CONTEMPORARY MESOZOOPLANKTON COMMUNITIES OF THE BEAUFORT SEA

By

Caitlin A. Smoot

RECOMMENDED: Kenneth O Coyle
Dr. Kenneth Coyle

Dr. Peter Winsor

Dr. Russell Hopcroft
Advisory Committee Chair

Dr. Katrin Iken
Program Head, Marine Sciences and Limnology

APPROVED:
Dr. Joan Braddock
Interim Dean, School of Fisheries and Ocean Sciences

John C Eichelberger
Dr. John Eichelberger
Dean of the Graduate School

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Date

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A

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By

Caitlin A. Smoot, B.S.

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Abstract

Zooplankton are critical trophic links and important modifiers of organic carbon cycles, yet are poorly characterized for much of the Arctic's Beaufort Sea, particularly in mesopelagic (> 200 m) waters.

Zooplankton were sampled with 150 and 505 µm mesh nets in the upper 200 m in sections of the Beaufort Sea between Barrow Canyon and the Mackenzie River during August and September 2010-2013 to characterize the species composition, abundance, and biomass of epipelagic Beaufort Sea zooplankton communities. I observed 106 taxonomic zooplankton categories during four field seasons across both mesh sizes; copepods exhibited the highest species richness (38 species), followed by cnidarians (16 species) and amphipods (14 species). Average holozooplankton abundance ranged from 1110-3880 ind. m^{-3} in the 150-µm net and 47-215 ind. m^{-3} in the 505-µm net. Average holozooplankton biomass ranged from 23.8-76.9 mg dry-weight (DW) m^{-3} and 13.9-57.6 mg DW m^{-3} in the 150-µm and 505-µm nets, respectively. Spatial structure of zooplankton communities reflected a blending of across- and along-shelf temperature and salinity gradients that were driven by relative contributions of different water mass types.

To characterize mesopelagic zooplankton communities of the Beaufort Sea, I collected stratified zooplankton samples and physical oceanographic data at stations along the Beaufort Sea slope during August 2013. I documented 93 taxonomic categories; greatest diversity was observed in the copepods (48 species), followed by the cnidarians (10 species) and amphipods (8 species). Distinct zooplankton communities were associated with the three main water masses in the study region: the Polar Mixed Layer (PML), Arctic Halocline Water (AHW), and Atlantic Water (AW). Average abundance and biomass were highest (1150 ind. m^{-3} and 27.1 mg DW m^{-3}, respectively) in the PML (0-50 m) and declined with depth, to a minimum in the 500-1000 m layer of AW (15 ind. m^{-3} and 0.6 mg DW m^{-3}). Conversely, species richness increased with depth. Community structure was highly correlated with salinity and depth, both in terms of abundance (Spearman correlation (ρ) = 0.84, $p < 0.01$) and biomass ($\rho = 0.81$, $p < 0.01$).

Zooplankton communities in the Beaufort Sea exhibit structure along three axes: along-shore, across-shore, and depth-related. Community structure along these axes reflects hydrographic gradients created by different water masses and physical factors in the study region. This work provides a contemporary benchmark for Beaufort Sea zooplankton community species composition, abundance, and biomass from which future change may be assessed.

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General Introduction

Zooplankton are critical components of the marine ecosystem, both in terms of sheer numerical dominance in the global ocean (Schminke, 2007) and in terms of the ecological roles they can play. Zooplankton serve as trophic links between primary producers and upper trophic levels (e.g., Moore *et al.*, 2010), contribute to carbon and nitrogen cycling, and modulate the flux of organic material to the seafloor (del Giorgio & Duarte, 2002; Robinson *et al.*, 2010; Alcaraz *et al.*, 2010). Arctic zooplankton have a suite of finely-tuned physiological, reproductive, and energetic adaptions to life in a harsh and seasonally pulsed environment (Clarke & Peck, 1991; Hagen & Auel, 2001). It is well established that the Arctic Ocean is currently undergoing dramatic changes in sea ice cover, temperature, and carbonate mineral saturation states (Serreze *et al.*, 2007; Bates *et al.*, 2009; Stroeve *et al.*, 2012; Bates *et al.*, 2013) and that the Arctic marine system will experience an amplification of climate change signals when compared to lower latitudes (Serreze & Barry, 2011). It is less certain how Arctic marine zooplankton communities will respond to changes in climate; however, it is likely that zooplankton will be among the first responders to climate change because they are poikilotherms and have relatively short life spans (Hays *et al.*, 2005; Richardson, 2008). Efforts to document the responses of Arctic marine biota to climate change include only nine reports of planktonic response, of which just four concern zooplankton (Wassmann *et al.*, 2011). The paucity of consistent baseline data for many Arctic ecosystems is one of the main challenges of quantifying and documenting zooplankton community response to climate change.

Zooplankton communities are influenced by the physical and chemical oceanographic features of their environment; as a result, distinct species assemblages are often associated with different water masses (e.g., Grainger, 1965, Ashjian *et al.*, 2003; Lane *et al.*, 2008; Hopcroft *et al.*, 2010; Questel *et al.*, 2013; Ershova *et al.*, 2015). The Beaufort Sea is characterized by extreme environmental gradients that are reflected in the biological community. These gradients can be viewed along three major axes: across-shelf, along-shelf, and depth-related (e.g., Grainger, 1965; Darnis *et al.*, 2008; Walkusz *et al.*, 2010, 2013). Inshore waters of the Beaufort Sea are under strong influence of freshwater discharge from many river systems along the coast, notably the Colville River (15 km^3 yr^{-1} mean annual discharge) in the western Beaufort and the large Mackenzie River (308 km^3 yr^{-1} mean annual discharge) in the east (Arnborg *et al.*, 1967; Millot *et al.*, 2003). The Mackenzie River inputs substantial amounts of freshwater and terrestrial material to the nearshore environment of the Beaufort Sea (Millot *et al.*, 2003; Dunton *et al.*, 2006) in a plume that can extend over large portions of the Alaskan and Canadian sectors of the Beaufort shelf dependent on physical forcing (Carmack *et al.*, 1989; MacDonald *et al.*, 1989; Dunton *et al.*, 2006). Seasonal pulses of freshwater to the nearshore environment produce estuarine conditions that stand in stark contrast to the more oceanic conditions encountered offshore.

In the western Beaufort, complex bathymetry around Barrow Canyon and the influence of the Chukchi Sea domain produce unique oceanographic conditions that impact biological communities (Okkonen *et al.*, 2009; Ashjian *et al.*, 2010). The shelf-break and slope of the Beaufort Sea fall under influence of Pacific origin waters in the form of a narrow and seasonally variable jet, known as the Beaufort Shelf-break Current, flowing eastward along the shelf-break (Pickart, 2004; Spall *et al.*, 2008; Nikolopoulos *et al.*, 2009). Moving eastward, shelf waters and biota come under increasing influence of the Mackenzie River (Grainger & Grohe, 1975; Carmack *et al.*, 1989; Darnis *et al.*, 2008; Walkusz *et al.*, 2010), which provides a general demarcation between the relatively narrow Alaskan Beaufort Shelf and the wider Canadian Mackenzie Shelf. Shelf waters are influenced by freshwater input, freezing and melting processes, and cross-shelf exchange mechanisms, such as mesoscale eddies and wind-driven upwelling events (Carmack & MacDonald, 2002; Llinas *et al.*, 2009). Upwelling events can bring deep water masses from the Beaufort Sea slope onto the shelf, along with associated nutrients and biota (Mathis *et al.*, 2012; Pickart *et al.*, 2013a; Pickart *et al.*, 2013b).

A generalized description of water masses present in the Canada Basin along the Beaufort Sea slope illustrates vertical oceanographic gradients that are encountered by biological communities and characterizes deep water masses that may be upwelled onto the shelf (e.g., McLaughlin *et al.*, 2005). Shallow waters (0-50 m) of the offshore Beaufort Sea are comprised of the Polar Mixed Layer (PML), which is modified by freshwater input, atmospheric exchange, and freezing and melting processes (Carmack *et al.*, 1989; Lansard *et al.*, 2012). Below the PML lies Arctic Halocline Water (AHW), extending from approximately 50-200 m, followed by warmer and saltier Atlantic Water (AW) beginning around 200-300 meters (Aagaard *et al.*, 1981; Codispoti *et al.*, 2005; Codispoti *et al.*, 2009). This system of vertically-layered water masses is typical of the Arctic and produces a vertical gradient of environmental conditions that host different biological communities (Blachowiak-Samolyk *et al.*, 2007; Kosobokova & Hopcroft, 2010; Kosobokova *et al.*, 2011).

The oceanographic environment and planktonic communities of the Beaufort Sea have been sampled sporadically over the past six decades. Early efforts to document zooplankton in the Alaskan Beaufort Sea were conducted during the USS *Burton Island* cruises in 1950 and 1951 (Johnson, 1956; Hand, 1961). The *Burton Island* cruises covered a wide geographical range and sampled the Chukchi and Beaufort seas, as well as waters of the Canada Basin; however, relatively few stations were sampled on the Beaufort shelf itself compared to offshore waters. The Western Beaufort Sea Ecological Cruise (WEBSEC) program sampled the western and central Alaskan Beaufort in the 1970s (Hufford *et al.*, 1974; McConnell, 1977; Hopcroft *et al.*, 2012), followed by the Outer Continental Shelf Environmental Assessment Program (OCSEAP) (Horner, 1978; Horner, 1979; Horner, 1980). These programs had relatively broad spatial coverage of the Beaufort shelf; however, the coarse mesh (≥333 μm) used resulted in a bias towards larger-bodied zooplankton taxa while neglecting numerically important small-bodied genera such as *Triconia*, *Oithona*, and *Pseudocalanus*. It is particularly notable that low taxonomic resolution reported during most OCSEAP Beaufort studies renders those data of limited use. Grainger (1965; 1975) and Mohammed & Grainger (1974) reported on sampling conducted east of the US-Canada border in coastal Canadian waters. The Canadian Beaufort was also sampled in the 1980s with the Northern Oil and Gas Action Program (NOGAP2) (Hopky *et al.*, 1994a; Hopky *et al.*, 1994c; Hopky *et al.*, 1994b).

More recent efforts in the Alaskan Beaufort include the Shelf-Basin Interactions (SBI) program (Lane *et al.*, 2008) and Bowfest (Ashjian *et al.*, 2010); these programs focused on waters in the western Beaufort around Barrow Canyon. Other modern efforts include the 2002 R/V *Mirai* cruise in the Chukchi and Beaufort seas, the CCGS *Nahidik* cruises (Walkusz *et al.*, 2010; Walkusz *et al.*, 2012; Walkusz *et al.*, 2013), the CASES program (Darnis *et al.*, 2008), and the Beaufort Regional Environmental Assessment (BREA) in Canadian waters. In summary, most modern efforts in Alaskan waters focus on the western Beaufort around Barrow Canyon, while Canadian efforts focus on waters of the Mackenzie Shelf, resulting in a modern data gap for zooplankton communities of the central and eastern Alaskan Beaufort Shelf. Additionally, efforts to characterize the zooplankton communities of the Beaufort Sea have focused on epipelagic waters (0-200 m), neglecting the poorly-studied mesopelagic realm. Studies documenting vertical structure of the Arctic's marginal seas are generally scarce (Kosobokova *et al.*, 1998; Arashkevich *et al.*, 2010; Walkusz *et al.*, 2013) and are entirely lacking for the deeper mesopelagic communities of the Beaufort Sea slope. Mesopelagic zooplankton communities are modifiers of sinking organic material (Robinson *et al.*, 2010), and represent considerable species diversity in the Arctic's basins (e.g. Kosobokova *et al.* 2011).

