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ORIGINAL PAPER

Inter-annual variability of summer mesozooplankton communities of the western Chukchi Sea: 2004–2012

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Abstract The Chukchi Sea shelf is a complex transition zone between the Pacific and Arctic Oceans, on which climate variation may have a profound impact. We examined summer zooplankton community structure of the western Chukchi Sea in Alaskan and Russian waters during 2004, 2009, 2010 and 2012 within the ongoing Russian-American Long-term Census of the Arctic program. The four study years were very different both in water mass properties and in zooplankton community structure. A "warm" year with an early ice retreat and highest water temperatures occurred in 2004, whereas the years 2009–2012 were "cold" with a later-than-average ice retreat and colder average water temperatures during the sampling period. The extent and prominence of different water masses (Bering Sea–Anadyr Water, Alaska Coastal Current, Siberian Coastal Current, Resident Chukchi Water) within the Chukchi Sea varied between years, which was in turn reflected within the zooplankton communities. Community structure was highly correlated with water mass properties, with bottom temperature being the most significant factor influencing communities. The "cold" summers of 2009–2012 had nearly twice the biomass and abundance of zooplankton compared with the "warm" summer of 2004. Biomass was dominated by the large copepod *Calanus glacialis* believed to originate from the Bering Sea, and abundance was dominated by small shelf species of copepods, such as *Pseudocalanus* spp., *Acartia* spp. and *Oithona similis*. We discuss the implications of the inter-annual variability of planktonic communities within the Chukchi Sea and the possible effects of longer-term climate change.

Keywords Chukchi Sea · Mesozooplankton assemblages · Climate change · Pelagic ecosystems

Introduction

The Chukchi Sea is a marginal Arctic sea that serves as the transitional zone between the Pacific and Arctic Oceans. While sharing many common features with other Arctic shelf seas, it differs by being an inflow system, with most of the water masses arriving directly from the Pacific Ocean via the Bering Sea (Carmack and Wassmann 2006). Unlike its Atlantic equivalent, the Barents Sea, it has a wide, shallow (<50 m deep) shelf with a very gentle slope that stretches all the way to the Arctic shelf break, which in combination with other factors creates a very different ecosystem. Also, unlike the Barents Sea, where incoming warm Atlantic water discourages extensive ice formation, the Chukchi region remains completely ice-covered during the winter, while waters entering through Bering Strait have near-freezing temperatures (Hunt et al. 2013).

The amount of Pacific water entering the Chukchi Sea annually is estimated at ~1–1.2 Sv (Woodgate et al. 2012) with the strongest flow occurring during the summer months (Coachman et al. 1975; Woodgate et al. 2012). Several distinct water masses compose the Chukchi Sea

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water during the summer, named for the currents that carry them. The Alaska Coastal Current (Alaska Coastal Water, ACW) brings in seasonally warmer (up to 12 °C), reduced-salinity (<31) coastal water from the southeastern Bering Sea shelf along the coast of Alaska (Springer et al. 1984). Anadyr Water (AW), which originates on the continental slope of the Bering Sea (Coachman et al. 1975), is a flow of nutrient-rich, cold (0–10 °C) and saline (32.3–33.3) oceanic water. A water type with intermediate properties that originates on the Bering Sea shelf (BSW) separates the two water masses; it mixes with AW to form Bering Shelf–Anadyr Water (BSAW) (Coachman et al. 1975). Together, these water masses carry with them large quantities of nutrients, phytoplankton and zooplankton and make the Chukchi Sea one of the most productive regions of the Arctic (Grebmeier and Maslowski 2014). The annual primary production of the Chukchi region is estimated to be $\sim$42 Tg C year^{-1}, or almost 15 % of all primary production in the Arctic Ocean (Sakshaug 2004).

The significant reduction in sea ice thickness, extent and timing of coverage that has been recorded across the entire Arctic in recent decades has been most pronounced in its Pacific sector (IPCC 2013). The Chukchi Sea pelagic ecosystem, which is finely tuned to the seasonal ice formation and retreat, is now experiencing a dramatic change with shifting sea ice cover. Models and some observations suggest an average increase in primary production, mainly driven by the increased area of open water, across the entire Arctic with greatest change in the Chukchi/Bering Sea area (Arrigo and van Dijken 2011). Alternately, others believe that nutrient limitation will ultimately restrain primary productivity in the Arctic, with little or no increase in annual production (Lee et al. 2012). Some studies suggest that the Arctic planktonic communities are nearing a threshold favoring a regime shift (*a.k.a.* tipping point) (Duarte et al. 2012). Shifts from diatom-dominated to picoplankton-dominated communities, driven by ocean warming and sea ice reduction, have already been recorded for several regions in the central Arctic Ocean, and some studies suggest that such a regime shift may occur within the foreseeable future (Li et al. 2009; Arrigo and van Dijken 2011; Tremblay et al. 2012). A protracted ice-free summer period within the Chukchi region could potentially benefit advected Pacific zooplankton species, permitting them to play a larger role in the summer planktonic communities and facilitate a northward shift of their ranges, likely at the expense of "resident" Arctic species.

A number of studies focusing on zooplankton communities of the Chukchi region have been done sporadically beginning with the middle of the twentieth century (for a review, see Hopcroft et al. 2010). These efforts have recently intensified, fueled by interest in both climate change and the extraction of oil and gas reserves (e.g., Questel et al. 2013). Notably, most historical and contemporary studies have focused on smaller-scale areas and have been spatially limited to either Russian or US waters, but for several decades, sampling has been confined to US waters (e.g., Springer et al. 1989; Lane et al. 2008; Matsuno et al. 2011; Eisner et al. 2012). The Russian-American Long-Term Census of the Arctic (RUSALCA) program, established in 2004, is a unique attempt to investigate a much wider territory—from the Bering Strait to north of Wrangel Island on both sides of the political border—over a long-term time period (Hopcroft et al. 2010).

In this study, we describe the summer zooplankton communities of the western Chukchi Sea, illuminating the poorly described Russian section. We examine the interannual variability within the plankton communities, which are strongly shaped by physical drivers (e.g., Hopcroft et al. 2010, Eisner et al. 2012). This effort contributes solid snapshots for monitoring climate-related change within the region, placing them into perspective with past, ongoing and future surveys. Such observations will enable us to better discriminate systematic environmental change from the natural year-to-year variability.

Methods

Three 3-week interdisciplinary cruises with emphasis on ecosystem components have been carried out within the framework of the RUSALCA program: August 4–25, 2004, September 4–27, 2009 and September 2–24, 2012. Plankton was also collected on a shorter oceanographic expedition August 1–11 2010 (Fig. 1). The initial sampling area in 2004 included 34 stations that sampled the Chukchi Sea on both sides of the US–Russian border from the Bering Strait northward to Herald Canyon (Hopcroft et al. 2010). The expeditions in 2009–2012 repeated sampling of the transects established in 2004. During 2009, many additional sections in the East Siberian Sea and surrounding Wrangel Island were also sampled, for a total of 60 stations. In 2012, due to poor weather conditions and sea ice, only 25 stations were sampled. In 2010, only the two southern study lines were occupied, plus an additional short transect in the East Siberian Sea, for a total of 16 stations.

Zooplankton samples were collected using vertically hauled 150-µm double-ring nets of 60 cm mouth diameters, sampling entire water column to within 3–5 meters of the ocean floor. While we recognize that the system often consists of different water masses overlaying each other, collecting stratified samples was not logistically possible. Total volume of water through the nets was measured using General Oceanics or Ocean Test flow meters, which were positioned at the mouth of each net and rigged not to spin during descent. Additionally, larger and

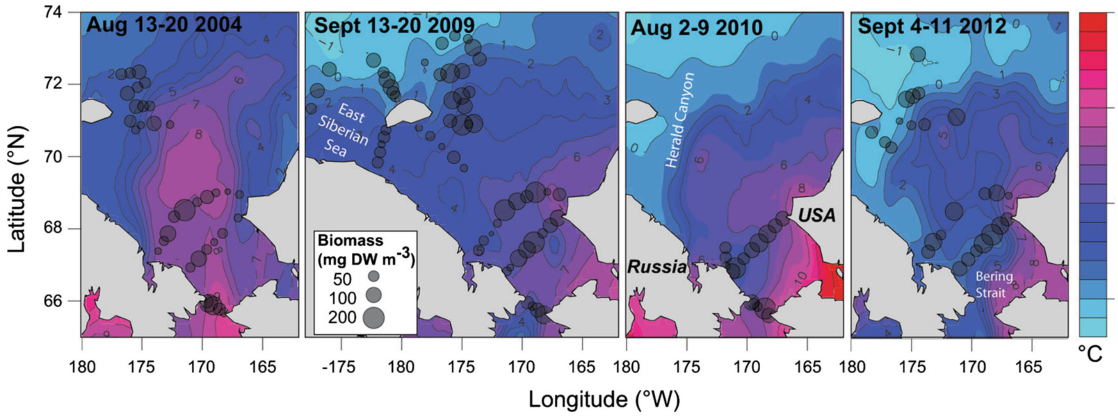

Fig. 1 Locations of sampling stations and holozooplankton biomass (estimated from the 150-µm vertical ring net) overlain on sea surface temperatures (SST, °C) averaged over a mid-cruise 7-day interval

Table 1 Length–weight relationship of gelatinous zooplankton species

Species	Regression equation	Units	Source
Bolinopsis infundibulum	$DW = 0.062TL^{2.34}$	mm mg	Kasuya et al. (2000)
Mertensia ovum	$DW = 0.104TL^{2.12}$	mm mg	Percy (1989)
Beroe ovata	$DW = 0.018TL^{2.69}$	mm mg	Kremer et al. (1986)
Cyanea capillata	$DW = 0.006BD^{2.721}$	cm g	Bailey et al. (1995)
Aeginura grimaldii (morphologically similar to *Aeginopsis laurentii*)	$DW = 5.04BD^{1.12}$	mm mg	Bailey et al. (1995)
Hydrozoan jellyfish	$DW = 0.00194TL^{3.05}$	mm mg	Matthews and Hestad (1977)

DW dry-weight, *TL* total length, *BD* bell diameter

rarer taxa were collected in 2009 and 2012 with obliquely towed flow-metered 505-µm Bongo nets, sampling at 2 knots (~1 m s^{-1}) to a depth near the bottom. Samples were collected during both the day and night. Upon retrieval, one of the samples from each net was preserved in 95 % molecular-grade ethanol, while the other 150-µm sample was preserved in 10 % formalin, and the 505-µm sample was live-sorted immediately for fragile gelatinous organisms on a light table prior to formalin preservation.

Fresh gelatinous specimens were keyed to species and measured, and then ctenophores were discarded, as they are known to quickly disintegrate in preservatives. The large (>5 cm) specimens were weighed using a scale; the weight of the smaller individuals was predicted from taxa-specific weight–length relationships of the same or similar species (Table 1). To reduce the inflated importance of cnidarians and ctenophores resulting from their low carbon content, we normalized their biomass through division by 4 (Kosobokova and Hopcroft 2010), in order to make their dry-weight (DW) more comparable with that of crustacean zooplankton (i.e., typically carbon is 10 % of dry-weight in gelatinous species vs. 40 % in crustaceans), while retaining the units of biomass most common in zooplankton literature (Larson 1986; Båmstedt 1986).

