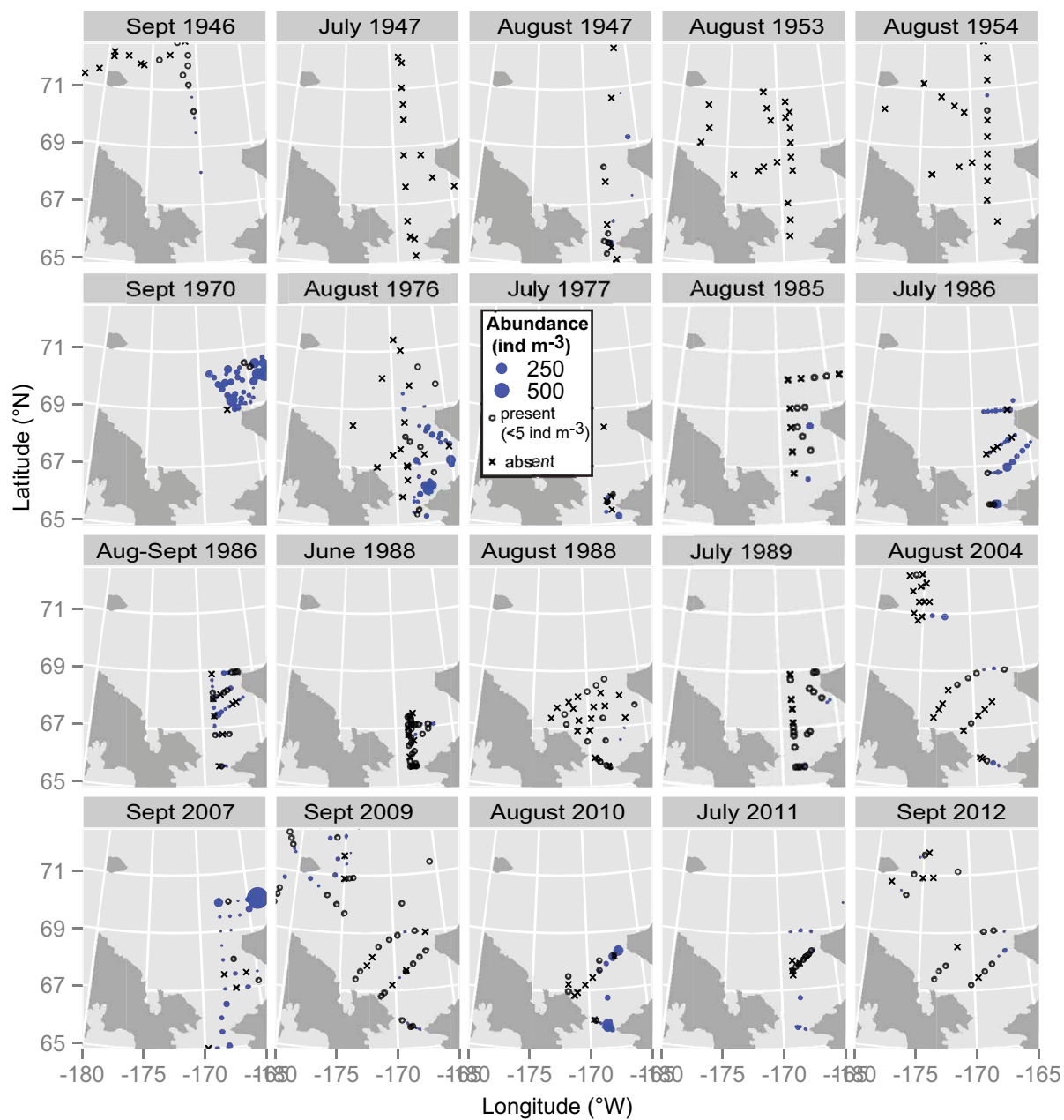| EXPEDITION/Ship | Year | Month | No. of Stations | Mesh size | CTD Data | Mean SST | Taxonomic Resolution | Biomass Method | Mean Biomass (mg DW m$^{-3}$) | Mean Abund. (ind m$^{-3}$) | Source |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Severnyj Polyus* | 1946 | Sep | 36 | 167 µm Juday | NO | 2.16 | High | 1 | 23.7 | 1,621 | Unpublished and Markhaseva et al. (2005) |
| *Nereus* | 1947 | July | 14 | 500 µm | YES | 2.14 | Medium | 1 | 13.5 | 2,500 | Johnson (1953) |
| *Cedarwood* | 1949 | August | 21 | ~150 µm | YES | 2.20 | High | 2 | 28.7 | 1,068 | Unpublished |
| *Lomonosov* | 1953 | August | 19 | 333 µm | YES | 3.27 | Low | 3 | 10.35 | 254 | Unpublished |
| *Lomonosov* | 1954 | August | 21 | 333 µm | YES | 3.41 | Medium | 3 | 84.75 | 2,986 | Unpublished |
| WEBSEC/CGC *Glacier* | 1970 | Sep-Oct | 39 | 570 µm | YES | 3.24 | Medium | 1 | 17.7 | 114 | Ingham et al. (1972) |
| *Mayak* | 1976 | August | 25 | 167 µm Juday | NO | 4.93 | Low | 3 | 46.3 | 4,104 | Pavshtiks (1984) |
| OSCEAP/*Discoverer* | 1976 | August | 25 | 333 µm | NO | 4.93 | Medium | 1 | 41.6 | 537 | Unpublished |
| OSCEAP/*Surveyor* | 1977 | July | 7 | 333 µm | NO | 3.64 | Medium | 1 | 49.1 | 1,212 | Unpublished |
| ISHTAR HX74/*Alpha Helix* | 1985 | Aug-Sep | 16 | 505 µm | YES | 4.72 | Low | 4 | 141.9 | 415 | Springer et al. (1989) |
| ISHTAR HX85/*Alpha Helix* | 1986 | July | 38 | 505 µm | YES | 4.24 | Medium | 4 | 84.4 | 252 | Springer et al. (1989) |
| ISHTAR HX88/*Alpha Helix* | 1986 | Aug-Sep | 38 | 505 µm | YES | 5.39 | High | 4 | 57.1 | 247 | Springer et al. (1989) |
| ISHTAR TT221/*Thomas Thompson* | 1988 | June | 24 | 505 µm | YES | 1.5 | Low | 4 | 13.4 | 225.5 | Unpublished |