This thesis attempts to fill the modern data gap for zooplankton communities on the Beaufort Sea shelf and slope by documenting the species composition, abundance, and biomass of the zooplankton communities in the Beaufort Sea survey areas during August and September from 2010-2013. It will characterize the zooplankton community along the three spatial axes (across-shelf, along-shelf, and depth-related) and relate the physical oceanographic environment to the observed community structure. This work serves as a modern benchmark for zooplankton community composition, abundance, and biomass from which future change may be gauged, and represents the first depth-stratified examination of Beaufort Sea zooplankton communities ranging from the surface to 1000 meters in depth.

1. The epipelagic zooplankton communities of the Beaufort Sea during 2010-13 and their relationship to hydrography[1]

Abstract

Zooplankton are poorly characterized for large portions of the Arctic's Beaufort Sea, despite their ecological and trophic importance. Biological, chemical, and physical oceanographic data were collected on the Beaufort Sea shelf between Point Barrow and the Mackenzie River during August and September from 2010-2013. Data were collected along cross-shelf transects ranging from the 20 m isobath to the 1000 m isobath with 150- and 505-µm nets; here we present data from the upper 200 m of the water column as the epipelagic community. Annual averages of holozooplankton abundance and biomass ranged from 1110-3880 ind. m^{-3} and 23.8-76.9 mg DW m^{-3} in the 150- µm net, while the 505-µm net ranged from 47-215 ind. m^{-3} and 13.9-57.6 mg DW m^{-3}, respectively. The zooplankton community was decidedly Arctic in faunal character during all field seasons, although Pacific expatriates were observed in extremely low abundances. The community was dominated in abundance and biomass by Arctic copepods, including *Calanus glacialis*, *Calanus hyperboreus*, *Metridia longa*, *Oithona similis*, *Triconia borealis*, *Microcalanus pygmaeus*, and the *Pseudocalanus* species complex; this group contributed 45-81% of the abundance and 52-64% of the biomass in the 150-µm net, and 42-92% of the abundance and 44-63% of the biomass in the 505-µm net. Zooplankton community structure reflected a blending of across-shelf and along-shelf gradients representative of the underlying hydrographic conditions. Community structure from the 150-µm net was most strongly related to temperature and salinity averaged over the upper 100 m in terms of abundance (Spearman correlation (ρ): 0.53, $p < 0.01$) and biomass ($\rho = 0.49$, $p < 0.01$). Community structure in the 505-µm net was best related to temperature averaged over the upper 200 m in terms of abundance ($\rho = 0.57$, $p < 0.01$) and biomass ($\rho = 0.50$, $p < 0.01$). This study serves as a contemporary benchmark for zooplankton communities of the Beaufort Sea and may be used to assess future change as the Beaufort Sea undergoes rapid environmental change and increased oil and gas exploration.

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[1] Smoot, C. and Hopcroft, R.R. The epipelagic zooplankton communities of the Beaufort Sea during 2010-13 and their relationship to hydrography. Prepared for submission in Journal of Plankton Research.

Introduction

Zooplankton are important trophic intermediaries in marine systems; in the Beaufort Sea, zooplankton communities connect the highly seasonal pulse of primary production to upper trophic levels, such as fish and marine mammals, that are of cultural and ecological significance (Lowry *et al.*, 2004; Walkusz *et al.*, 2011). It is well established that the Arctic Ocean is undergoing changes in sea ice cover, temperature, and carbonate mineral saturation states (Serreze *et al.*, 2007; Bates *et al.*, 2009; Stroeve *et al.*, 2012; Bates *et al.*, 2013); it is less certain how Arctic marine zooplankton communities will respond to these changes. Zooplankton will likely be among the first responders to climate change due to their poikilothermic nature and relatively short lifespans (Hays *et al.*, 2005; Richardson, 2008). The paucity of consistent baseline data for many Arctic ecosystems is one of the main challenges of quantifying and documenting zooplankton community response to climate change (e.g., Wassmann *et al.*, 2011); therefore, as the Beaufort Sea undergoes rapid environmental change, concurrent with industrial development, it is critical to monitor its biological communities. This work contributes to a multi-year and multi-disciplinary effort to characterize the physical and biological oceanography of the Beaufort Sea, and serves as a spatially comprehensive assessment of contemporary epipelagic zooplankton communities in the Beaufort Sea.

The Beaufort Sea is a seasonally ice-covered interior sea of the Arctic Ocean. Early efforts to characterize the physical oceanography and zooplankton communities of the Beaufort Sea include Johnson's (1956) work on the USS *Burton Island* cruises. The *Burton Island* cruises spanned the Beaufort and Chukchi Seas and southern Canada Basin; however, relatively few samples were collected from the Alaskan Beaufort shelf. The Western Beaufort Sea Ecological Cruise (WEBSEC) program in the 1970s (Hufford *et al.*, 1974; McConnell, 1977; Hopcroft *et al.*, 2012) and the Outer Continental Shelf Environmental Assessment Program (OCSEAP) (Horner, 1978; Horner, 1979; Horner, 1980) provided better spatial coverage of the Alaskan Beaufort shelf; however, the coarse mesh (≥ 333 μm) used in these programs resulted in a bias toward larger bodied taxa while completely excluding small-bodied and numerically dominant taxa. Data from OCSEAP do not provide species-level taxonomic resolution; rather, organisms were grouped into broad taxonomic categories, thus rendering its data of limited use. Very shallow (< 10 m) nearshore stations of the Beaufort Sea in the vicinity of Prudhoe Bay were also sampled by Horner and Murphy (1985) during the winter ice-covered period. Early efforts in the

Canadian Beaufort include Grainger (1965, 1975) and Mohammed & Grainger (1974). The Canadian Beaufort was also extensively sampled by the Northern Oil and Gas Action Program (NOGAP2) in the 1980s (Hopky *et al.*, 1994a; Hopky *et al.*, 1994c; Hopky *et al.*, 1994b). These early efforts provide important historical perspective; however, gear biases, inadequate taxonomic resolution of key groups, and limited spatial coverage preclude rigorous comparisons between many data sets, and highlight the paucity of consistent baseline ecological data for zooplankton communities of the Beaufort Sea. More recent efforts in the Alaskan Beaufort Sea have focused on the oceanographically complex area around Barrow Canyon (e.g. Lane *et al.* 2008, Ashjian *et al.* 2010), while Canadian efforts include the 2002 R/V *Mirai* cruise in the Chukchi and Beaufort Seas, the CCGS *Nahidik* cruises (Walkusz *et al.*, 2010; Walkusz *et al.*, 2012; Walkusz *et al.*, 2013), the Canadian Arctic Shelf Exchange Study (CASES) (Darnis *et al.*, 2008), and the Beaufort Regional Environmental Assessment (BREA). As a result, a large contemporary data gap exists for much of the central and eastern Alaskan Beaufort Sea.

Zooplankton communities are associated with water masses and their underlying hydrographic properties (e.g., Darnis *et al.*, 2008; Lane *et al.*, 2008; Hopcroft *et al.*, 2010; Ershova *et al.* 2015); as a result knowledge of the underlying physical oceanographic conditions can provide insight into likely faunal assemblages. Understanding zooplankton assemblages and their hydrographic associations is particularly critical in light of a rapidly changing Arctic. The volume of Pacific water flow through Bering Strait into the Arctic has increased in recent years (Woodgate *et al.*, 2012), upwelling events have increased in frequency and strength in the Beaufort Sea (Pickart *et al.*, 2013), and modelling efforts suggest that Mackenzie River discharge, along with other Arctic rivers, may increase in a warming climate (Nijssen *et al.*, 2001; Nohara *et al.*, 2006). Changes in these physical parameters can impact biological communities; therefore, knowledge of faunal associations can provide insight into shifts in community structure that may result from environmental forcing. Given the trophic importance of zooplankton, changes in community structure have the potential to reverberate throughout Arctic food webs. This study identifies the species composition, abundance, and biomass of the contemporary Beaufort Sea shelf zooplankton communities, relates community structure to underlying hydrography, and characterizes broad-scale community patterns as this region experiences a period of rapid environmental change and increasing commercial activities.

Methods

Study region

The Beaufort Sea is a seasonally ice-covered interior shelf sea of the Arctic Ocean. The Alaskan Beaufort is bounded on the west by Barrow Canyon, where the shelf is relatively narrow (~80 km), and in the east by Mackenzie Canyon, where it widens slightly in Canadian waters. Near-shore and surface waters of the Beaufort Sea are profoundly influenced by seasonally variable freshwater input, both in the Alaskan and Canadian sectors. The Alaskan sector of the Beaufort Sea receives freshwater input from numerous small rivers, the largest of which is the Colville River. The Canadian sector is dominated by input from the large Mackenzie River (Dunton *et al.*, 2006). The mean Mackenzie River freshwater discharge is approximately 308 km^3 yr^{-1} at the mouth (Millot *et al.*, 2003) and the plume can extend over large portions of the Alaskan and Canadian sectors of the Beaufort shelf and slope depending on physical forcing (Carmack *et al.*, 1989, Dunton *et al.*, 2006, MacDonald *et al.*, 1989). By comparison, the Colville River and the Sagavanirktok River are the two largest rivers draining into the Beaufort Sea from Alaska's North Slope and discharge approximately 15 km^3 yr^{-1} and 2 km^3 yr^{-1}, respectively (Arnborg *et al.*, 1967; Rember & Trefry, 2004). Together, sea ice meltwater and riverine input create highly freshened conditions in surface waters of Beaufort shelf during summer months (Carmack *et al.*, 1989; Dunton *et al.*, 2006).