At each station, oceanographic data were collected with a Seabird 911 + CTD equipped with an oxygen sensor, transmissometer and fluorometer (Pickart et al. 2010; Pisareva et al., accepted), with all data binned into 1-m intervals during post-processing. Chlorophyll samples were collected by Niskin bottles on the CTD rosette every 5 m from the surface to bottom, filtered at low pressure onto GF/F filters and analyzed fluorometrically (e.g., Lee et al. 2007).

The formalin-preserved samples were processed in the laboratory to determine community composition, abundance and biomass. The entire samples were scanned for large and uncommon species, which were identified and measured. The remainder of the sample was then split using a Folsom splitter such that there were about 100 individuals of the most common species in the terminal split. Increasingly larger splits were scanned for rarer taxa; a minimum of 400 individuals were examined from each sample, with 500–600 typically identified. All organisms were measured using a computer-assisted measurement system (ZoopBiom software, Roff and Hopcroft 1986), and the dry-weight (DW) of each specimen was predicted from a length–weight regression relationship known for the same species, or a morphologically similar organism (Hopcroft et al. 2010). Copepods were staged and keyed to species; juveniles within some genera (such as *Pseudocalanus* spp. and *Acartia* spp.), which are morphologically undistinguishable, were grouped together. The species complex *Calanus glacialis/marshallae*, which is also undistinguishable morphologically, was considered to be *C. glacialis* within our region (Nelson et al. 2009). Meroplankton was grouped to the macrotaxa or to the family level (in the case of shrimp larvae). Copepod nauplii were counted only in 2009, 2010 and 2012. Here and hereafter, the copepods *C. glacialis*, *Neocalanus* spp., *Metridia* spp. and *Eucalanus bungii* are referred to as “large copepods”; all other copepods are considered “small copepods.” Only the 150-µm net samples are discussed in detail in this paper; however, the 505-µm net samples were included in the overall species lists with biomass values from the 505-µm nets only presented for the live-sorted gelatinous organisms.

Water masses were separated by cluster analysis using Euclidean distances on the normalized temperature and salinity values. Surface (averaged for 0–10 m), bottom (averaged for 10 m above sea floor), and midwater layers (10–10 m above sea floor) at each station were examined separately to partially account for the complex-stratified oceanography of the region and to determine where multiple water types may be present at a single location. The resulting groups (surface and bottom only) were plotted on a *T–S* diagram for quantitative separation and on a map of the study area. Increasing the surface and bottom depth intervals to 15–20 m thickness resulted in an identical separation of clusters, but slightly lower correlations to biological data. The midwater layer was not included in analysis because it was highly auto-correlated to the bottom and surface layers. High-resolution satellite SST data were extracted from the NOAA website at http://www.esrl.noaa.gov/psd/. The R packages “maps,” “mapplots” and “ggplot2” were used to create figures and plots (Wickham 2009; Becker and Wilks 2013; Gerritsen 2013).

Differences in total abundance and biomass, as well as abundance and biomass of taxonomic groups and individual species between years, were examined using ANOVA with station location as a blocking factor. Significant interactions between years were established using the Tukey’s HSD test. Due to different spatial coverage during the 4 years, only the southern Chukchi domain (three southern transects) was included in this analysis. Full domain community patterns were explored using the “vegan” package in R (Dixon 2009; Oksanen et al. 2013). Both the abundance and biomass datasets were examined independently for the stations pooled from all years. The datasets were power-transformed (fourth root), and the Bray–Curtis similarity index was calculated for all stations for each year. All taxonomic categories that contributed at least 3 % after transformation to any sample were included in the analysis; categories that were employed only during some of the years (e.g., copepod nauplii, crab megalopa) were excluded from analysis. Hierarchical cluster analysis using average linkage was carried out, and qualitative separation of groups was established by overall similarity (~30–35 %), the SIMPROF routine (significance at $\alpha = 0.05$) (Clarke and Gorley 2005) and subjective biological interpretation. These resulting groups were superimposed on 2D and 3D plots of nonparametric multidimensional-scaled (nMDS) datasets and spatial plots of the study area. The correspondence between zooplankton community patterns and physical data were explored using the BIOENV routine (Clarke and Ainsworth 1993), which establishes correlations between these two data matrices. The significance of these correlations was established using Mantel’s test of associations (Mantel 1967).

Results

Water masses

August 2004 was the warmest sampling period, with an average sea surface temperature (SST) across the sampled domain of 6.3 °C and with water as warm as 8 °C entering the Herald Canyon region (Fig. 1). The coldest temperatures were observed in September 2012, averaging only 3.4 °C, nearly three degrees colder than 2004. The warm waters of the Alaska Coastal Current (ACW), and the resultant temperature gradient across the shelf, were most pronounced in 2010 and 2012, while in 2009, the surface water temperatures were the most uniform.

Cluster analysis of surface and bottom water properties (Temperature and Salinity) within each year splits them into 11 distinct groups; these were subsequently grouped into six water types, as recognized by the literature characterizations (i.e., Eisner et al. 2012) (Fig. 2). While this approach is an oversimplification, particularly within the surface waters, which are influenced by melting, mixing and radiative forcing, it provides us with a broad-scale picture of the physical environment within our study. The fresh and warm Alaska Coastal Water (ACW, red) was the most recognizable assemblage, which includes three cluster groups: extremely warm low-salinity water, present only in 2004 and at one station in 2010; colder low-salinity water present only in 2012 (and one station in 2004, which was most likely an outlier); and colder higher-salinity water visible in all years except 2009. ACW waters were most

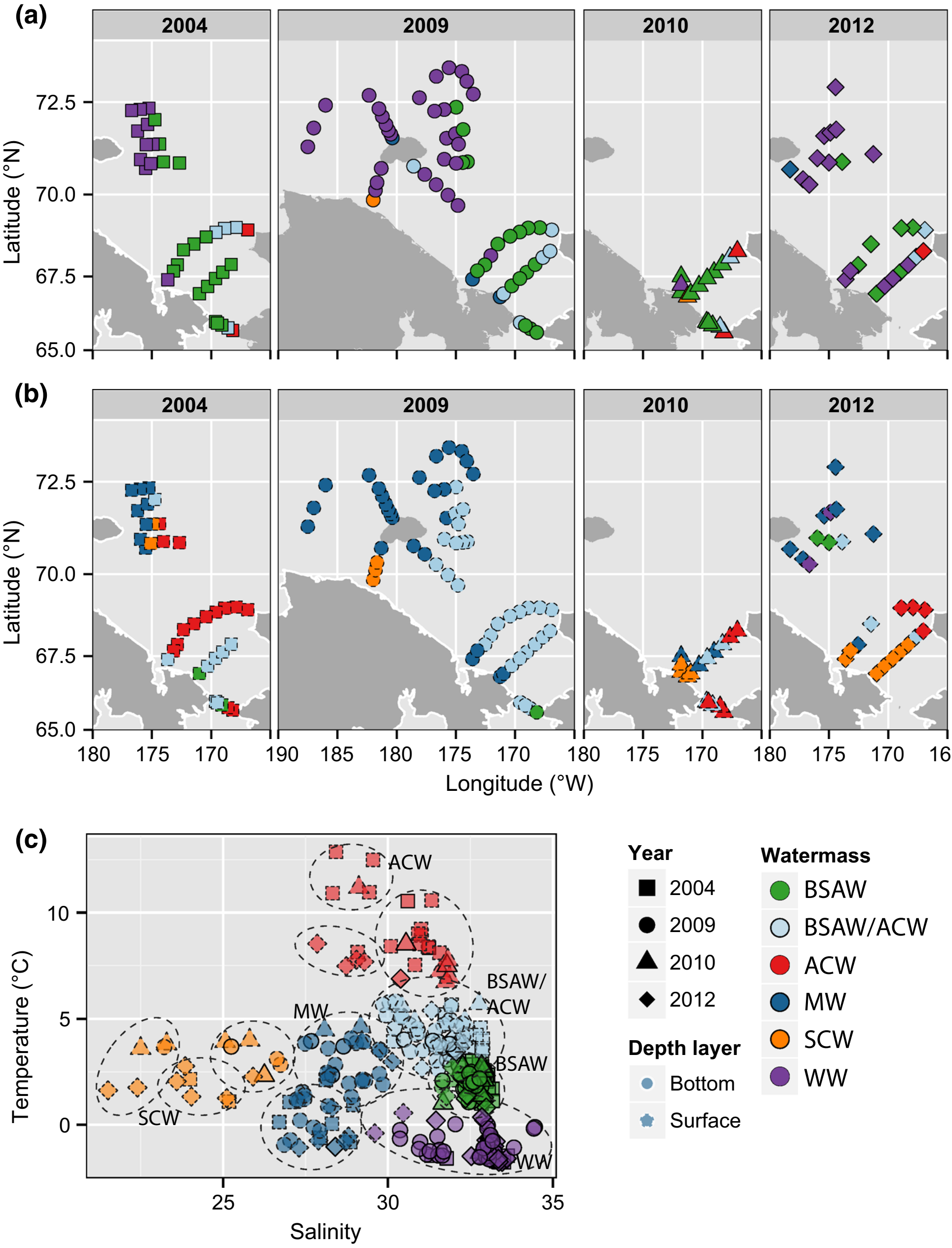

Fig. 2 Cluster analysis of depth-integrated temperature/salinity observations in the Chukchi Sea, **a** bottom waters, **b** surface waters, **c** temperature–salinity plot. *Dashed line* boundaries indicate individual clusters; each cluster has been assigned a water mass type. Water mass abbreviations: BSAW, Bering Sea–Anadyr Water; ACW, Alaska Coastal Water; SCW, Siberian Coastal Water; MW, melt water; WW, winter water

pronounced in 2004, when they were found in surface waters across the entire offshore section of the southern Chukchi, and even as far north as eastern Herald Canyon. The higher-salinity and colder Bering Sea–Anadyr Water (BSAW, green) was present in bottom waters throughout the southern Chukchi and as far north as 72°N in Herald Canyon in 2004 and 2009. An intermediate water type, most likely a mixture of ACW and BSAW (BSAW/ACW, light blue) (Pisareva et al., accepted), was found within the surface waters of the southern Chukchi during all years, particularly in 2009, when it reached far north into the Herald Canyon. Resident Chukchi Winter Water (WW, purple) was the dominating bottom water type in western Herald Canyon and was typically overlain by BSW/BSAW or lower-salinity melt water (dark blue). The surface waters of the northernmost stations (in 2009) and the stations surrounding Wrangel Island (in 2004 and 2012) also contained a very cold, low-salinity water type most likely resulting from ice melt (melt water, dark blue). The very low-salinity (<27), cold waters of the Siberian Coastal current (SCW, orange) were visible along the Siberian coast in 2009 and 2010 and farther offshore in 2012.