| BERPAC/*Akademik Korolev* | 1988 | August | 32 | 505 µm | YES | 3.92 | Medium | 4 | 33.1 | 147 | Kulikov (1992) |
| ISHTAR HX128/*Alpha Helix* | 1989 | July | 42 | 505 µm | YES | 3.62 | Medium | 4 | 106.7 | 337 | Unpublished |
| *Oshoro-Maru* | 1991 | July | 27 | 333 µm | YES | 5.0 | Medium | 3 | 117.5 | 1,616 | Matsuno et al. (2011) |
| *Oshoro-Maru* | 1992 | July | 34 | 333 µm | YES | 4.7 | Medium | 3 | 76.4 | 1,110 | Matsuno et al. (2011) |
| RUSALCA/*Khromov* | 2004 | August | 34 | Bongo 150 µm | YES | 6.3 | High | 2 | 49.7 | 5,762 | Hopcroft et al. (2010) |
| *Oshoro-Maru* | 2007 | August | 31 | 333 µm | YES | 8.9 | Medium | 3 | 91.7 | 1,728 | Matsuno et al. (2011) |
| *Oscar Dyson* | 2007 | Sep | 25 | 505 µm/150 µm | YES | 9.6 | High | 1 | 175/57 | 64/1,348 | Eisner et al. (2012) |
| *Oshoro-Maru* | 2008 | July | 28 | 333 µm | YES | 3.4 | Medium | 3 | 119.2 | 2,771 | Matsuno et al. (2011) |
| *Laurier* | 2009 | July | 5 | Bongo 150 µm | NO | 4.9 | High | 2 | 76.4 | 4,061 | Unpublished |
| RUSALCA/*Khromov* | 2009 | Sept | 60 | Bongo 150 µm | YES | 3.2 | High | 2 | 72.1 | 8,967 | Ershova et al. (2015) |
| *Laurier* | 2010 | July | 16 | Bongo 150 µm | NO | 5.4 | High | 2 | 170 | 16,313 | Unpublished |
| RUSALCA/*Khromov* | 2010 | August | 17 | Bongo 150 µm | YES | 5.6 | High | 2 | 70.7 | 14,070 | Ershova et al. (2015) |
| *Laurier* | 2011 | July | 23 | Bongo 150 µm | NO | 5.5 | High | 2 | 126.6 | 12,327 | Unpublished |
| RUSALCA/*Khromov* | 2011 | July | 9 | Bongo 150 µm | NO | 5.5 | High | 2 | 98.1 | 2,359 | Unpublished |
| RUSALCA/*Khromov* | 2012 | Sep | 25 | Bongo 150 µm | YES | 2.6 | High | 2 | 85.4 | 3,224 | Ershova et al. (2015) |