Pacific-influenced waters east of Barrow Canyon form a seasonally variable Beaufort Shelf-Break Jet (BSJ) flowing eastward along the Beaufort shelf break. In summer months this jet is surface intensified and carries buoyant Alaska Coastal Water (ACW), while in spring and winter months transformed winter water is transported in a subsurface jet (Pickart *et al.*, 2005; Nikolopoulos *et al.*, 2009). ACW is seasonally variable and is generally characterized by warm (0-10°C) and freshened (< 32) water (Codispoti *et al.*, 2005). Cross-shelf exchange is common in the Beaufort Sea and can exert a strong structuring force on biological communities. Mesoscale eddies can carry shelf waters and biota into the basin (Llinas *et al.*, 2009), and winds produced by variations in the Beaufort High, as well as storms generated by the Aleutian Low, can cause reversal of the BSJ, resulting in upwelling events. During upwelling events, slope waters from intermediate depths (i.e., Arctic Halocline Water (AHW) and Atlantic Water (AW)) can move onto the Beaufort shelf, transporting nutrients and biota from depth (Pickart *et al.*, 2009; Pickart *et al.*, 2011; Mathis *et al.*, 2012). The hydrographic characteristics and relative influence of freshened surface waters, resident shelf waters, deeper intermediate waters, and waters of Pacific-origin subsequently shape the composition and distribution of Beaufort Sea zooplankton communities.

Sample collection and processing

Data were collected during four field seasons during August and September of 2010-13 (Table 1.1), primarily during daylight hours. Due to differences in station locations between surveys, we present zooplankton community structure and species composition relative to water mass type, rather than in terms of inter-annual differences. Oceanographic data were sampled along cross-shelf transects at stations ranging from 20 m to 1000 m in depth from Point Barrow to the Mackenzie River (Fig. 1.1). Here we focus on observations from the epipelagic realm (0-200 m).

Physical oceanographic data were collected with a Seabird SBE25 CTD, and averaged into 1-m vertical intervals. Chlorophyll-*a* and macro-nutrient samples were collected with a 6 Niskin bottle SBE-55 rosette attached to the CTD. Water samples for chlorophyll-*a* and macro-nutrient analysis were taken at the surface, 10, 20, 30, 40, and 50 m; when stations were shallower than 50 m, the deepest water sample was collected approximately three meters from the sea floor. Water for chlorophyll-*a* analysis was filtered under low pressure onto Whatman GF/F filters; filters were then frozen at -40 °C for post-cruise analysis following Parsons *et al.* (1984). In 2013, 20 μm polycarbonate filters and Whatman GF/F filters were used to size fractionate cells. Nutrient samples were filtered with 0.45 μm cellulose-acetate filters and frozen immediately at -40°C for post-cruise analysis following the methods of Gordon *et al.* (1993).

Smaller zooplankton were collected with a vertically-hauled twin-ring 60-cm diameter net fitted with 150-μm mesh at all stations in 2010 and 2011. In 2012 and 2013, the twin-net was used at shallow stations, while a Hydrobios Midi-Multinet (150-μm mesh nets; mouth aperture: 0.25 m^2) was used at stations greater than 50 m depth to collect vertically-stratified samples. Larger, more mobile zooplankton were targeted with a 60-cm Bongo net fitted with 505-μm mesh hauled obliquely at approximately two knots. All nets were outfitted with annually-calibrated General Oceanics flowmeters to estimate volume of water filtered. Samples were preserved in 10% buffered formalin and returned to the laboratory for processing.

During laboratory processing, samples were subsampled using a Folsom splitter until a given aliquot contained approximately 100 individuals of the most abundant taxa. Increasingly larger fractions were examined for less abundant taxa. Organisms were identified, enumerated, measured, and staged (when appropriate) to determine species composition, abundance, and biomass. Measurements were completed using the ZoopBiom program (Roff & Hopcroft, 1986). The weight of measured animals was predicted from species-specific length-weight relationships (Questel *et al.*, 2013) or from relationships of morphologically similar species. Typically, 400-600 animals were measured within each sample. Organisms were identified to lowest taxonomic level possible. Data from stratified samples were integrated to produce a single stratum over the upper 200 m for these analyses.

Data processing and statistical analyses

Analyses were performed separately for both abundance and biomass using 4th root-transformed data pooled across all years for each mesh size. Community associations were assessed using the Bray-Curtis similarity index (Bray & Curtis, 1957) and community structure was subsequently explored with cluster analysis and non-parametric Multi-Dimensional Scaling (nMDS) using PRIMER (v6) (Clarke & Warwick, 2010). Statistical significance of clusters was assessed using the SIMPROF routine. Taxa that contributed to community similarity were identified using Primer's SIMilarity PERcentage (SIMPER) routine. Finally, we related the observed biological community patterns to a suite of explanatory environmental variables using Primer's BEST bio-env routine. The BEST routine relates matrices of multidimensional biological and environmental data using both forward-selection and backward-elimination techniques (Clarke & Warwick, 2010).

Results

Oceanographic conditions

Temperature and salinity averaged over the upper 200 m of the water column reveal the dominant hydrographic features experienced by the zooplankton communities sampled by our nets in the epipelagic realm of the Beaufort Shelf (Fig. 1.2). On average, the western Beaufort sampled in 2011 experienced much warmer temperatures (5-6 °C) than other survey years, due to strong influence of ACW near Point Barrow. Midshelf stations from 2011 were characterized by warm (~3 °C) temperatures and lower salinities (~30), once again likely due to influence of ACW. Inshore stations from 2012 were also characterized by warm (~4 °C) and fresh (~26) waters. Stations from 2010, eastern inner-shelf and shelf-break stations from 2011, shelf-break and slope stations from 2012, and the majority of stations from 2013 were characterized by cold (0-2 °C) temperatures and salinities ranging from 30-33 °C. Surface waters of the region were variably influenced by meltwater and riverine input in all field seasons; the freshest surface waters were observed in the vicinity of the Mackenzie River in 2013. Additionally, AW intruded into the upper 200 m of the water column at shelf-break and slope stations in 2011 and 2012 (Fig. 1.3). These years also exhibited upwelling favorable winds during the survey period.

Chlorophyll-*a* and macro-nutrients

Surface nitrate was generally depleted throughout the study region during all surveys, while phosphate and silicate were typically low but non-limiting (Fig. 1.4). Higher nitrate and phosphate concentrations were observed most frequently with increasing depth during all surveys, except 2010 when phosphate concentration was unrelated to depth. In 2013 we observed elevated silicate levels in surface waters of the study region, with highest concentrations at stations closest to the mouth of the Mackenzie River. Chlorophyll-*a* concentration was also generally low (always < 2.5, and typically <0.5 mg m^{-3}) throughout the region in all surveys, and similarly, peak concentrations were observed in subsurface waters (Fig. 1.4). Depletion of both nutrients and chlorophyll-*a* indicates that all sampling periods occurred after the summer phytoplankton bloom. Nutrient data were not available for the 2011 field season, nor were complete chlorophyll-*a* or fluorescence datasets.

Zooplankton

General patterns

We observed 106 taxonomic categories over the course of the four field seasons in the two mesh sizes (Tables 1.2, 1.3). Copepods exhibited the highest diversity (38 species), followed by the cnidarians (16 species) and amphipods (14 species). We also observed 5 euphausiid, 4 ctenophore, 3 chaetognath, 2 cladoceran, 2 pteropod, and 2 mysid species. Numerous meroplanktonic taxa were observed; abundances were highest in the western Beaufort and in the nearshore vicinity of the Mackenzie River, where the meroplankton was dominated by polychaete and bivalve larvae. In the 150-µm net, average holozooplankton abundance and biomass ranged from 1110-3880 individuals m^{-3} and 23.8-76.9 mg DW m^{-3}, respectively (Table 1.1). Average zooplankton abundance and biomass captured in the 505-µm net ranged from 47-215 individuals m^{-3} and 13.9-57.6 mg DW m^{-3}, respectively (Table 1.1). Copepods dominated in terms of abundance and biomass in all years in both nets; however, larvaceans and predators, primarily cnidarians and chaetognaths, made important contributions that varied both between and within years (Fig. 1.5). The community was dominated by the traditional guild of Arctic copepods in all sampling regions across all field seasons, including *Calanus glacialis*, *Calanus hyperboreus*, *Metridia longa*, *Oithona similis*, *Triconia borealis*, *Microcalanus pygmaeus*, and the *Pseudocalanus* species complex. Numerically, these copepods accounted for 45-81% of zooplankton abundance and 52-64% of the biomass in the 150-µm net across all survey years, while in the 505-µm net this guild composed 42-92% of the abundance and 44-63% of the biomass.

Species-specific patterns

The 150-µm net provides insight to patterns in the numerically dominant small-bodied taxa, such as *Pseudocalanus* spp., *Oithona similis*, *Triconia borealis*, and *Microcalanus pygmaeus*. *Pseudocalanus* species were found across the shelf, with highest abundances observed at inshore stations in all survey years. *Oithona similis* was distributed across the shelf, with no immediately apparent spatial pattern; *Triconia borealis* was also found across the shelf; however, it was most abundant in the eastern Beaufort. *Microcalanus pygmaeus* exhibited highest abundances at stations influenced by colder water, and was largely absent from warmer waters influenced by ACW (Fig. 1.6). Less dominant taxa also provide insight to habitat associations; the ostracod *Boroecia maxima* and the copepod *Heterorhabdus norvegicus* were largely restricted to stations over the shelf-break and slope that were influenced by deeper waters. Euryhaline and freshwater taxa, such as *Eurytemora* spp., the marine cladocerans *Podon leuckartii* and *Evadne nordmanni*, and rotifers, were found at freshened stations, mostly in the vicinity of the Mackenzie River (Fig. 1.7).

With respect to the 505-µm net, *Calanus hyperboreus*, considered an oceanic species, was present in moderate numbers on the shelf in all years, indicating some degree of shelf-slope exchange (Fig. 1.8). Abundances were highest in cooler waters that likely originated offshore. *Calanus glacialis* was present across the shelf in all years, with no obvious spatial pattern. *Paraeuchaeta glacialis* and *Metridia longa* were largely absent in warmer waters influenced by ACW and reached highest abundances at offshore stations or stations influenced by waters originating off of the shelf (Fig. 1.8). Euphausiids were found in low numbers throughout the entire survey area (Fig. 1.9a,b). *Thysanoessa raschii* and *Thysanoessa inermis* were the most common euphausiid species, although *Thysanoessa longipes* was encountered in extremely low abundances (< 0.01 ind. m^{-3}) in offshore waters. Two notable expatriate euphausiids were encountered in the study region; one individual of the Atlantic-affinity *Meganyctiphanes norvegica* was observed at an offshore station in 2012 captured in a midwater trawl and one individual of the Pacific-affinity *Thysanoessa spinifera* was observed at an inshore station in 2013. Juvenile euphausiid distribution was extremely patchy and abundances were generally low; juvenile stages were encountered most frequently in the western Beaufort and were not encountered in the eastern Beaufort in 2013.

We observed several Pacific expatriate copepod species in the study region in extremely low abundances (<1 ind. m^{-3}) in both nets; namely *Neocalanus cristatus, Eucalanus bungii,* and *Metridia pacifica*. *Neocalanus flemingeri* and *Neocalanus plumchrus* were observed at only a few stations across all survey years. Pacific taxa were observed most frequently at western Beaufort stations influenced by ACW sampled in 2011, but were encountered as far east as the Mackenzie River region sampled in 2013. Aside from the portion of the western Beaufort that was influenced by ACW in 2011, presence of Pacific expatriates generally followed the described path of the Beaufort Shelf-break Jet (e.g. Nikolopoulos *et al.*, 2009), with the exception of the 2013 survey year, when Pacific taxa were found across the entire study region (Fig. 1.9c).