Zooplankton taxa

Total holozooplankton abundance estimated by the 150-μm nets varied across a wide range: from 400 individuals (ind) m^{-3} to 25,000 ind m^{-3}. Abundance averaged ~3000 ± 2500 ind m^{-3} in 2004 and 2012; in 2009 and 2010, it was almost three times higher, averaging ~8000 ± 6500 ind m^{-3}, mainly due to the extremely high abundance of small copepods during those 2 years (copepod nauplii are excluded from all counts). The total holozooplankton biomass varied by almost two orders of magnitude across the studied domain during the four study years, with the minimum observation being around 8 mg dry-weight (DW) m^{-3} and the maximum 360 mg DW m^{-3} (Fig. 1). The lowest biomass (averaged across the entire domain) was observed in 2004, averaging 44 ± 31 mg DW m^{-3} (here and henceforth values are mean ± SD); biomass was somewhat higher in 2010, averaging 63 ± 35 mg DW m^{-3}. During 2009 and 2012 years, the observed biomass was relatively similar, averaging ~75 ± 40 mg DW m^{-3}. Across the southern Chukchi domain, which was common for all four cruises, difference in overall biomass was significant, with lower values observed in 2004 than in 2009 and 2012 (ANOVA, $p < 0.05$, Tukey's HSD); abundance was significantly higher in 2009 than in 2004 and 2012 (Table 3).

A total of 82 unique taxa from 13 taxonomic groups were encountered during the four study years (Table 2). The majority of these were advected subarctic Pacific species, which are shared with the Bering Sea. However, a number of species, including the majority of the observed hydrozoan jellyfish and some copepods (marked by asterisks in Table 2), are generally not found south of the northern Bering Sea/Chukchi region and can therefore be considered resident Arctic species. Copepods dominated both community biomass and abundance (Table 2; Fig. 3)—large copepods, mainly *Calanus glacialis* (Fig. 4), dominated the biomass at most locations, while small copepods dominated the abundance. Other large copepods, such as *Metridia pacifica*, *Euclanus bungii* and *Neocalanus* spp., were present mainly in Bering Sea waters, with numbers declining to the north and toward the Siberian coast (Fig. 4; Online Resource 1). Small copepods, such as *Pseudocalanus* spp., *Oithona similis* and *Acartia* spp. were common throughout the study region, but were particularly abundant near the coasts (Figs. 6 7; Online Resource 1). Study year 2009 stood out by significantly higher (2–3 times) average abundance of small copepods: juvenile *Pseudocalanus* spp. and *O. similis* (Fig. 3; Table 3). Warm-water euryhaline copepods, such as *Eurytemora herdmani* and *Centropages abdominalis* (not shown), were generally only found in Alaska coastal waters; in 2009, however, these species were found throughout the southern Chukchi domain (Fig. 5). The pelagic harpacticoid copepod *Microsetella norvegica* was a prominent member of zooplankton communities in the Herald Canyon region and around Wrangel Island and was mostly absent from Bering Sea and Alaskan waters (Fig. 5). The presence of a number of Arctic taxa in 2009 (i.e., *Calanus hyperboreus*, *Metridia longa*, *Chiridius obtusifrons*) was largely due to the extended sampling region during that year.

A number of other non-copepod groups were also of high importance. Hydrozoan jellyfish, such as *Aeginopsis laurentii* and *Halitholis cirratus*, was common within waters around Wrangel Island and along the Siberian coast; *A. laurentii* was particularly abundant in 2009 (Fig. 6) and *H. cirratus* in 2012 (not shown). *Aglantha digitale*, on the other hand, was widespread throughout the study region during all years, particularly in waters influenced by Alaska Coastal Water, and was especially abundant in 2010 (Fig. 6). Other groups contributed variably across the area and between the studied years. Pteropods (*Limacina helicina* and *Clione limacina*) were extremely numerate in 2009 and 2010, especially near the Alaskan coast, but were rare in 2012 and completely absent in 2004 (Table 2, Online Resource 2). Similarly, cladocerans were completely absent from the zooplankton in 2009. The larvacean *Oikopleura vanhoeffeni* (Online Resource 2) was an important contributor in terms of abundance in 2004 (particularly in the Herald Canyon region) and in 2010 (Table 2). Despite much lower overall numbers in 2012, the much larger size of the individuals resulted in an exceptionally high biomass of this species during that year (significantly higher than in all other years) (Table 3). It is noteworthy that in 2009, the biomass and abundance of larvaceans were extremely low. The predatory chaetognath *Parasagitta elegans* (Online Resource 2) was present at all sampling locations; its abundance (and biomass) was highest in 2009, especially in Herald Valley and around Wrangel Island. Cirripeda larvae were also common during all years throughout the studied region and were particularly abundant during the two summer surveys (2004 and 2010) (Online Resource 2). As with copepods, the presence of a number of Arctic jellyfish species in 2009 was largely due to the extended sampling region during that year.

When properly accounted for (in 2009 and 2012), ctenophores and large jellyfish were important contributors to the community biomass, resulting in a 2–10 % average increase in the biomass estimated by preserved samples. At several stations, particularly in 2012, the normalized biomass of large gelatinous taxa was over 40 mg DW m^{-3} and exceeded copepod biomass (Fig. 6). The ctenophore *Mertensia ovum* (Fig. 6) was the most abundant species, particularly in 2012, when it occurred at nearly every station and contributed an average of 2 mg DW m^{-3} to the overall holozooplankton biomass (and up to 10 mg DW m^{-3}). In 2009, we only encountered *M. ovum* above 69°N, but its average contribution to biomass across the entire area was nevertheless high at 0.8 mg DW m^{-3}. The

Table 2 Species encountered during RUSALCA 2004–2012 cruises in the Chukchi Sea

	Abundance (ind m^{-3})				Biomass (mg DW m^{-3})			
	2004	2009	2010	2012	2004	2009	2010	2012
Amhipoda								
Gammaridae	0.05	0.06	+	0.40	0.14	0.11	+	0.13
Apherusa glacialis[b]	−	Obs	−	0.02	−	Obs	−	0.06
Monoculodes sp.	−	Obs	−	Obs	−	Obs	−	Obs
Hyperiidae	−	0.10	−	0.01	−	+	−	+
Hyperoche sp.	−	0.14	+	0.03	−	0.20	+	0.05
Themisto libellula	0.03	0.05	0.20	0.05	+	1.40	4.80	0.48
T. pacifica/abyssorum	0.04	0.01	0.01	0.03	0.07	0.02	+	0.07
Hyperia galba	−	−	−	+	−	−	−	+
Scina borealis	−	−	−	+	−	−	−	+
Sum	0.12	0.36	0.21	0.14	0.20	1.73	4.81	0.66
Appendicularia								
Fritillaria borealis	85.09	308.50	1470.30	2.61	0.01	0.03	0.11	+
Oikopleura vanhoeffeni	256.60	27.95	375.10	63.64	4.12	0.14	1.76	5.34
Sum	341.69	336.45	1845.40	66.26	4.13	0.17	1.88	5.34
Chaetognatha								
Eukrohnia hamata[b]	0.43	+	8.68	−	0.34	0.05	0.23	−
Parasagitta elegans	5.69	109.16	40.52	23.72	4.77	17.15	3.97	11.22
Sum	6.12	109.17	49.19	23.72	5.11	17.20	4.20	11.22
Cladocera								
Evadne nordmanni	11.35	−	196.85	−	0.04	−	1.55	−
Podon leuckarti	14.51	−	103.85	0.25	0.06	−	0.57	+
Sum	25.85	−	300.70	0.25	0.10	−	2.12	+
Copepoda								
Acartia hudsonica	2.52	14.19	7.28	11.26	0.01	0.05	0.04	0.04
Acartia longiremis	199.43	67.12	507.20	101.67	0.41	0.14	0.72	0.16
Acartia tumida	+	0.36	−	−	+	+	−	−
Calanus glacialis	35.67	144.72	78.67	263.73	6.70	24.55	14.14	35.03
Calanus hyperboreus[b]	−	0.08	−	−	−	0.06	−	−
Centropages abdominalis	190.23	78.24	135.91	64.31	0.50	0.48	0.53	0.27
Epilabidocera amphitrites	−	0.01	0.20	0.02	−	+	0.03	+
Chiridius obtusifrons	−	0.04	−	+	−	+	−	+
Aetideidae	−	0.01	0.19	+	−	+	+	+
Eucalanus bungii	14.62	7.80	146.64	3.02	1.33	0.43	3.37	0.30
Paraeuchaeta glacialis[b]	+	+	−	+	+	0.01	−	+
Eurytemora herdmani	5.69	16.95	1.09	22.26	0.03	0.10	0.01	0.09
E. pacifica	+	0.07	−	−	+	+	−	−
Jaschnovia brevis[b]	−	0.05	−	0.32	−	+	−	0.01
J. tolli[b]	0.32	−	−	−	0.01	−	−	−
Mesocalanus tenuicornis	+	−	−	−	+	−	−	−
Metridia longa[b]	−	1.36	−	−	−	0.28	−	−
M. pacifica	39.75	71.60	367.48	11.29	1.41	1.81	10.01	0.15
Microcalanus pygmaeus	8.18	2.17	32.09	1.88	0.01	+	0.05	+
Neocalanus cristatus	0.94	0.06	0.27	0.75	6.38	0.36	1.75	5.19
N. flemingeri	7.09	2.40	7.84	2.59	4.50	0.28	4.21	1.46
N. plumchrus	2.10	0.29	0.23	0.11	1.42	0.22	0.14	0.07