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**TABLE S2.** (a) Summary and (b) comparisons between least squares means for factors (only significant comparisons reported) for the mixed model log(Biomass) ~ Year + Month + PDO + Water mass +Gear + 1|Facet. PDO = Pacific Decadal Oscillation. ACW = Alaska Coastal Water. BSAW = Bering Sea/Anadyr Water. WW = Winter Water. SCW = Siberian Coastal Water.

| (a) | Factor | Estimate | Standard Error | df | t-value | p-value |
|---|---|---|---|---|---|---|
| Intercept | – | −22.5428 | 2.5479 | 451 | −8.8475 | *** |
| Year | – | 0.0119 | 0.0012 | 451 | 9.3447 | *** |
| PDO index | – | −0.0949 | 0.0272 | 451 | −3.4839 | ** |
| Month | June | 0.7555 | 0.1148 | 536.7 | 6.58 | *** |
| | July | 1.6596 | 0.0782 | 366 | 21.23 | *** |
| | August | 1.4347 | 0.0735 | 362.5 | 19.52 | *** |
| | September | 1.4416 | 0.0746 | 391 | 19.33 | *** |
| Water mass (bottom water mass/surface water mass) | ACW | 1.1815 | 0.0778 | 193.2 | 15.19 | *** |
| | BSAW | 1.4871 | 0.0484 | 66.3 | 30.72 | *** |
| | BSAW/ACW | 1.4308 | 0.0518 | 83.8 | 27.6 | *** |
| | BSAW/SCW | 1.4518 | 0.1556 | 363 | 9.33 | *** |
| | BSAW/WW | 1.1901 | 0.2552 | 576.5 | 4.66 | *** |
| | SCW | 0.7784 | 0.1708 | 302.4 | 4.56 | *** |
| | WW | 1.3178 | 0.0766 | 275.6 | 17.2 | *** |
| | WW/BSAW | 1.2919 | 0.0945 | 349.3 | 13.67 | *** |
| | WW/SCW | 1.1051 | 0.151 | 516.4 | 7.32 | *** |

| (b) | Factor A | Factor B | Estimate (difference) | Error | p-value |
|---|---|---|---|---|---|
| Month | June | September | −0.7 | 0.1002 | *** |
| | July | June | 0.9 | 0.1045 | *** |
| | July | September | 0.2 | 0.0602 | *** |
| | August | July | −0.2 | 0.0588 | *** |
| | August | June | 0.7 | 0.0973 | *** |
| Water mass (bottom water mass/surface water mass) | ACW | BSAW | −0.3 | 0.0812 | *** |
| | ACW | BSAW/ACW | −0.2 | 0.0749 | *** |
| | ACW | SCW | 0.4 | 0.182 | * |
| | BSAW | SCW | 0.7 | 0.1745 | *** |
| | BSAW | WW | 0.2 | 0.0856 | * |
| | BSAW | WW/BSAW | 0.2 | 0.1037 | . |
| | BSAW | WW/SCW | 0.4 | 0.155 | * |
| | BSAW/ACW | SCW | 0.7 | 0.1721 | *** |
| | BSAW/ACW | WW/SCW | 0.3 | 0.1524 | * |
| | BSAW/SCW | SCW | 0.7 | 0.2142 | ** |
| | BSAW/SCW | WW/SCW | 0.3 | 0.2038 | . |
| | SCW | WW | −0.5 | 0.1846 | ** |
| | SCW | WW/ACW | −1.2 | 0.5231 | * |
| | SCW | WW/BSAW | −0.5 | 0.1907 | ** |
| | WW/ACW | WW/SCW | 0.9 | 0.5155 | . |

p-value codes:

*** <0.001

** <0.01

* <0.05

. <0.1

**TABLE S3.** Mixed model results of *Calanus glacialis* abundance in Bering Sea/Anadyr Water. Best model reported as predicted by the Akaike Information Criterion (AIC). (a) Results and (b) comparisons between least squares means for month (only significant comparisons reported) for the model log(Abundance+1) ~ Year + Month + PDO + (Gear) + 1|Facet. PDO = Pacific Decadal Oscillation.

| (a) | Factor | Estimate | Std. Error | df | t-value | p-value |
|---|---|---|---|---|---|---|
| (Intercept) | – | −17.50 | 3.14 | 402.00 | −5.57 | *** |
| Year | – | 0.01 | 0.00 | 402.00 | 5.98 | *** |
| PDO index | – | −0.11 | 0.03 | 386.50 | −3.30 | ** |
| Month | June | 1.14 | 0.11 | 257.10 | 10.51 | *** |
| | July | 1.60 | 0.08 | 130.40 | 19.26 | *** |
| | August | 1.32 | 0.06 | 51.30 | 22.58 | *** |
| | September | 1.16 | 0.07 | 81.00 | 17.24 | *** |

| (b) | Estimate | Std. Error | df | t-value | p-value |
|---|---|---|---|---|---|
| July–June | 0.50 | 0.12 | 373.50 | 3.75 | *** |
| July–September | 0.40 | 0.09 | 387.40 | 5.03 | *** |
| August–July | −0.30 | 0.08 | 396.50 | −3.39 | *** |
| August–September | 0.20 | 0.07 | 400.70 | 2.25 | * |

p-value codes:
*** <0.001
** <0.01
* <0.05

**TABLE S4.** Mixed model results of *Metridia pacifica* abundance in BSAW. Best model reported as predicted by AIC. (a) Results and (b) comparisons between least squares means for month (only significant comparisons reported) for the model log(Abundance+1) ~ Year + Month + Surface T + (Gear) + 1|Facet.