Community structure and relation to hydrography

150-µm net

The zooplankton community exhibited complex structure that represents a mixing of along- and across-shelf gradients and the underlying hydrographic conditions. Four major community groupings were present when community similarity was assessed with abundance (Fig. 1.10). All station groupings exhibited high abundances of calanoid nauplii, *Oithona similis*, and the *Pseudocalanus* spp., with differences of relative contributions of dominant taxa and less common taxa serving to differentiate community groupings (Table 1.4). Group 1 consisted of stations from 2011 under strong ACW influence and was characterized by high abundances of the larvacean *Fritillaria borealis*, meroplanktonic larvae, and the neritic chaetognath *Parasagitta elegans*. Group 2 consisted of stations from the mid-shelf in 2011; these stations exhibited high abundances of the larvaceans *Fritillaria borealis* and *Oikopleura vanhoeffeni*, the hydrozoan

Aglantha digitale, and lower abundances of the key copepod species when compared to other groups. Group 3 included stations from 2010, 2011, 2013; these stations were characterized by high abundances of *Oithona similis* and *Pseudocalanus* spp., as well as more oceanic taxa, including *Calanus hyperboreus* and *Microcalanus pygmaeus*, reflecting the influence of cold offshore waters at these stations. Finally, Group 4 included stations from 2011, 2012 and 2013. These stations exhibited high abundances of the copepods *Triconia borealis*, *Calanus glacialis*, *Microcalanus pygmaeus*, and *Calanus hyperboreus*. This group exhibited additional internal structure, with stations separating largely according to location relative to the shelf-break and relative influence of the freshened surface lens and offshore waters (Fig. 1.11). Within Group 4, the "upwelling/weak plume" group consisted of inshore stations that were more faunally similar to offshore stations than other inshore stations. This more oceanic faunal character, combined with prevailing easterly winds during the study period and the cold (< 0°C) and saline (~32) waters at these stations in this group (Fig. 1.12), suggests that upwelling occurred during the study period, bringing waters and biota from offshore to the nearshore stations.

When considering pooled data from all field seasons, the structure in the zooplankton community according to abundance was correlated with temperature and salinity averaged over the upper 100 m (Spearman correlation (ρ): 0.53, p <0.01). The addition of station depth to the model did not improve the relationship, nor did the use of different layers of the water column (Table 1.5). Individual analyses of 2010, 2012, and 2013 datasets showed that the addition of chlorophyll-*a*, macro-nutrients, and fluorescence did not improve BEST models, suggesting the absence of such data for 2011 was inconsequential. The community structure according to biomass was very similar to that observed according to abundance, despite the fact that these metrics emphasize a different suite of species. A small number of stations were shuffled between groups and analysis using biomass data produced more outliers (Fig. 1.13), but overall community structure was consistent with that observed using abundance data. The combination of temperature and salinity averaged over the upper 100 m of the water column was the best explanatory variable for the observed community structure according to biomass (ρ= 0.49, p <0.01). Once again, the use of station depth and different depth layers did not improve the relationship (Table 1.5).

505-µm net

Community structure sampled with the 505-µm net was generally similar to that observed in the 150-µm net, regardless of whether abundance (Fig. 1.14) or biomass (Fig. 1.15) was used to assess community similarity, although more unique community groupings were identified. Seven major community groupings were identified. *Calanus* species and *Aglantha digitale* were important contributors to all community groupings (Table 1.6). Large-scale community structure was preserved across both mesh sizes and both community metrics (abundance and biomass); however, community structure in the 505-µm net was more heterogeneous than that observed in the 150-µm net. The same four groups described in the multivariate analysis of 150-µm data can be identified in multivariate analysis of the 505-µm data. Group 1 was characterized by high abundances of the hydrozoan *Aglantha digitale*, *Calanus glacialis*, meroplanktonic larvae, pteropods, and juvenile euphausiids. Group 2 was characterized by high abundances of *Aglantha digitale*, *Oikopleura vanhoeffeni*, and *Fritillaria borealis*. *Calanus glacialis*, *Oikopleura vanhoeffeni*, and *Calanus hyperboreus* characterized Group 3. Group 4 was characterized by *Calanus glacialis*, *Metridia longa*, and *Calanus hyperboreus*. The remaining groups generated by multivariate analysis of the 505-µm data consisted of a few stations each; Group 5 consisted of stations from 2011 in the western Beaufort that were more faunally similar to offshore stations and stations influenced by colder water. Group 6 consisted of inshore stations from 2012, and was characterized by higher abundances of *Calanus glacialis*. Finally, Group 7 consisted of stations from 2010 and 2011 on the inner- and mid- shelf and was characterized by *Calanus glacialis*, *Calanus hyperboreus*, hydrozoans, and hyperiid amphipods. Community structure in the 505-µm net according to abundance was correlated to temperature averaged across the upper 200 m ($\rho = 0.57$, $p < 0.01$). The addition of salinity and station depth, alone or in combination, did not improve the model, nor did the use of different water layers (Table 1.7). Community structure according to biomass was best explained by temperature averaged over the upper 200 m of the water column ($\rho = 0.50$, $p < 0.01$). Once again, the addition of other variables (salinity, station depth) or the use of different depth layers did not improve the model (Table 1.7).

Discussion

Our surveys provide a spatially comprehensive assessment of the zooplankton communities of the Alaskan Beaufort Sea; however, this spatial coverage comes at the expense of the ability to quantify inter-annual variability in the community, because very few locations were sampled repeatedly. Our multivariate analyses indicate that, while there is likely an element of inter-annual variability in our data set, hydrographic conditions play a considerable role in structuring epipelagic zooplankton communities, both within and across years. With respect to the 150-µm net, western stations from 2013 clustered with stations from 2010 and 2011 that experienced similar hydrographic conditions, indicating that physical parameters, rather than the survey year itself were driving much of the observed community structure.

Given that nMDS stress increases with the number of points in a dataset (Clarke & Warwick, 2010), the relatively high 2-dimensional (2D) stress values (2D stress: 0.21 and 0.19 for abundance and biomass, respectively) of nMDS plots for the 150-µm net are not surprising. Stress is reduced with increasing dimensionality of ordination; therefore, lower three-dimensional (3D) values (3D stress: 0.13 for both abundance and biomass) are expected. The general agreement between the dendrogram produced from hierarchical clustering and the 2D nMDS plots suggests that the 2D representation of our multidimensional dataset is reasonable, even if some distortion is caused during the compression of the dataset from three dimensions to two dimensions.

Community structure

In the Arctic, zooplankton communities are tied to the underlying hydrographic conditions; this relationship has been observed in the Chukchi Sea (Hopcroft *et al.*, 2010; Matsuno *et al.*, 2011; Questel *et al.*, 2013; Ershova *et al.*, 2015), the Canadian Beaufort (Walkusz *et al.*, 2010), the Canada Basin (Kosobokova & Hopcroft, 2010), and now in the Alaskan Beaufort. The community groupings described in the present study reflect underlying hydrographic conditions and processes in the region and allow some general characterizations of gradients across the Beaufort shelf as a whole. The Beaufort Sea around Barrow Canyon represents a transitional zone between the Pacific-affinity, benthic-rich Chukchi Sea and the Beaufort Sea, as reflected in its relatively high abundances of meroplanktonic larvae and Pacific expatriate taxa when compared to the rest of the Beaufort. High abundances of meroplankton in the western Beaufort were likely swept into the region from Chukchi Sea via the ACW entering around Point Barrow.

The western Beaufort exhibited highest abundances of Pacific-derived taxa (e.g., *Neocalanus* spp.), demonstrating the hydrographic connectivity between the subarctic Pacific, the Chukchi Sea, and the Beaufort Sea. In contrast, the central and eastern Beaufort are more traditionally Arctic in faunal character, with the influence of the Chukchi Sea and Pacific-derived waters increasingly weakened towards the Mackenzie River. The eastern Beaufort near the Mackenzie River is generally more estuarine than the rest of the Alaskan Beaufort, although conditions at specific locations likely vary seasonally as well as from year to year depending on the extent of the river plume. Estuarine species assemblages include *Eurytemora* spp., *Limnocalanus* spp., and rotifers, as demonstrated by our study and others from the Canadian Beaufort (e.g. Walkusz *et al.*, 2010; Hopky *et al.*, 1994,a,b,c), as well as other marginal Arctic seas influenced by major riverine input (e.g. Abramova & Tuschling, 2005).

Across-shelf gradients associated with the Mackenzie River plume extent have been recognized in the Canadian Beaufort. Walkusz *et al.* (2010) report ecological zones associated with intensity of the Mackenzie River plume, noting an "intense plume" assemblage, a "diffuse plume" assemblage, and an "offshore" assemblage. Our findings mirror this description; stations from the 2013 survey year exhibit internal structure associated with location relative to the shelf-break and the degree of freshwater influence. In both our work and that of Walkusz *et al.* (2010), the "intense plume" assemblage is characterized by euryhaline and brackish water taxa, such as cladocerans, *Eurytemora* spp., and *Limnocalanus* spp. The "diffuse plume" grouping represents a transitional group, with euryhaline, neritic, and some oceanic taxa; the "offshore" assemblage is primarily composed of oceanic taxa. The across-shelf transition from neritic to more oceanic taxa is also evident beyond the river plume extent; Grainger (1965) reported species assemblages associated with Arctic surface waters and coastal surface waters. Similarly, Darnis *et al.* (2008) report a distinct off-shelf assemblage and a neritic assemblage. In all of these surveys, including the present one, *Pseudocalanus* species usually typify neritic shelf assemblages, while the oceanic *Calanus hyperboreus* and *Microcalanus pygmaeus* are characteristic of offshore assemblages.

Localized physical processes, such as upwelling, may blur the gradients described above. For example, in 2013 the inshore "upwelling/weak plume" stations within Group 4 were more faunally similar to offshore stations than to other inshore stations (see Fig. 1.11). The more oceanic faunal character of these stations (e.g., elevated abundances of *Calanus hyperboreus*, see Fig. 1.8) stands in contrast to the neritic faunal character that would be expected based on the inshore location of these stations. Prevailing easterly winds during the survey, as well as colder

(< 0 °C) and more saline (~32) waters at these stations (see Fig. 1.12), lend further support that upwelling was occurred during our survey. In summary, along-shelf gradients in the Beaufort Sea represent a transition from Pacific and Chukchi influenced waters in the western Beaufort, to more traditionally Arctic conditions in the central Beaufort, to an estuarine environment in the eastern Beaufort. This gradient is reflected in the zooplankton community. Across-shelf gradients represent a transition from neritic assemblages typified by *Pseudocalanus* spp. to more oceanic assemblages typified by *Calanus hyperboreus* and *Microcalanus pygmaeus*. The region around the Mackenzie River represents an extreme example of across-shelf gradients, with a "plume" assemblage, characterized by euryhaline copepods such as *Eurytemora* spp., in addition to the traditional neritic and oceanic assemblages. These gradients intersect and can be modified by localized processes, such as upwelling.