Table 2 continued

	Abundance (ind m^{-3})				Biomass (mg DW m^{-3})			
	2004	2009	2010	2012	2004	2009	2010	2012
Pseudocalanus acuspes[b]	38.55	78.72	34.50	31.79	0.51	0.77	0.41	0.34
P. mimus	−	3.24	26.22	1.72	−	0.03	0.25	0.01
P. minutus[b]	71.81	8.21	46.33	9.80	0.89	0.11	0.84	0.17
P. newmani	92.80	141.23	41.66	22.59	0.55	0.72	0.23	0.12
Pseudocalanus spp.	1606.62	4150.74	1739.67	1655.06	4.51	9.45	4.61	4.30
Scolecitrichidae	−	0.30	−	0.05	−	0.01	−	+
Spinocalanus sp.	−	0.03	−	−	−	+	−	−
Tortanus discaudatus	−	0.06	−	0.02	−	+	−	+
Harpacticus sp.	−	7.24	6.24	0.03	−	0.03	0.02	+
Microsetella norvegica[b]	19.26	59.72	550.89	14.94	0.09	0.42	2.92	0.09
Oithona similis	701.95	2471.66	1721.77	490.42	0.77	3.37	2.65	0.66
Triconia borealis	65.02	12.96	87.71	6.85	0.10	0.02	0.29	0.01
Calanoid nauplii	NA	618.91	1119.95	289.55	NA	0.43	1.27	0.25
Sum	5106.56	9969.49	8670.02	5018.02	30.14	44.16	48.49	48.73
Ostracoda								
Boroecia sp.[b]	0.01	0.03	−	−	+	+	−	−
Polychaeta								
Tomopteris sp.	+	+	−	+	0.01	+	−	+
Ctenophora (505 µm net)								
Beroe abyssicola	**NA**	**−**	**NA**	**+**	**NA**	**−**	**NA**	**0.04**[a]
Beroe cucumis	**NA**	**+**	**Obs**	**0.01**	**NA**	**0.05**[a]	**Obs**	**1.71**[a]
Mertensia ovum	**Obs**	**0.06**	**Obs**	**0.31**	**Obs**	**0.82**[a]	**Obs**	**1.56**[a]
Bolinopsis infundibulum	**Obs**	**+**	**Obs**	**0.01**	**Obs**	**0.60**[a]	**Obs**	**0.37**[a]
Sum	NA	0.06	NA	0.33	NA	1.48	NA	3.67
Decapoda and other Crustacea								
Cumacea	−	0.13	−	−	−	0.21	−	−
Hippolytidae	−	0.31	0.23	0.10	−	0.02	0.21	0.10
Eualus gaimardii	−	0.05	−	0.03	−	0.06	−	0.02
Pandalidae	−	0.02	−	0.03	−	0.03	−	0.34
Sum	0.00	0.50	0.23	0.16	0.00	0.31	0.21	0.45
Euphausiidae								
Thysanoessa inermis	0.14	0.02	−	0.13	0.44	0.19	−	0.60
T. raschii	0.03	0.34	0.05	0.36	0.08	2.89	0.46	1.81
Thysanoessa juveniles	6.12	5.09	63.13	9.14	0.66	1.55	0.12	3.85
Sum	6.30	5.46	63.17	9.62	1.17	4.63	0.58	6.27
Cnidaria								
Aeginopsis laurentii[b]	−	4.89	−	0.31	−	0.48[a]	−	0.07[a]
Aglantha digitale	5.35	5.63	44.76	1.89	0.95[a]	0.20[a]	0.51[a]	2.00[a]
Aurelia aurita	−	+	−	−	−	0.01[a]	−	−
Eumedusa birulai[b]	−	0.02	0.10	+	−	0.05[a]	0.01[a]	0.01[a]
Euphysa flammea	0.06	0.01	−	−	0.08[a]	+	−	−
Melicertum octocostatum[b]	0.01	0.01	−	0.09	0.01[a]	0.02[a]	−	0.01[a]
Obelia longissima[b]	0.40	0.16	2.49	0.03	+	0.01[a]	0.13	+
Catablema/Halitholis sp.[b]	+	0.01	+	0.12	0.02[a]	0.03[a]	0.01[a]	0.64[a]
Plotocnide borealis[b]	−	0.40	−	0.29	−	+	−	0.01[a]
Polyorchis penicillatus	+	−	−	−	0.02[a]	−	−	−

Table 2 continued

	Abundance (ind m^{-3})				Biomass (mg DW m^{-3})			
	2004	2009	2010	2012	2004	2009	2010	2012
Rathkea octopunctata[b]	11.60	0.12	15.56	0.06	0.02[a]	+	0.03[a]	+
Sarsia tubulosa	+	0.06	–	+	0.02[a]	0.15[a]	–	+
Dimophyes arctica[b]	–	+	–	–	–	+	–	–
Bougainvillia superciliaris[b]	–	–	0.01	–	–	–	0.01	–
Sum (150 µm)	17.43	11.31	62.92	2.80	1.20	0.95	0.69	2.74
Cnidaria (505 µm net)								
Cyanea capillata	**NA**	**+**	**NA**	**0.02**[a]	**NA**	**0.10**[a]	**NA**	**1.96**[a]
Mitrocomella polydiademata	**NA**	**–**	**NA**	**+**	**NA**	**–**	**NA**	**0.80**[a]
***Catablema vesicarium/Halitholis* cirratus**	**NA**	**+**	**NA**	**0.04**[a]	**NA**	**0.01**[a]	**NA**	**0.07**[a]
Sarsia tubulosa	**NA**	**0.01**[a]	**NA**	**+**	**NA**	**0.02**[a]	**NA**	**0.01**[a]
Eumedusa (=Calycopsis) birulai	**NA**	**+**	**NA**	**+**	**NA**	**+**	**NA**	**+**
Chrysaora melanaster	**NA**	**–**	**Obs**	**+**	**NA**	**–**	**Obs**	**1.16**[a]
Aeginopsis laurentii[b]	**NA**	**1.40**[a]	**NA**	**0.09**[a]	**NA**	**0.15**[a]	**NA**	**0.18**[a]
Aglantha digitale	**NA**	**0.75**[a]	**NA**	**0.38**[a]	**NA**	**0.04**[a]	**NA**	**0.11**[a]
Sum (505 µm)	NA	2.16	NA	0.53	NA	0.32	NA	4.29
Meroplankton								
Bipinnaria	–	0.32	12.50	1.00	–	+	0.02	+
Echinodermata larvae	795.56	46.03	1437.76	19.38	0.37	0.05	0.29	+
Bivalvia larvae	148.31	217.77	1730.72	49.38	0.05	0.12	2.72	0.02
Cirripeda larvae	1235.55	102.68	1181.63	39.57	5.28	1.49	2.03	0.58
Decapoda zoea	0.31	0.04	0.08	0.24	0.21	0.04	+	0.02
Fish larvae	0.20	+	0.10	0.01	0.88	0.25	0.02	0.51
Megalopa (crab larvae)								
Actinula (anenome larvae)	0.24	0.16	–	0.30	0.30	0.13	–	0.06
Pagurus zoea	0.32	0.60	0.52	0.28	0.11	0.09	+	+
Polychaete larvae	81.85	70.28	642.19	3.56	0.81	0.37	2.31	0.05
Pilidium (nemertine larvae)	–	–	3.12	–	–	–	+	–
Sum	2262.35	437.89	5008.63	113.74	8.01	2.49	7.40	1.29
Mysidae								
Mysis oculata	+	0.02	–	0.01	0.04	0.02	–	0.01
Neomysis awatschensis	–	Obs	–	–	–	Obs	–	–
Pteropoda								
Clione limacina	–	0.22	0.42	0.15	–	0.03	0.04	0.42
Limacina helicina	–	101.94	76.97	0.45	–	1.45	0.27	+
Sum	0.00	102.16	77.39	0.60	0.00	1.48	0.31	0.43

Species marked in bold were estimated using the 505-µm net

Obs, species were observed during the cruise, but not noted (or counted) within the samples; "–," species not observed; "+," < 0.01; NA, no data available

[a] Biomass standardized through division by 4

[b] Arctic species

ctenophores *Bolinopsis infundibulum* and *Beroe cucumis* (not shown) were less common, occurring at 15–25 % of the stations sampled, but due to their large size and weight, their average contribution to biomass is also substantial during both years (Table 2). The large scyphomedusan *Cyanea capillata* was also common in 2012, with smaller individuals (up to 20 cm) occurring throughout the collections and contributing an average of 2 mg DW m^{-3} to the biomass (Table 2); in 2009, we only observed this jellyfish at three stations.

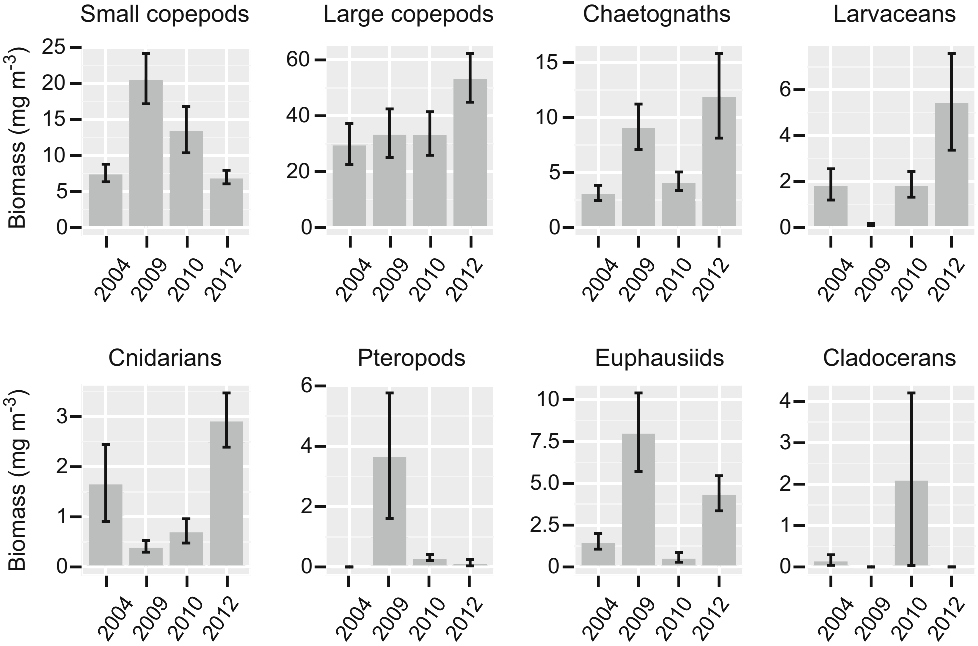

Fig. 3 Inter-annual variability in mean biomass (mg DW m^{-3}) of major zooplankton groups across the Southern Chukchi Sea (southern 3 sampling sections), *black bars* standard error

Community structure

Twelve station groups were identified by cluster analysis for all years (Fig. 7a). The nMDS ordination largely reinforces (Fig. 7c) the results of cluster analysis, with improvement in stress from 0.21 to 0.14 when increasing from two to three dimensions. Generally, the stations separate by year, with several exceptions. Specifically, the Chukchi communities in 2009 clustered together with the Chukchi/SCW stations in 2012; the ACW-influenced communities in 2012 were grouped together with most of the stations of the southern Chukchi in 2009. Overall, 2004 was more similar to 2010, and 2009 to 2012, and it is notable that the former two cruises took place in August, and the other two in September. A strong cross-shelf (east to west) gradient in community structure of the southern Chukchi was evident in 2004, 2010 and 2012, with an ACW-influenced community along the Alaskan coast being replaced by Bering Sea communities farther offshore and by Siberian coastal/Chukchi communities closer to the Siberian Coast. In 2009, there was no distinct separation of communities across the southern Chukchi using either biomass or abundance, with several stations (dark purple) being most similar to the Siberian communities in 2010. Stations on the east edge of Herald Canyon were generally characterized by Bering Sea/Chukchi communities, yet the western stations were more similar to the SCW stations.