| (a) | Factor | Estimate | Std. Error | df | t-value | p-value |
|---|---|---|---|---|---|---|
| (Intercept) | | −26.97 | 6.30 | 372.70 | −4.28 | *** |
| Year | | 0.01 | 0.00 | 372.70 | 4.40 | *** |
| Mean Bottom Temperature | | 0.37 | 0.07 | 371.00 | 5.22 | *** |
| Month | June | 0.07 | 0.18 | 315.00 | 0.40 | |
| | July | 0.72 | 0.13 | 212.00 | 5.45 | *** |
| | August | 1.03 | 0.10 | 117.00 | 10.34 | *** |
| | September | 1.05 | 0.12 | 170.00 | 8.97 | *** |

| (b) | Estimate | Std. Error | df | t-value | p-value |
|---|---|---|---|---|---|
| June–September | −1.00 | 0.17 | 367.70 | −5.90 | *** |
| July–June | 0.70 | 0.18 | 356.00 | 3.69 | *** |
| July–September | −0.30 | 0.14 | 363.80 | −2.37 | * |
| August–June | 1.00 | 0.17 | 363.80 | 5.50 | *** |
| August–July | 0.30 | 0.12 | 362.50 | 2.57 | * |

p-value codes:
*** <0.001
** <0.01
* <0.05

**TABLE S5.** Mixed model results of *Eucalanus bungii* abundance in Bering Sea/Anadyr Water. Best mixed model reported as predicted by AIC. (a) Results and (b) comparisons between least squares means for month (only significant comparisons reported) for the model log(Abundance+1) ~ Year + Month + Bottom T + (Gear) + 1|Facet.

| (a) | Factor | Estimate | Std. Error | df | t-value | p-value |
|---|---|---|---|---|---|---|
| (Intercept) | – | −24.65 | 4.74 | 323 | −5.19 | *** |
| Year | – | 0.01 | 0.00 | 323 | 5.10 | *** |
| Mean Bottom Temperature | – | 0.46 | 0.06 | 323 | 7.82 | *** |
| Month | June | 0.83 | 0.18 | 335.9 | 0.69 | *** |
| | July | 0.28 | 0.12 | 220.5 | 1.46 | * |
| | August | 0.83 | 0.08 | 107.5 | 10.62 | *** |
| | September | 0.95 | 0.10 | 175.5 | 10.06 | *** |

| (b) | Estimate | Std. Error | df | t-value | p-value |
|---|---|---|---|---|---|
| June–September | −0.1 | 0.18 | 372.4 | −0.66 | *** |
| July–June | −0.5 | 0.16 | 368.8 | −3.28 | ** |
| July–September | −0.7 | 0.12 | 361.8 | −5.70 | *** |
| August–July | 0.50 | 0.10 | 360.1 | 5.51 | *** |

p-value codes:

*** <0.001

** <0.01

* <0.05

**TABLE S6.** Mixed model results of *Neocalanus* spp. abundance in Bering Sea/Anadyr Water. Best model reported as predicted by AIC. (a) Results and (b) comparisons between least squares means for month (only significant comparisons reported) for the model log(Abundance+1) ~ Year + Month + (Gear) + 1|Facet.

| (a) | Factor | Estimate | Std. Error | df | t-value | p-value |
|---|---|---|---|---|---|---|
| (Intercept) | – | −10.24 | 3.62 | 370.8 | -3.43 | *** |
| Year | – | 0.01 | 0.00 | 371.4 | 3.53 | *** |
| Mean bottom temperature | – | 0.19 | 0.05 | 368.8 | 3.53 | *** |
| Month | June | 0.50 | 0.14 | 217.5 | 3.61 | |
| | July | 0.42 | 0.08 | 204.9 | 6.71 | *** |
| | August | 0.58 | 0.05 | 122.0 | 10.88 | *** |
| | September | 0.21 | 0.07 | 227.7 | 2.96 | *** |

| (b) | Estimate | Std. Error | df | t-value | p-value |
|---|---|---|---|---|---|
| June–September | 0.30 | 0.15 | 312.6 | 2.31 | * |
| July–September | 0.30 | 0.13 | 363.1 | 3.56 | *** |
| August–September | 0.40 | 0.07 | 364.5 | 5.35 | *** |

p-value codes:

*** <0.001

** <0.01

* <0.05