Regional comparison

Our results indicate that zooplankton abundance and biomass in the Beaufort Sea can rival, and even surpass, those reported in the Chukchi (Hopcroft *et al.*, 2010; Questel *et al.*, 2013; Ershova *et al.*, 2015) and that diversity in the epipelagic realm of the Beaufort Sea is similar to that observed in the shallow Chukchi Sea, despite distinct faunal differences between the mostly Arctic-affinity Beaufort and mostly Pacific-affinity Chukchi Sea. The influence of Pacific-origin waters is revealed by the presence of subarctic copepods that occur predominantly in the western Beaufort. The penetration of Pacific expatriate taxa into the Beaufort Sea has been previously recorded by Johnson (1956) and across the Chukchi Plateau and into Central Basin (Hopcroft *et al.*, 2005; Nelson *et al.*, 2009; Kosobokova & Hopcroft, 2010; Nelson *et al.*, 2014), reflecting the penetration of these taxa well into the Arctic Ocean proper. We report low numbers of euphausiids; net avoidance and aggregation near the bottom (Coyle & Pinchuk, 2002) may partially explain these results, although it has also been suggested euphausiids populations are not self-sustaining in the Pacific-Arctic (Berline *et al.*, 2008). Our results are also consistent with species inventories from the epipelagic realm in the Canada Basin (Kosobokova & Hopcroft, 2010; Hunt *et al.*, 2014), although we report higher abundances of neritic taxa, as would be expected given our shelf emphasis. High abundances of euryhaline taxa in the vicinity of the Mackenzie River are consistent with influence of major river systems (Abramova & Tuschling, 2005; Walkusz *et al.*, 2010), as noted previously.

Historical context and future outlook

It is notable that the species composition of the major players of the Beaufort Sea mesozooplankton community appear to have remained relatively stable over the past decades; historical studies (e.g., Johnson, 1956; Grainger, 1975; Grainger & Grohe, 1975; McConnell, 1977; Hopky *et al.*, 1994a,b,c) show a clear dominance of the key Arctic copepods also reported in this study, as do other contemporary studies (e.g., Lane *et al.*, 2008) . Our results, as well as others in the western Arctic (Ashjian *et al.*, 2003; Hopcroft *et al.*, 2005; Lane *et al.*, 2008; Kosobokova & Hopcroft, 2010), suggest increased zooplankton standing stock in the modern Arctic when compared to early work, although we note there is quite a large range in abundances. Other caveats include methodological differences that may have resulted in an underestimate of historical abundance and biomass (see Ashjian *et al.*, 2003; Hopcroft *et al.*, 2008). Nonetheless, available data point to an upward trend in abundances of several key copepod species in the Beaufort Sea region. Concomitant with this apparent increase, the Arctic has undergone rapid declines in sea ice extent and thickness (Comiso, 2002; Serreze *et al.*, 2007; Kwok & Rothrock, 2009). Loss of sea ice increases the area of open water available for phytoplankton production (e.g., Arrigo *et al.*, 2008), thereby increasing resources available to herbivorous copepod grazers that dominate the Beaufort Sea ecosystem, and potentially accelerating life cycles due to higher water temperatures (e.g., Ringuette *et al.*, 2002). Increased resource availability could result in increased zooplankton abundance. Average abundances of the key herbivore *Calanus glacialis* and the small-bodied omnivore *Oithona similis* seem to have increased over the past decades in the Beaufort Sea region (Fig. 1.16); however, additional data are needed to rigorously assess this trend. Other groups, such as the microcalanids (*Microcalanus pygmaeus* and *Pseudocalanus* spp.) and larvaceans, do not show a clear trend (Fig. 1.16). We note that the difficulties associated with collection and preservation of larvaceans (see Hopcroft, 2005) make comparisons particularly challenging, as they are very likely underrepresented in all of the above-mentioned collections, including the present study. The key Arctic *Calanus* species undergo extensive seasonal vertical migration; the timing of this seasonal migration, diapause, and reproduction are tightly coupled to the timing of the spring/summer phytoplankton bloom and can vary across the Arctic (Daase *et al.*, 2013). While the current and near-future climate environment may favor a prolonged bloom that *Calanus* spp. will still be able to exploit (e.g. Lavoie *et al.*, 2010), extreme shifts in bloom phenology could result in a mismatch between the timing of *Calanus* spp. reproduction and the highly pulsed food environment that these Arctic copepods are physiologically fine-tuned to exploit (e.g., Søreide *et al.*, 2010, Leu *et al.*, 2011). This could result in a future environment that is more favorable to small-bodied copepod species (e.g., *Pseudocalanus* spp. and *Oithona similis*) (Daufresne *et al.*, 2009) or subarctic species (Falk-Petersen *et al.*, 2006). Such shifts would have the potential to profoundly impact Arctic food webs and energy flow (e.g., Falardeau *et al.*, 2014).

In addition to large-scale changes in sea ice extent and phenology, more localized impacts of climate change may impact Beaufort Sea zooplankton communities on seasonal and annual time scales. Changes in relative influence of different water masses on the Beaufort shelf have the potential to actuate changes in zooplankton community structure and magnitude; more frequent upwelling events (e.g. Pickart *et al.*, 2013) could bring the large-bodied and lipid-rich copepod *Calanus hyperboreus* onto the shelf more often or in higher abundances, providing high quality food for upper trophic levels utilizing the shelf environment. Upwelling events can also bring AHW that is under-saturated with respect to aragonite from the slope onto the shelf (Mathis *et al.*, 2012), resulting in unfavorable conditions for marine calcifiers, such as the pteropod *Limacina helicina*. Conversely, increased freshwater input from river systems along the coast may create conditions more beneficial to neritic and euryhaline taxa than to oceanic taxa.

Continued efforts to survey Beaufort Sea zooplankton communities as the region undergoes environmental change will be critical in efforts to quantify community shifts and inform process-based examinations of the region. Efforts to quantify change associated with a warmer climate [i.e. Intergovernmental Panel on Climate Change (IPCC, 2014)] or anthropogenic activities must necessarily consider the natural variability of the biological system of the Beaufort Sea; therefore, future efforts to quantify inter-annual variability in zooplankton communities of the Beaufort Sea would be particularly valuable. The interplay between climate change and zooplankton communities is complex and likely species-specific; therefore, robust datasets are needed to assess any future change. This work describes broadscale gradients across and along the Beaufort shelf, highlights faunal associations driven by underlying hydrographic characteristics, and provides a modern characterization of epipelagic zooplankton communities in the Beaufort Sea that may be used to assess future change.

Figures

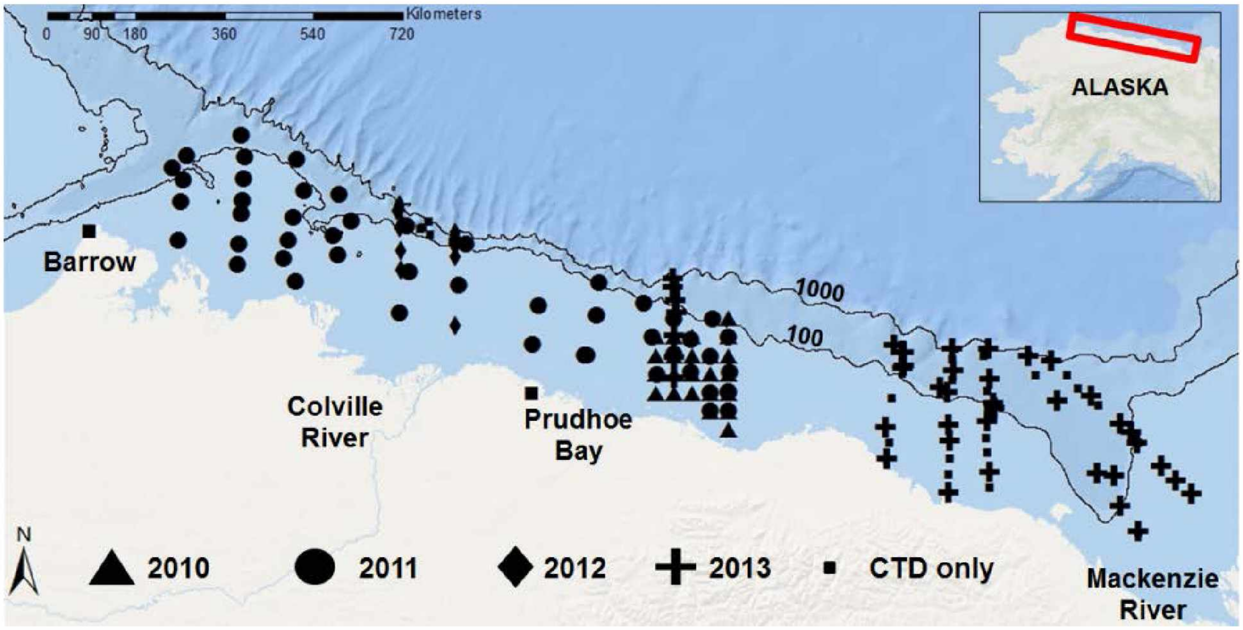

Figure 1.1. Beaufort Sea study area with stations indicated for each field season 2010-13.