In terms of species composition (Fig. 8), the ACW communities were the most recognizable assemblage, characterized by the presence of several of warmer-water euryhaline taxa: the cladocerans *Evadne nordmanni* and *Podon leuckarti*; the copepods *Pseudocalanus newmani*, *Acartia hudsonica*, *Centropages abdominalis* and *Epilabidocera longipedata*. The Bering Sea communities were dominated by shelf species, such as the copepods *Pseudocalanus* spp., *Oithona similis*, *Acartia* spp., cirriped larvae as well as the more oceanic copepods *Calanus glacialis*, *Metridia pacifica*, *Neocalanus* spp and *Euclanus bungii*. The communities associated with the Chukchi Winter Waters, while sharing a large number of advected Pacific species with the Bering Sea communities, were characterized by a lower overall biomass of copepods, particularly *C. glacialis*, and by the increased presence of Arctic taxa, such as several hydrozoan jellyfish species, as well as the copepod *Microsetella norvegica*. Several other Arctic and ice-associated species, such as the copepods *Metridia longa* and *Jaschnovia* spp., and the amphipod *Apherusa glacialis* also occurred within these communities. The SCW assemblages (2009 and 2010) were similar to the Chukchi communities, but with a reduced presence of Pacific taxa. Large copepods were nearly absent from these communities, with biomass dominated by small copepods and adult euphausiids. Interestingly, in 2010, these communities contained a number of entrained warm-water neritic species, such as the copepods *P. newmani* and *C. abdominalis*, while in 2009, they were nearly absent. While the copepod *C. glacialis* was present in all communities during all years, the distribution of developmental stage of this species reveals patterns suggesting multiple origins (Fig. 9). Within BSAW, the *C. glacialis* population consisted mainly of C5 copepodites, while within the resident Chukchi/Siberian Coastal Waters, subadult C5s

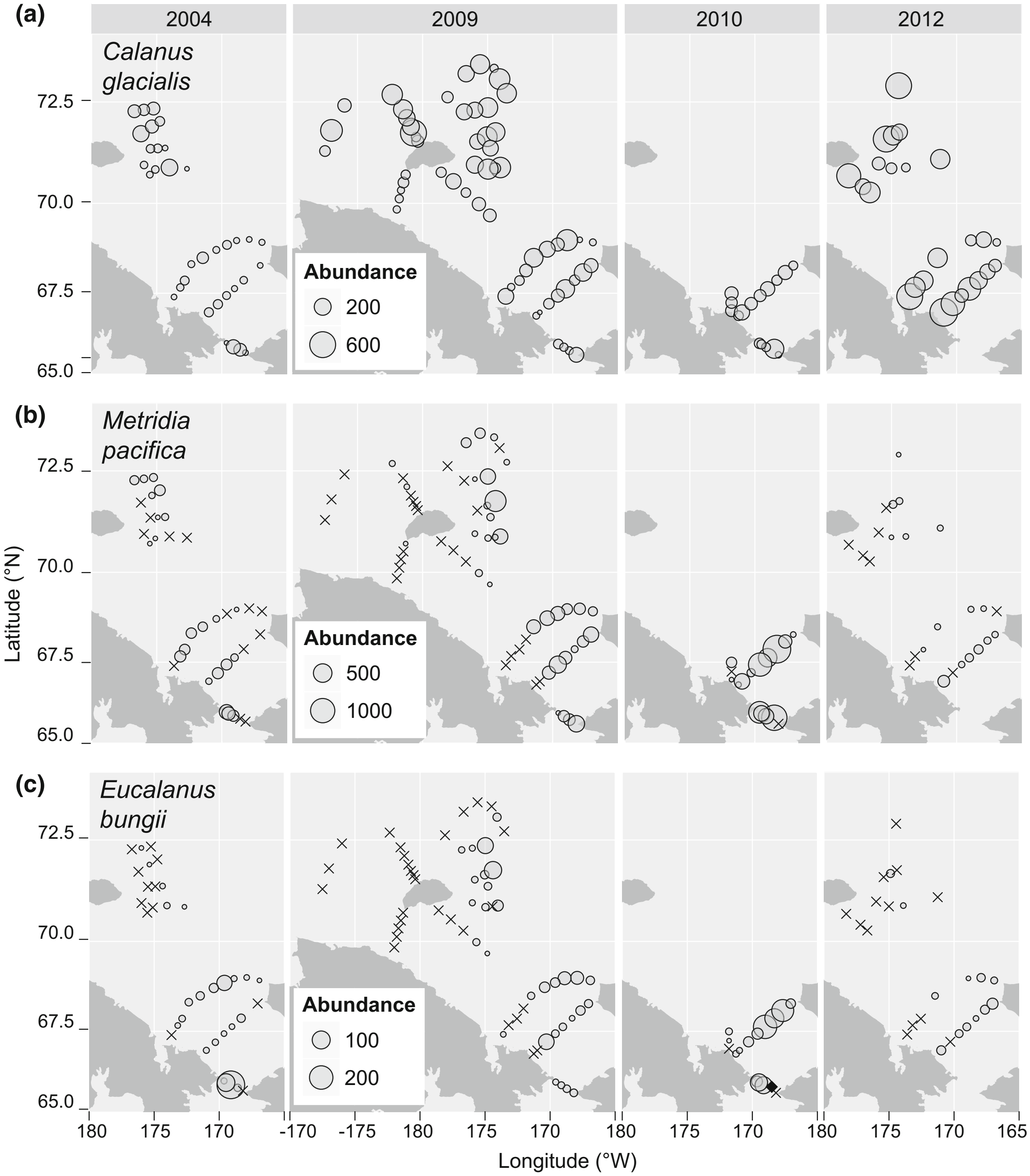

Fig. 4 Abundance of large copepods (ind m^{-3}) across the Southern Chukchi Sea; *cross symbol* species absent at this location

were scarce or absent, and the population consisted mainly of young C1–C4 copepodites. Younger copepodites also dominated within the ACW *C. glacialis* populations.

We found the community structure within each year to be strongly correlated with environmental parameters via the BIOENV routine. Bottom temperature was the most important variable during most years (with the exception of 2012, when surface temperature was the highest-correlated variable) (Table 4—as also apparent from the nMDS temperature overlay, Fig. 7c). Other variables that improved the model included bottom salinity, surface temperature and salinity, station depth, and distance from Bering Strait (Table 4). Using biomass and abundance matrices produced very similar results. Including more than three parameters or other variables (Fluorescence, Chlorophyll, Oxygen) produced no significant (<3 %) improvement in correlations. Bottom temperature also had a strong inverse relationship to prosome length in several

Table 3 One–way ANOVA results for the southern Chukchi Sea domain during all years for (a) total holozooplankton (b) taxonomic groups (c) individual copepod species

	Abundance (ind m^{-3})					Significant interactions	Biomass (DW m^{-3})					Significant interactions
	2004	2009	2010	2012	*p*		2004	2009	2010	2012	*p*	
(a) Total	3295.6	10,605.1	7944.5	3218.8	***	2009 > 2004, 2012	46.1	78.5	62.0	86.2	*	***2004 < 2009, 2012***
(b)												
Large copepods	116.2	237.6	601.3	287.5	**	2010 > 2004, 2009	29.9	33.7	33.7	53.6	NS	None
Small copepods	2823.1	9672.8	4938.6	2825.2	***	2009 > 2004, 2010, 2012	7.6	20.7	13.6	7.0	***	2009 > 2012, 2004
Chaetognaths	4.2	58.5	49.2	26.0	NS	None	3.2	9.2	4.2	12.0	*	2012 > 2004
Larvaceans	277.3	432.3	1845.4	60.4	***	2010 > 2004, 2009, 2012	1.9	0.1	1.9	5.5	**	2012 > ***2004***, 2009, ***2010***
Cnidarians	22.5	1.8	68.3	3.9	***	2010 > 2004, 2009, 2012	1.7	0.4	0.7	2.9	*	2012 > 2009, 2010
Euphausiids	9.2	5.7	63.2	14.0	*	2010 > ***2004,*** 2009	1.5	8.1	0.6	4.4	**	2009 > 2004, 2010
Pteropods	0.0	196.2	77.4	0.8	*	2009 > 2004	0.0	3.7	0.3	0.1	NS	None
Cladocerans	43.1	0.0	300.7	0.6	NS	None	0.2	0.0	2.1	0.0	NS	None
Amphipods	0.1	0.2	0.2	0.3	NS	None	0.1	2.6	4.8	0.6	NS	None
Decapods	0.0	0.0	0.2	0.1	NS	None	0.0	0.0	0.2	0.1	*	2010 > 2004, ***2009***
(c)												
Calanus glacialis	20.9	98.6	78.7	270.3	***	2012 > 2004, 2009, 2010	5.7	27.8	14.1	44.7	**	2012 > 2004, 2010; ***2009 > 2004***
Metridia pacifica	55.3	126.1	367.5	9.9	***	2010 > 2004, 2009, 2012	2.3	4.5	10.0	0.1	**	2010 > 2004, 2012
Neocalanus flemingeri	10.7	1.3	7.8	1.6	*	2004 > 2009, ***2012***	6.8	0.4	4.2	1.1	**	2004 > 2009, 2012
Pseudocalanus spp.	1356.3	5103.1	1888.4	1756.3	**	2009 > 2004, 2010, 2012	5.2	13.5	6.3	5.0	**	2009 > 2004, 2010, 2012
Oithona similis	946.6	4154.5	1721.8	665.2	***	2009 > 2004, 2010, 2012	1.0	5.3	2.6	0.9	***	2009 > 2004, ***2010,*** 2012
Eurytemora herdmani	7.4	42.6	1.1	42.0	*	2009 > 2004, 2010	0.0	0.2	0.0	0.2	**	2009 > 2004, 2010

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. Significant interactions ($p < 0.05$) via Tukey HSD test; bold italic indicates significance at $p = 0.1$ level

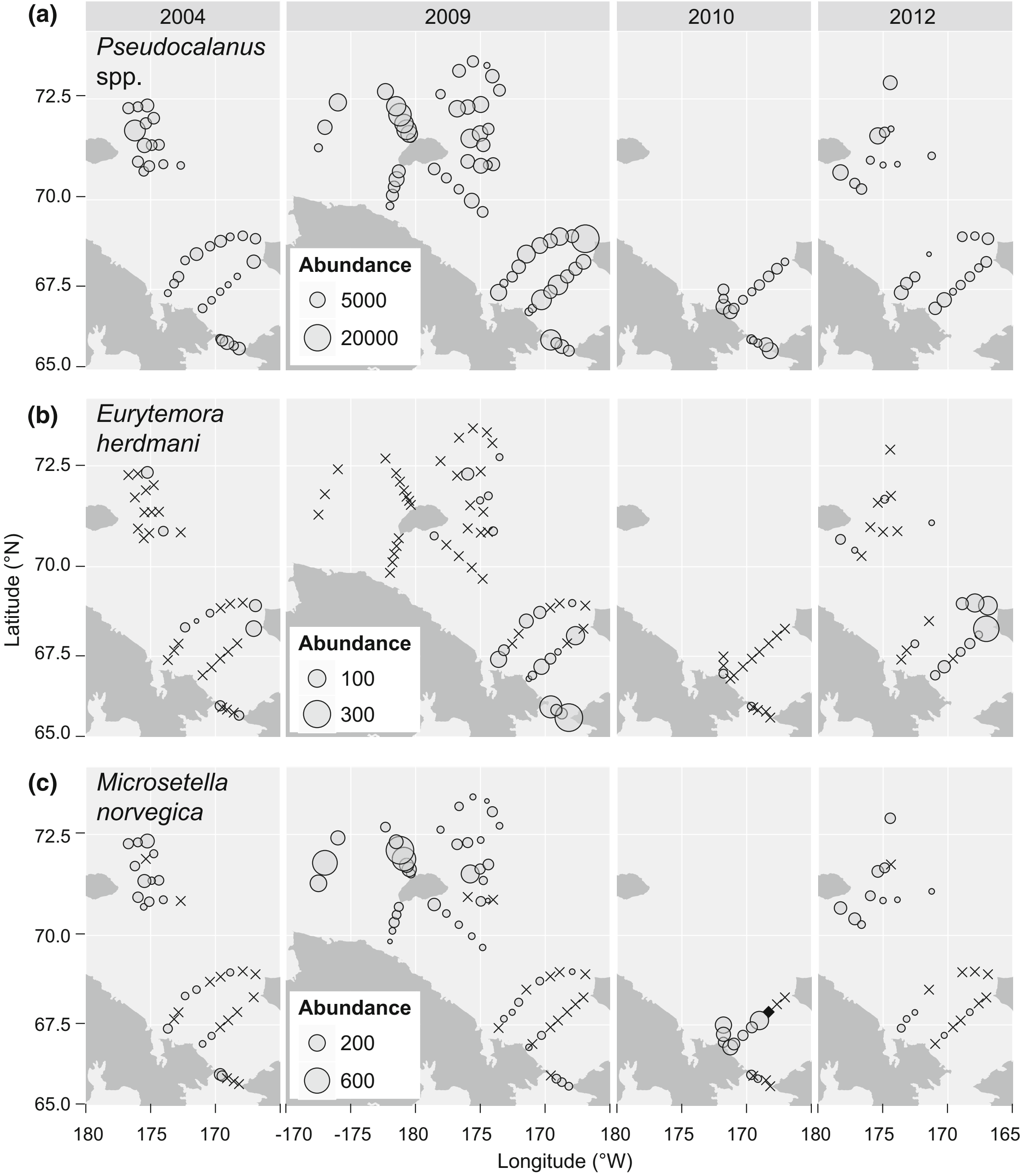

Fig. 5 Abundance of small copepods (continued) (ind m^{-3}) across the Southern Chukchi Sea; *cross symbol* species absent at this location

copepod species, such as *C. glacialis*, *M. pacifica*, *Pseudocalanus acuspes* and *P. newmani* ($R^2 = 0.36$, 0.28, 0.35. 0.25, respectively) (Fig. 10).

Discussion

While the relationship between zooplankton communities and water masses within this region has been well documented by studies beginning as early as the 1930 s (e.g., Stepanova 1937; Pavshtiks 1984; Kulikov 1992), no prior study has encompassed as many different water masses (ACW, BSAW, SCW, WW) within a single survey. Furthermore, repeated sampling over several years allowed us to observe the spatial variability of these relationships and their spatial manifestations. Within our study, four broad community types were identified: Alaska Coastal, Bering Sea (Pacific), Chukchi/Arctic and Siberian Coastal in broad agreement with study by Hopcroft et al. (2010) based on only 2004 data. Within these assemblages, the Alaska Coastal communities were the most identifiable, marked by the presence of a number of warm-water

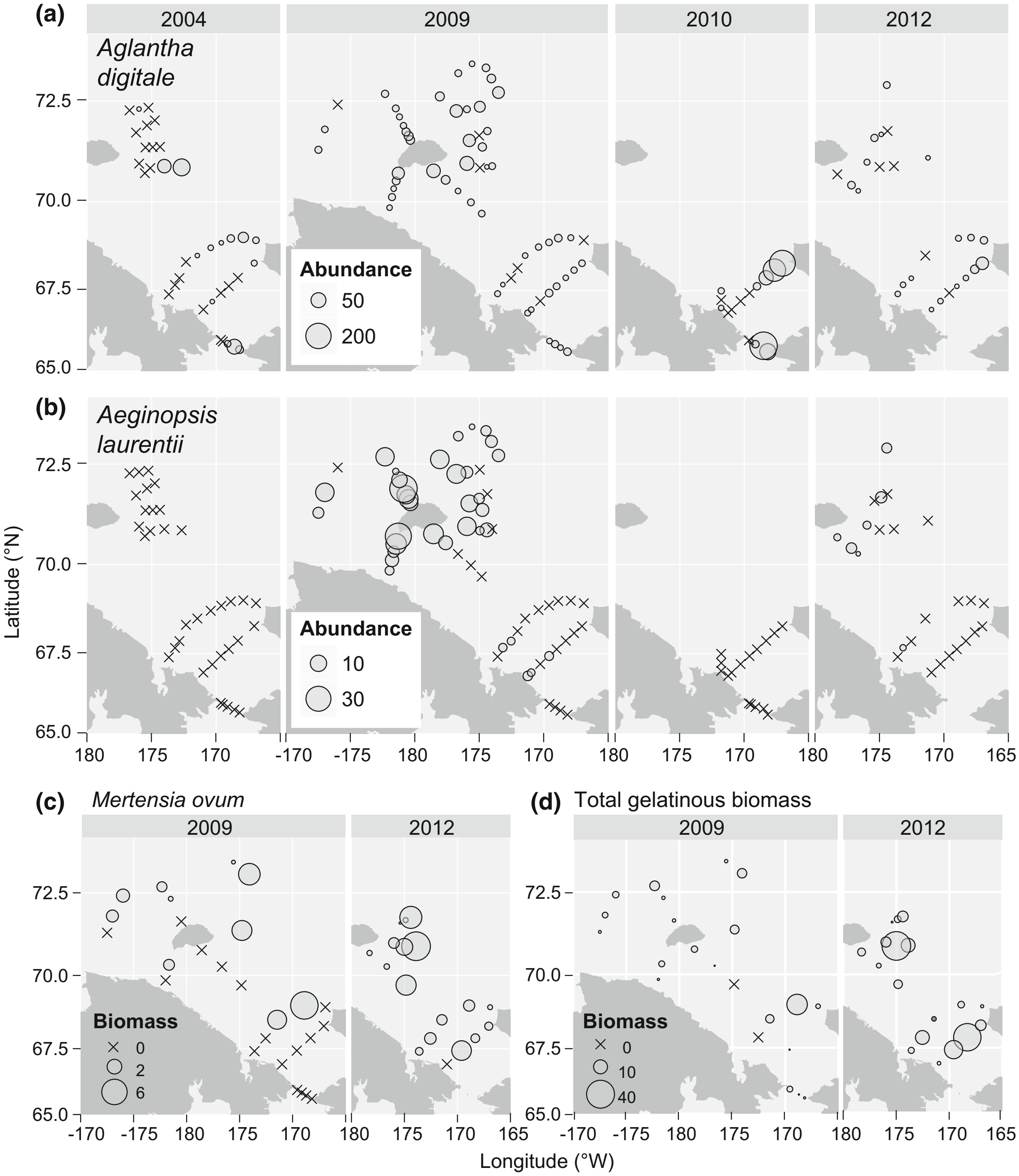

Fig. 6 **a**, **b** Abundance of gelatinous species (ind m^{-3}) across the Southern Chukchi Sea; *cross symbol* species absent at this location; **c** total biomass (mg DW m^{-3}) of gelatinous plankton in the Chukchi Sea as estimated by 505-µm nets

euryhaline taxa. In two of the study years (2004 and 2010), a marked boundary in both the physical properties and zooplankton communities separated these communities from adjacent BSAW waters; in 2012, this boundary was weaker, and in 2009, it was nearly absent, with species characteristic of the ACW found in diluted numbers across the entire southern Chukchi shelf. The boundary between Bering Sea oceanic and shelf communities, as described by Springer et al. (1989) and Hopcroft et al. (2010) for 2004, was variable and often obscured by mixing and layering of water masses of different origins. As a result, shelf and oceanic Bering water properties and communities were grouped into a broad BSAW category, which carries both oceanic and shelf zooplankton species in varying proportions, presumably as influenced by corresponding water masses.

An important transitional zone between Pacific and Arctic communities was formed in Herald Canyon. Most of

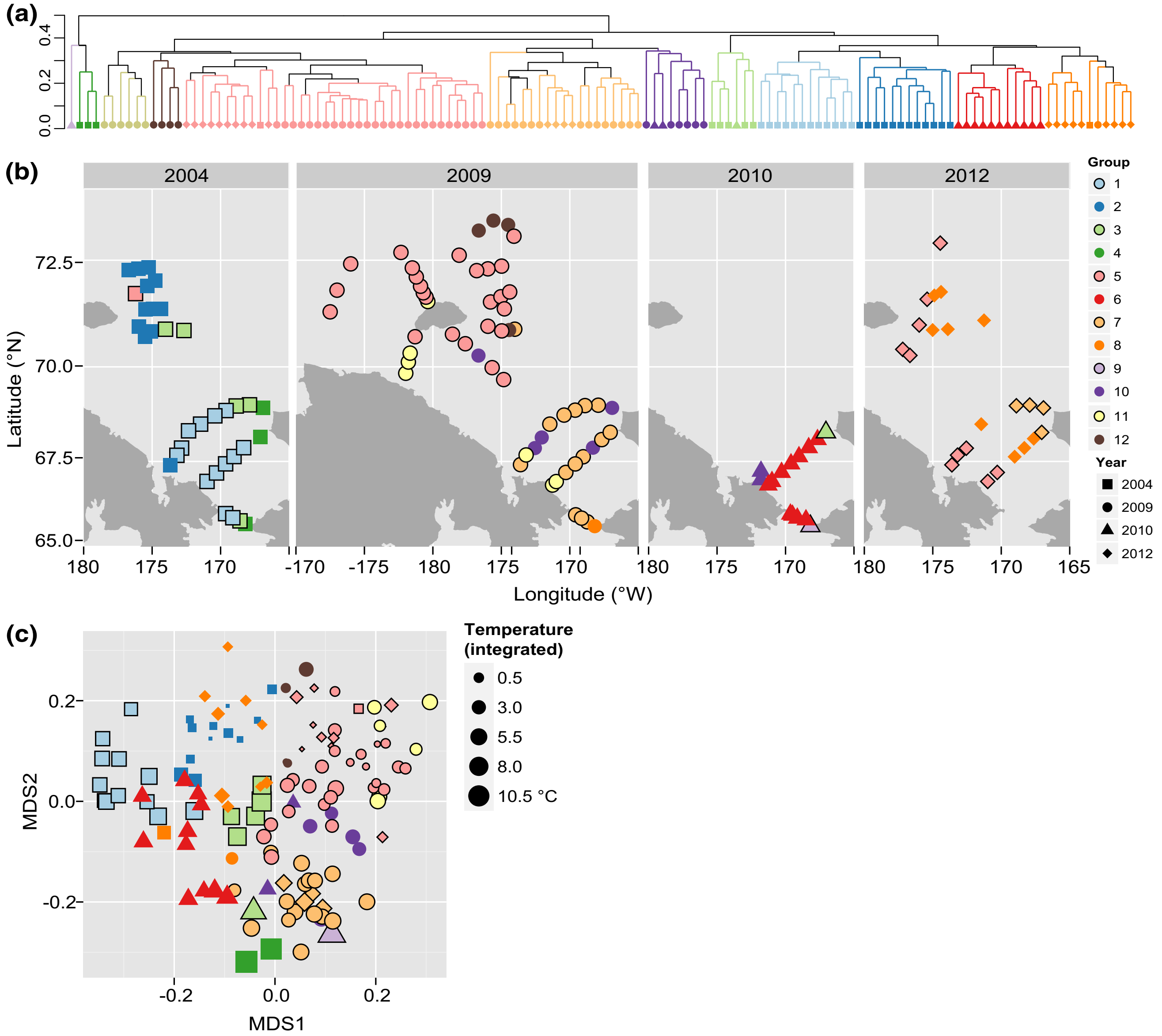

Fig. 7 Zooplankton abundance. **a**, **b** Cluster analysis and **c** nMDS ordination plot (first two axes) for combined 2004, 2009, 2010 and 2012 stations in the Chukchi Sea. Bottom temperature overlaying nMDS plot indicates strong relationship with community structure. *Solid colors* connect clusters that were significant at α = 0.05 level; *same colors* indicate 35 % similarity