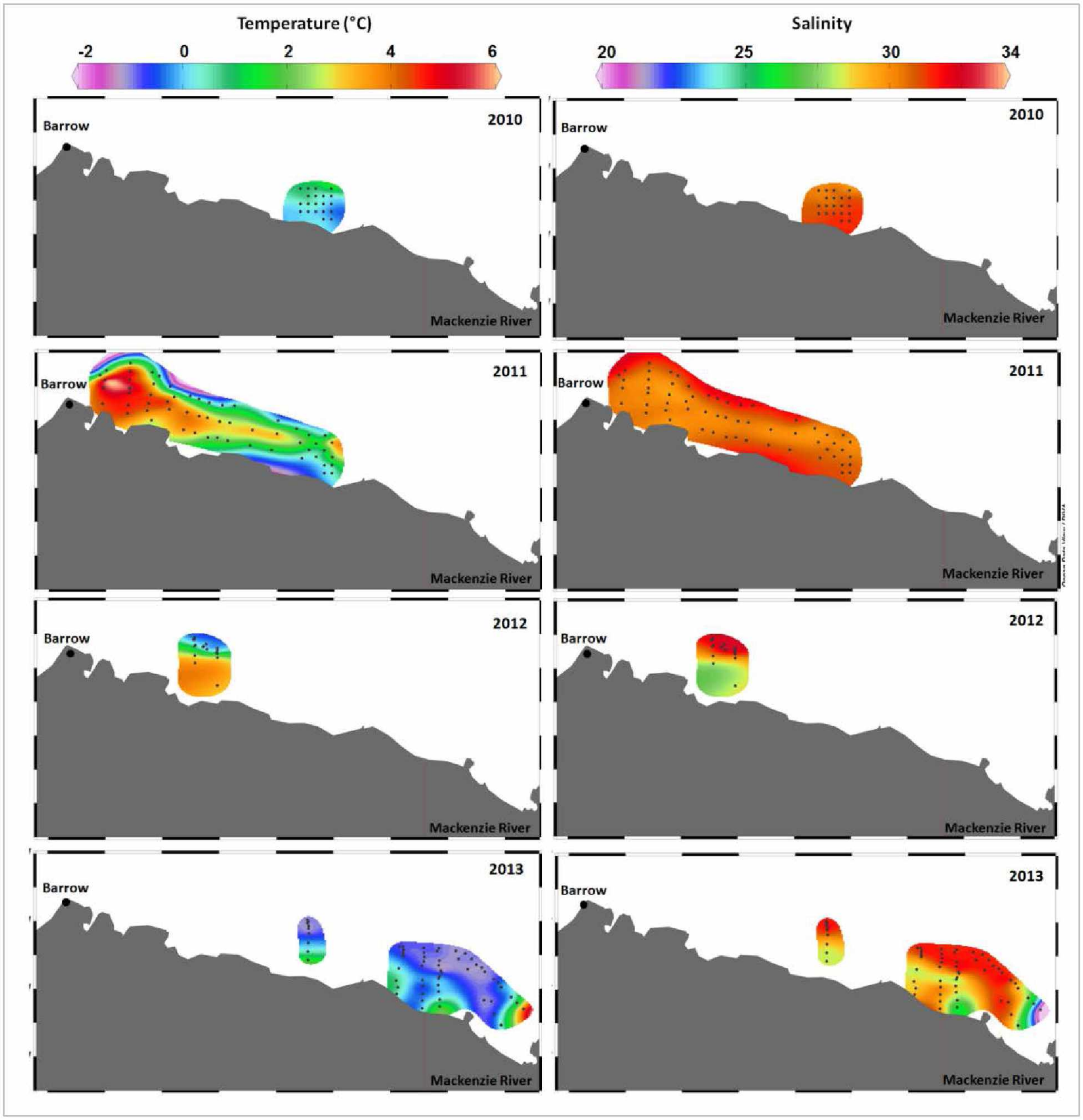

Figure 1.2. Mean temperature (°C) and salinity in the upper 200 m along the Beaufort Sea shelf during 2010-2013.

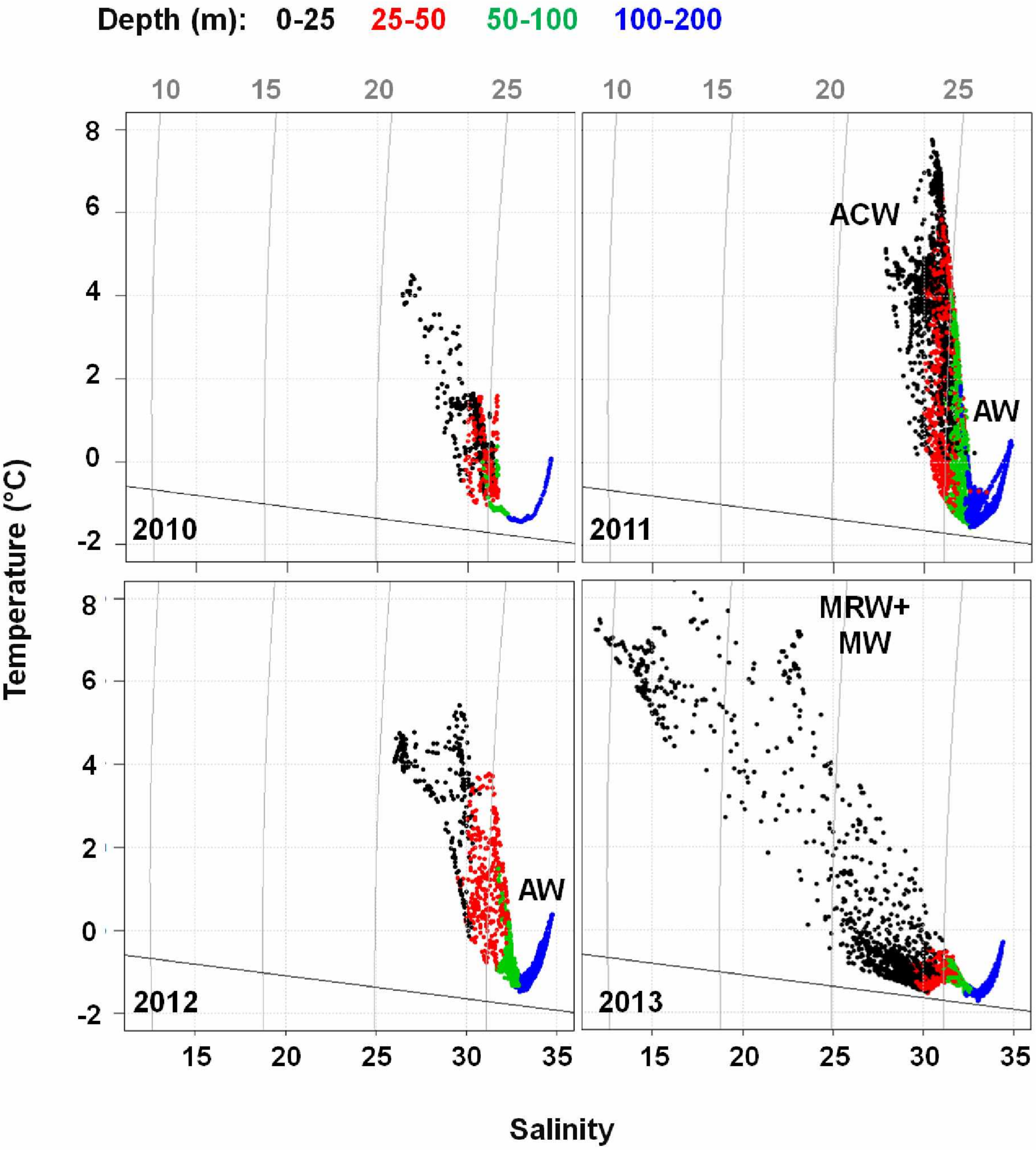

Figure 1.3. Temperature – salinity diagrams from the upper 200 m of the Beaufort Sea shelf during summer 2010-2013. Color represents depth interval. Grey lines & numbers represent isopycnals. *ACW* = Alaska Coastal Water, *AW* = Atlantic Water, *MRW* = Mackenzie River Water, *MW* = Melt Water.

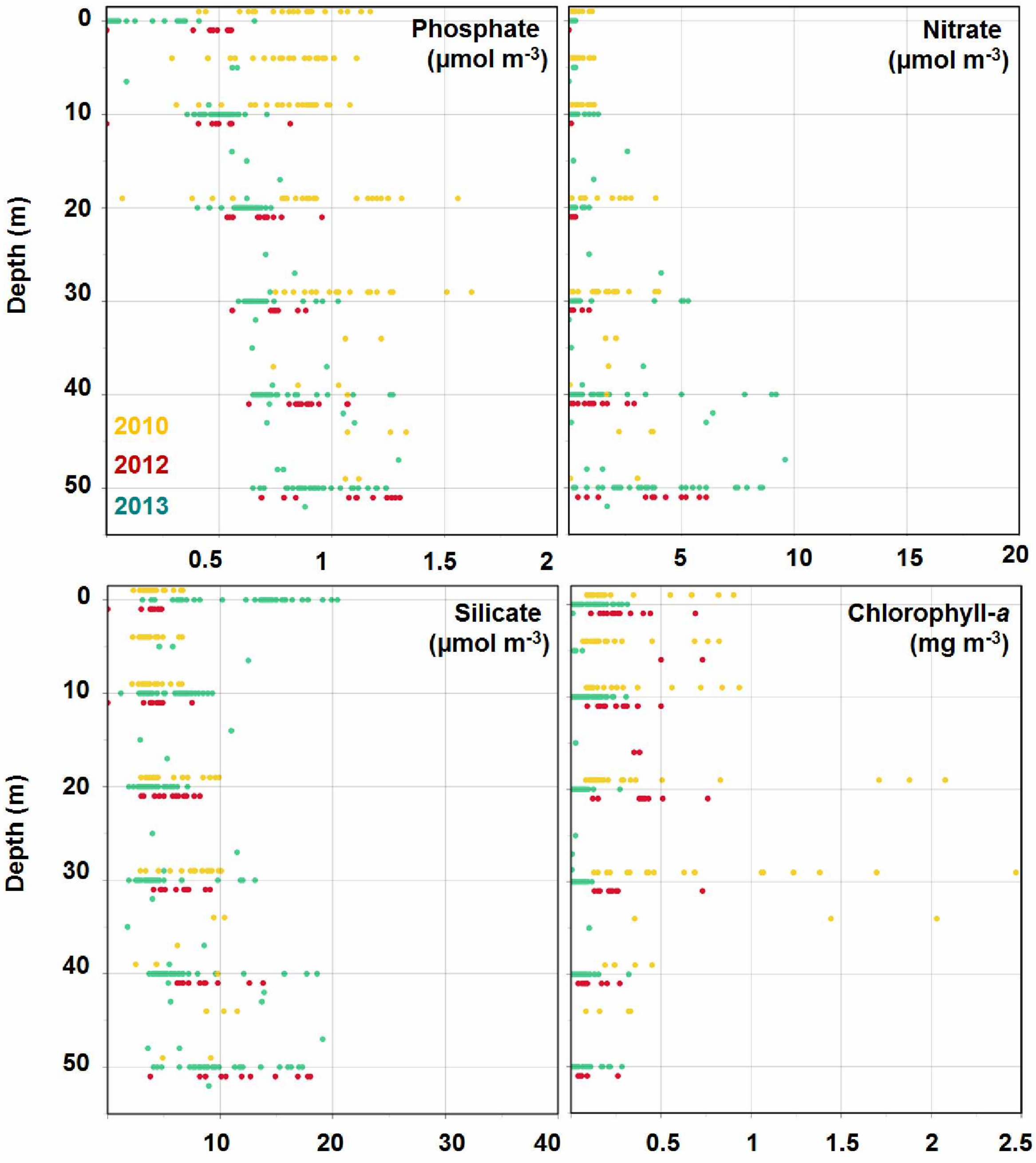

Figure 1.4. Inorganic macro-nutrient (phosphate, nitrate, silicate) and chlorophyll-*a* concentrations in the study area of the Beaufort Sea during 2010-13. Data at target depths offset slightly to facilitate comparison.