the plankton observed on the eastern side of the canyon was strongly influenced by Bering Sea communities, with more resident Chukchi and Siberian coastal groups appearing to the west, accepting that our methodology weakens the intensity of some patterns when two water masses co-occur at a single station. The northward boundary, where Arctic zooplankton communities begin to replace Pacific communities, was visible in the deeper northernmost stations in 2009. Siberian coastal communities were characterized by lower biomass compared with the adjoining Chukchi Sea and were similar to those found in other shallow river-influenced Arctic seas, dominated by small neritic copepods (*Pseudocalanus* spp., *O. similis*, *M. norvegica*), hydrozoan jellyfish, and chaetognaths (Pavshtiks 1994).

The very low numbers of the copepod *C. glacialis* in the SCW and resident Chukchi communities strongly suggest that most of the *C. glacialis* population in the shallow Chukchi Sea was advected from the Bering Sea rather than the Arctic basins, and thus was not composed of resident individuals. This point is further reinforced by the distribution of copepodite stages of *C. glacialis* (Fig. 9), suggesting that during all the years, there were at least two distinct populations with different timing of life histories

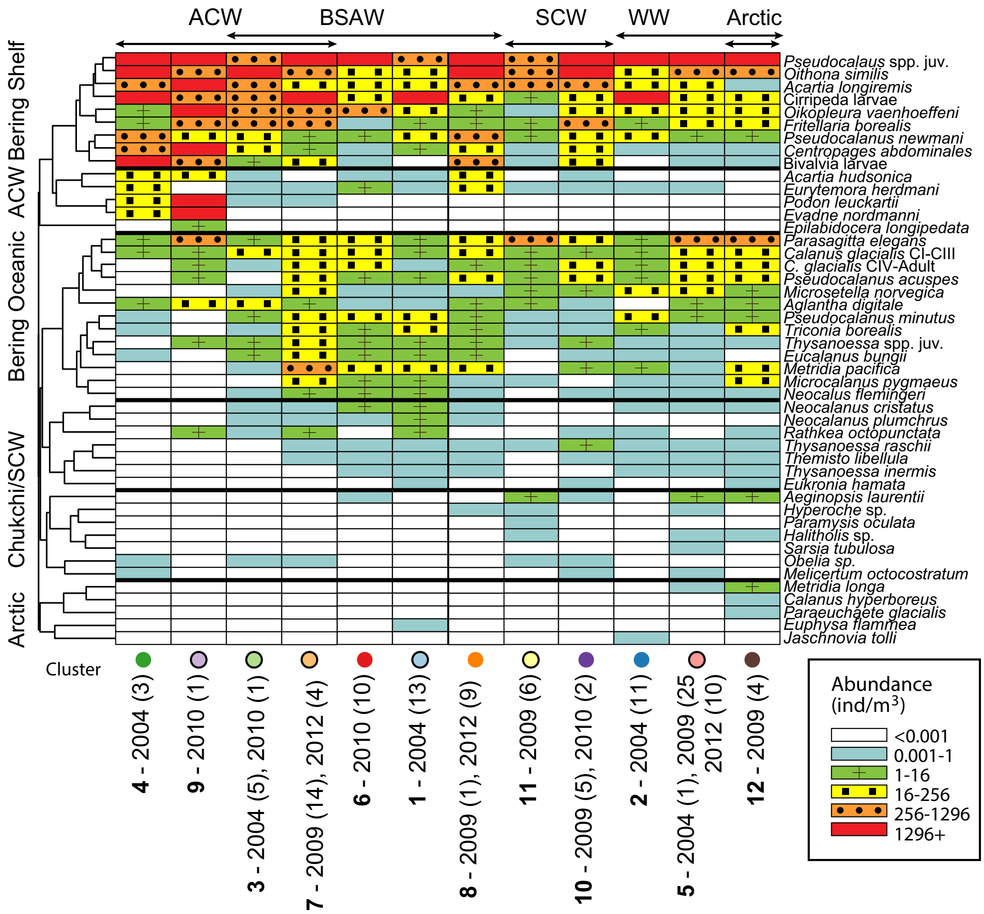

Fig. 8 Results of cluster analysis of species composition (*columns*) and stations (*rows*) in the Chukchi Sea. Text labels along axes indicate correspondence to water mass types; *column names* indicate cluster number (as defined in Fig. 10). *Numbers in parentheses* indicate number of stations per cluster and years observed

across the Chukchi Sea. A Pacific population presumably advected from the Bering Sea shelf and dominated by late copepodite stages IV–V was the main contributor to community biomass within the offshore section of the Southern Chukchi and the eastern side of Herald Canyon. In contrast, a resident Arctic population, composed of mainly early stages copepodite stages I-III and some adults, was found in the WW and SCW. This observation is consistent with results of population genetics, which also show two distinct haplotypes present in the Pacific Arctic: a Bering Sea haplotype which follows the Bering Sea water into the Chukchi Sea and a resident lineage, which is found throughout the marginal Arctic seas (Nelson et al. 2009). The latter may also sometimes be carried into the southern Chukchi by the SCW and even into the northern Bering Sea during occasional wind-driven current reversals.

The heightened presence of adult euphausiids in the East Siberian waters during 2009 and 2010 is also noteworthy. Surveys of marine mammals along the Chukotka coast show that this area may be an important feeding area for bowhead whales, which are known to actively prey upon euphausiids (Moore et al. 1995; Shelden and Mocklin 2013). Euphausiids are also active swimmers that are able to successfully avoid plankton nets; their increased presence in net tows may indicate reduced fitness in the cold and freshened waters of the Siberian Coastal Current.

While the primary members of the zooplankton communities remained the same between years, there was strong variability between years on the absolute and relative contribution to the communities by different taxa. For example, larvaceans, which were a very prominent component of the system in 2004 and 2012 (up to 40 % of total biomass at some stations), were nearly absent in 2009. Concurrent surveys in the northeastern Chukchi in 2009 also indicated extremely low larvacean abundance in that area (Questel et al. 2013) compared with 2012 (Hopcroft et al. 2014). Moreover, while our average abundance of *Oikopleura vanhoeffeni* in 2004 was two times higher than that of 2012, the biomass was significantly higher in 2012, due to the much larger sizes of the animals encountered. Most likely, this is the result of the combined effect of overall lower water temperature observed during 2012

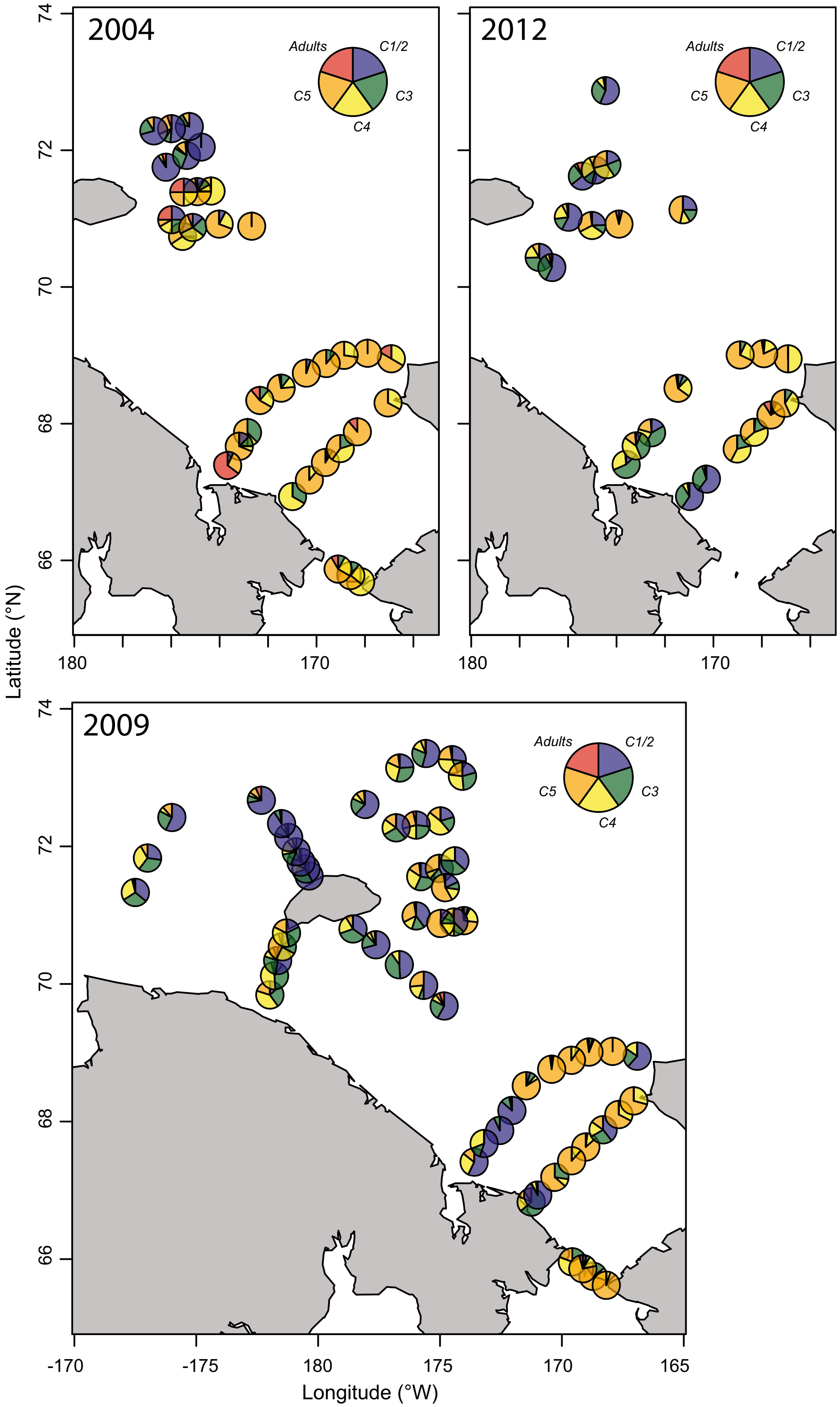

Fig. 9 Distribution of developmental stages of *Calanus glacialis* in the Chukchi Sea during 2004, 2009 and 2012 cruises

Table 4 Pearson's correlations between environmental variables and transformed abundance data in the Chukchi Sea

	2004	ρ	2009	ρ	2010	ρ	2012	ρ
1	S.btm	0.5690	dist	0.4653	T.btm	0.6985	**T.surf**	**0.5570**
2	**T.btm, S.btm**	**0.6454**	T.btm, dist	0.5435	Depth, T.btm	0.7370	T.surf, T.btm	0.5468
3	T.btm, S.btm, T.surf	0.6287	**T.btm, S.btm, dist**	**0.5933**	**T.btm, Depth, T.surf**	**0.7599**	T.surf, T.btm, S.surf	0.5406

All results presented are significant at $\alpha = 0.05$ level. Best correlations highlighted in bold

T temperature, *S* salinity, *btm* bottom layer, *surf* surface layer, *dist* distance from Bering Strait, *Depth* station depth

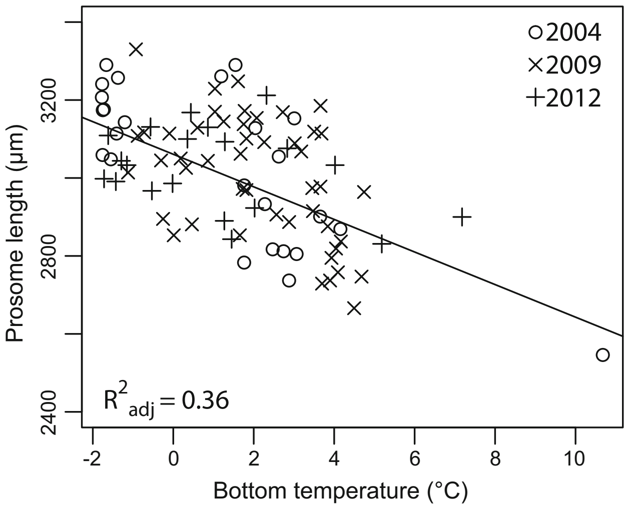

Fig. 10 Prosome length of C5 *Calanus glacialis* versus bottom temperature across all Chukchi Sea stations in 2004, 2009 and 2012

(whereby slower growth at lower temperature results in larger body size) and later timing of that cruise (thus encountering individuals at a later stage of their life cycle).

Abundance of other taxa, such as pteropods (completely absent in 2004), hydrozoan medusae and other gelatinous species, also showed very strong variability in contribution to communities during the different study years. Such year-to-year shifts from crustacean-dominated communities to communities with a higher contribution of gelatinous taxa may have important implications for the higher trophic levels. Jellyfish are predators of both zooplankton and fish larvae and can be detrimental to fish populations, which in turn are exploited by marine mammals (Brodeur et al. 2002, 2008). Since very few higher trophic levels can prey on gelatinous plankton, it also often represents a trophic "dead end" in the pelagic system.

The biomass and abundance values (42–80 mg DW m^{-3}, 3000–8000 ind m^{-3}) we observed within our study during the 4 years are comparable to estimates obtained by other historical and contemporary studies, some of which overlap our study in temporal and spatial coverage. The survey with the most comparable cross-shelf coverage ISHTAR (Springer et al. 1989) reported an average biomass of ~2–5 g DW m^{-2} (~40–100 mg DW m^{-3}) for the northern Bering Sea/southern Chukchi region, which is close to the range that we observed in our work, although our study uses different methods to arrive at biomass estimates. Older surveys, while imperfectly comparable due to different sampling techniques, generally report both biomass and abundance values within a similar range (see review in Hopcroft et al. 2010). The most recent estimates for the Eastern Chukchi (Matsuno et al. 2011) are also comparable, averaging 28–36 g WW m^{-2} (assuming DW to be ~10–15 % of WW). Interestingly, concurrent work in the northeastern Chukchi (Questel et al. 2013) found much lower overall biomass (~16 mg DW m^{-3}) from 150-µm nets in 2009 than we observed within our study, while the same study in 2010 reports much higher abundance and biomass values than were recorded by us during the same time period (101 mg DW m^{-3}/16,000 ind m^{-3}). The observed communities in 2012, however, are directly comparable, with similar biomass (66 mg DW m^{-3}) and an exceptionally high contribution of *C. glacialis* (Hopcroft et al. 2014). These observed differences may indicate that different processes are responsible for shaping zooplankton communities in the east and west Chukchi regions. Compared to other Arctic shelf systems, the biomass values observed in the Chukchi sea (2–5 g DW m^{-2}) are higher than that in most other regions, with the exception of the much deeper Barents Sea inflow system; biomass with the Barents Sea is reported to be 1–10 g DW m^{-2}, with estimates usually closer to the upper range (5–10 g DW m^{-2}) (Hunt et al. 2013). Biomass of summer zooplankton within the non-inflow shelf systems, such as the Laptev, Kara and White seas, is significantly lower, being of the order of ~1–2 mg DW m^{-2} (Kosobokova and Pertsova 2012).

It is important to note that while our results are presented as "snapshots," the Chukchi Sea is a highly dynamic system, where detectable seasonal change may occur over only a few weeks (Questel et al. 2013). It is not uncommon for wind activity to slow down or even reverse currents (Weingartner et al. 1999), as we observed during the 2009 cruise (Pisareva et al., accepted). Fronts of different water masses may also advance seasonally (Weingartner et al. 2013), replacing the community type present at a specific geographic location. These processes, which may have occurred on smaller timescales than the duration of the cruises, may have obscured the patterns observed. Nevertheless, the strong relationships between environmental factors and community structure during all years indicate that communities are very strongly structured by physical processes within the water column.

Inter-annual comparisons were also confounded by the slightly different seasonality of the cruises, including different timings relative to the spring breakup. The study years 2004 and 2010 both were sampled in early August, with the zooplankton communities observed during those years markedly different from those observed in 2009 and 2012 when sampling occurred in September. For example, meroplankton abundance was an order of magnitude higher in the two summer surveys; many meroplankton groups are only found in the plankton over a period of days or weeks before settling out to the benthos. Relatively large changes in community structure can occur over such timescales (Questel et al. 2013). Trophic interactions within the zooplankton communities may also play a large role in seasonal successions. The extremely high biomass of the chaetognath *Parasagitta elegans* observed in both September cruises (2009 and 2012), which at some stations exceeded the biomass of its prey, may indicate the transition of zooplankton communities from summer to autumn, when copepod production slows down, but the higher trophic levels are still capitalizing on the abundant food.

Indices of climate variability, such as the Pacific decadal oscillation (PDO), provide us with an opportunity to observe the effect that longer-term climate change may have on an ecosystem. PDO-related anomalies have been studied extensively within the Bering Sea, with zooplankton and fish communities visibly responding to changes in temperature and ice cover (Hunt et al. 2011). Namely, colder years with later ice retreat seem to benefit the shelf populations of large copepod *C. glacialis*, while abundances of small copepods and cnidarians decrease during cold years (Eisner et al. 2014). The Chukchi Sea's thermal regimes should reflect the conditions observed in the same years in the Bering Sea, as well as the shifts in zooplankton communities (Coyle et al. 2011; Eisner et al. 2014). Our 2004 survey was the only "warm" (positive PDO) year during our study period; it was also the year with the lowest observed biomass in the Chukchi Sea. The coldest year, 2012, was also the year with the highest biomass of advected *C. glacialis* across the Chukchi Sea, as also observed to the Northeast (Hopcroft et al. 2014). We did not observe a decrease in the numbers of small copepod species in 2009–2012, as was observed for the same period in the Bering Sea (Eisner et al. 2014); on the contrary, 2009 stands out by an almost twofold increase in small copepod abundance. This is indicative of the fact that the faster-growing small copepod populations may be more responsive to local conditions than to processes upstream.

While warm years such as 2004 may be examined as somewhat representative of what will happen to zooplankton communities as climate warms and sea ice retreats, for any permanent shift to occur within the plankton communities, such conditions must be maintained. The extent of variability observed within our study and other studies in the Chukchi (e.g., Questel et al. 2013; Hopcroft et al. 2014) indicates that the system is highly flexible and responsive to year-to-year shifts in climatic forcing. While a longer warm-water summer period, as observed in 2004, may provide an opportunity for boreal Pacific species to play an increased role in summer communities within the Chukchi Sea, during the winter and spring, the Northern Bering Sea remains at least partially ice-covered, and waters entering and within the Chukchi Sea during the winter have near-freezing temperatures. Thus, advected species are unlikely to survive the winter and establish permanent populations with the Chukchi (Wassmann et al., accepted). This is in contrast to the North Atlantic inflow system of the Barents Sea, where year-round above-freezing conditions may allow for permanent range expansion of southern species with warming water temperatures (Kwasniewski et al. 2012; Hunt et al. 2013).

Small copepods, such as *Pseudocalanus* spp. and *Oithona similis*, may play a proportionately larger role in a warmer Chukchi, although other local factors such as food availability may be more important in determining their ultimate success. Although a prolonged ice-free period may increase primary production and potentially benefit some zooplankton groups and higher trophic levels, a decrease and/or mismatch in sea ice algae production may affect Arctic species that are tuned to the spring ice algae bloom. Furthermore, an overall increase in productivity may be accompanied by a shift to smaller phytoplankton species (Arrigo and van Dijken 2011), which may cycle more production within the microbial loop and be detrimental to herbivorous species that specialize on large phytoplankton cells. Since body size is inversely related to temperature (Hop et al. 2006) (and as observed for several species within our study, Fig. 10), a downward shift in zooplankton size distribution even within species would be expected. Smaller zooplankton may be less effectively preyed upon by vertebrate predators, with significant consequences to many higher trophic levels (e.g., Kwasniewski et al. 2012).

Conclusions

The structure, biomass and productivity of zooplankton communities within the Chukchi Sea clearly reflect variations in physical properties of the water column, as well as seasonal differences and intensity of downstream productivity and Pacific water transport. While our results are snapshots of an extremely dynamic system, broad patterns are nevertheless emergent and together with other concurrent studies and historical data may be used to infer the fate of the pelagic communities both upstream and downstream of the studied region. Here, we establish spatial and inter-annual variability of summer plankton communities across a broad area within the Chukchi Sea, which is strongly shaped by different water masses. Future surveys, including those during "warm" years, should seek to capture more of the seasonal and inter-annual dynamics of the system and their responses to progressive climatic forcing.

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