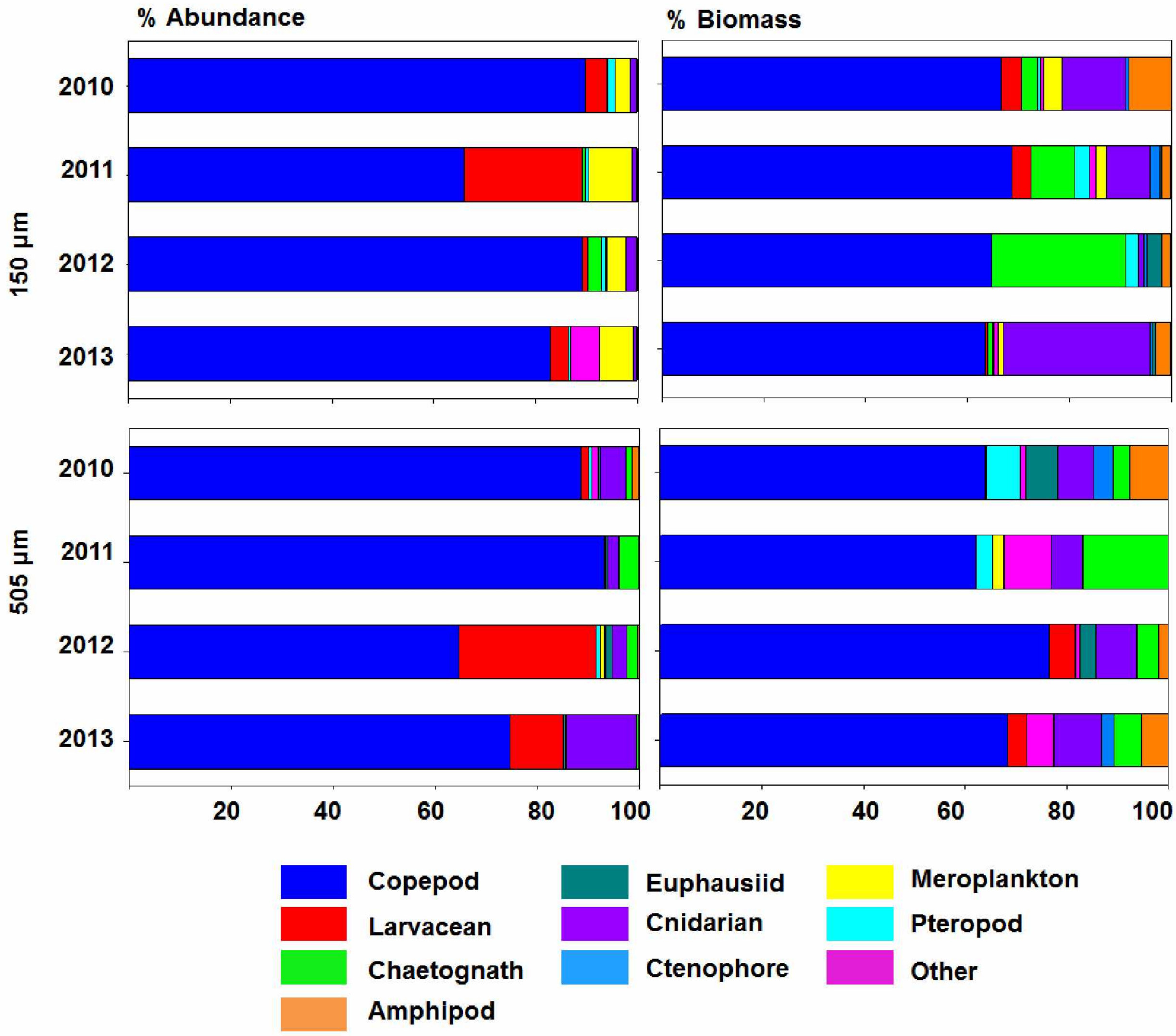

Figure 1.5. The relative contribution of major zooplankton taxonomic groups in terms of abundance and biomass in the Beaufort Sea during 2010-13 for the 150- and 505-µm nets.

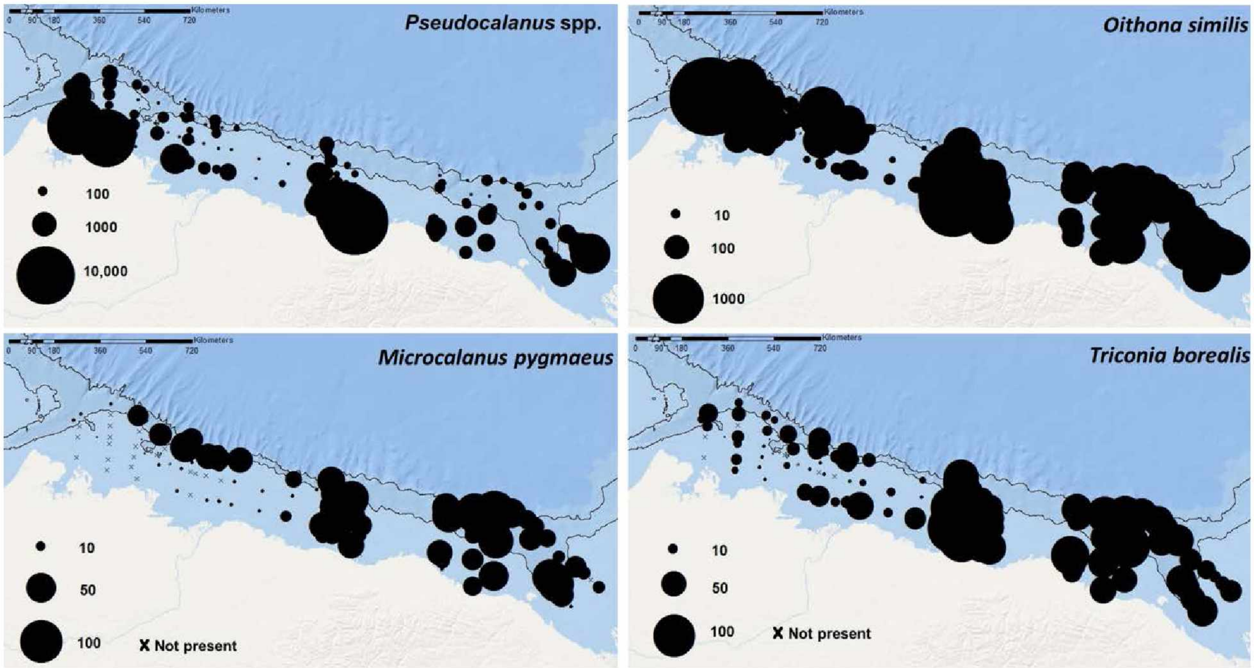

Figure 1.6. Abundance (ind. m^{-3}) of dominant copepod taxa in the 150-µm net in the Beaufort Sea during 2010-2013.

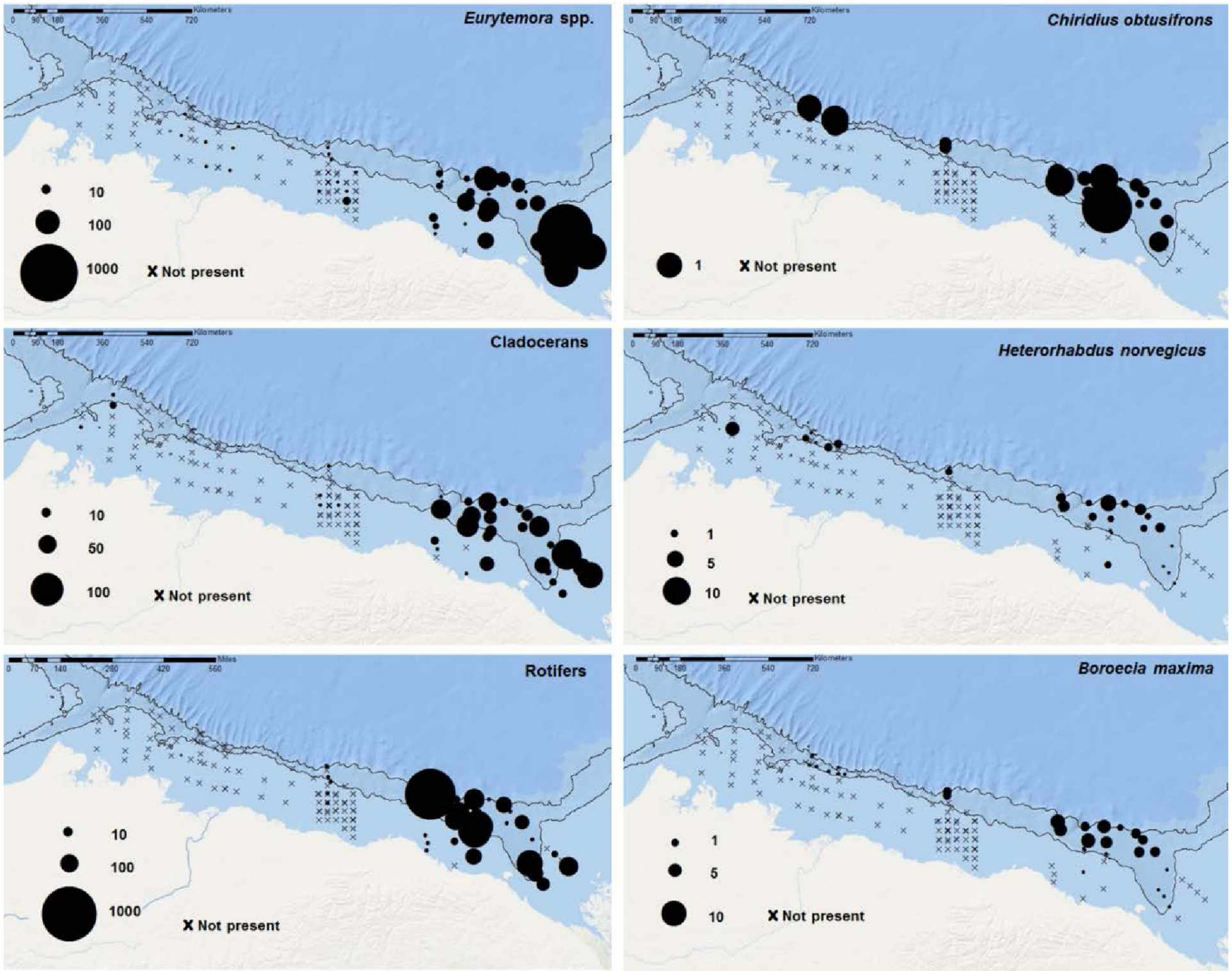

Figure 1.7. Abundance (ind. m^{-3}) of selected taxa from the 150-µm net in the Beaufort Sea during 2010-2013.

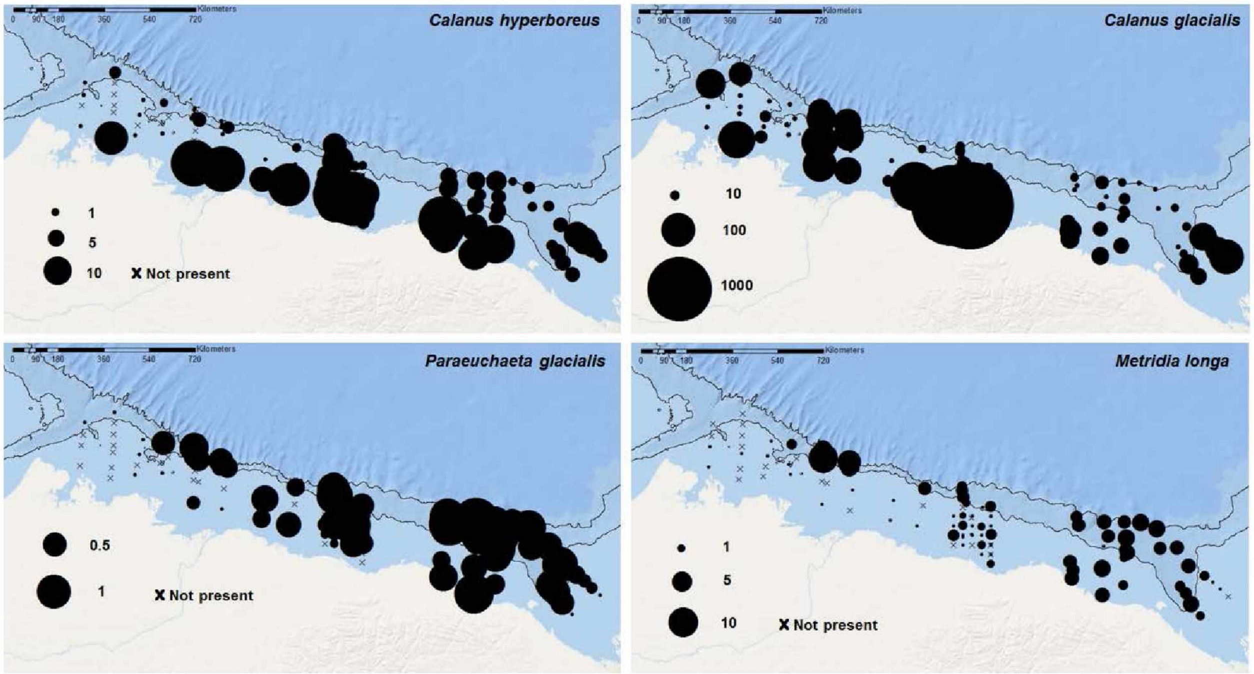

Figure 1.8. Abundance (ind. m^{-3}) of dominant copepods from the 505-µm net in the Beaufort Sea during 2010-2013.

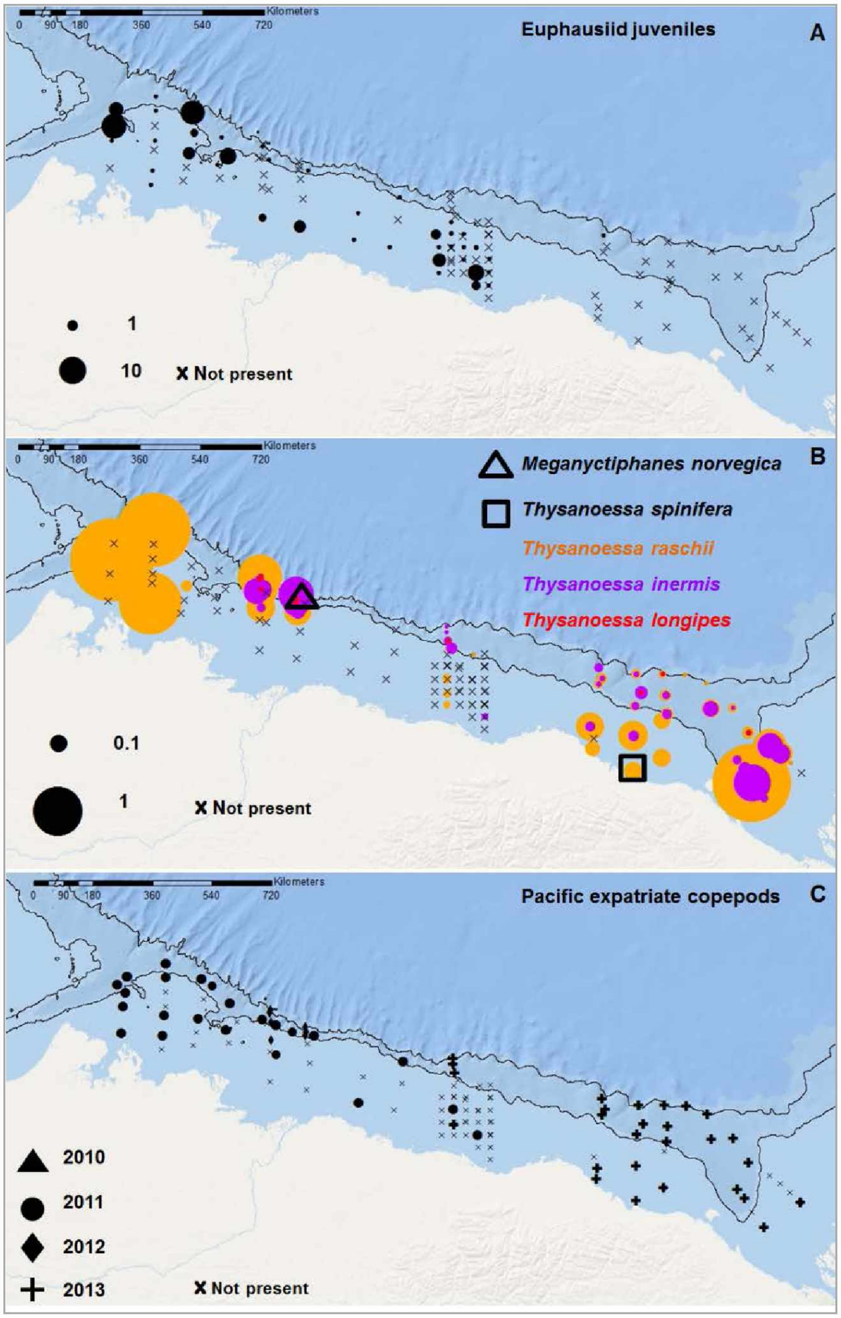

Figure 1.9. Expatriate zooplankton taxa in the Beaufort Sea during 2010-13. A) Juvenile euphausiid abundance (ind. m^{-3}) from the 150- and 505-µm nets. B) Euphausiid abundance (ind. m^{-3}) from the 505- µm net. Square and triangle indicate presence of *Meganyctiphanes norvegica* and *Thysanoessa spinifera*, respectively. C) Presence of Pacific expatriate copepods from the 150- and 505-µm nets.

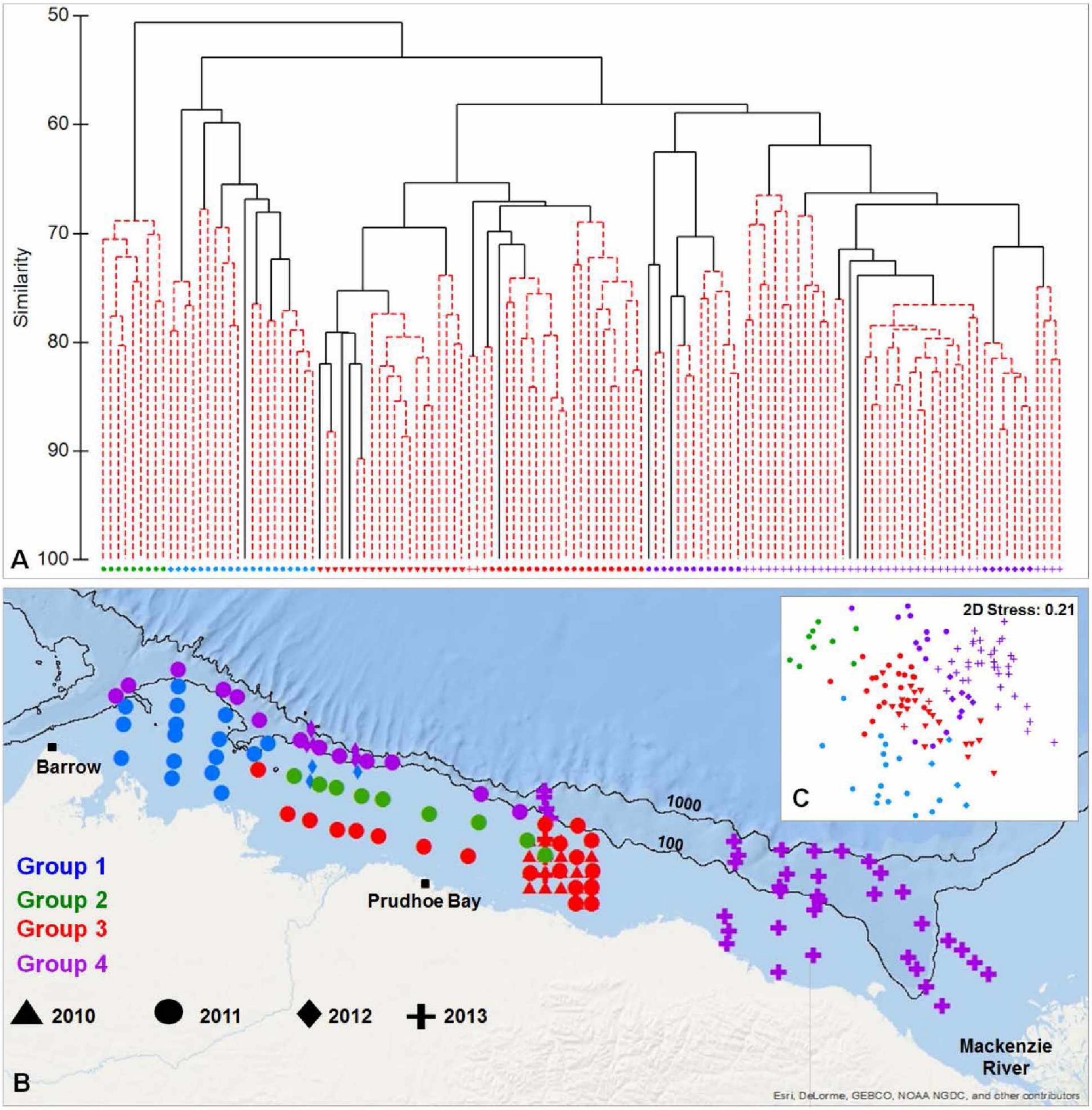

Figure 1.10. Beaufort Sea zooplankton community structure for 150-µm net abundance data from 2010-13. Shapes indicate year. Colors indicate faunal grouping. A) Bray-Curtis sample similarity as determined by hierarchical clustering on species abundance. Dotted red lines connect samples that are not statistically unique (SIMPROF, $p < 0.05$). B) Spatial distribution of observed community groups. C) Non-parametric Multidimensional Scaling (nMDS) of zooplankton community overlain with observed groupings.

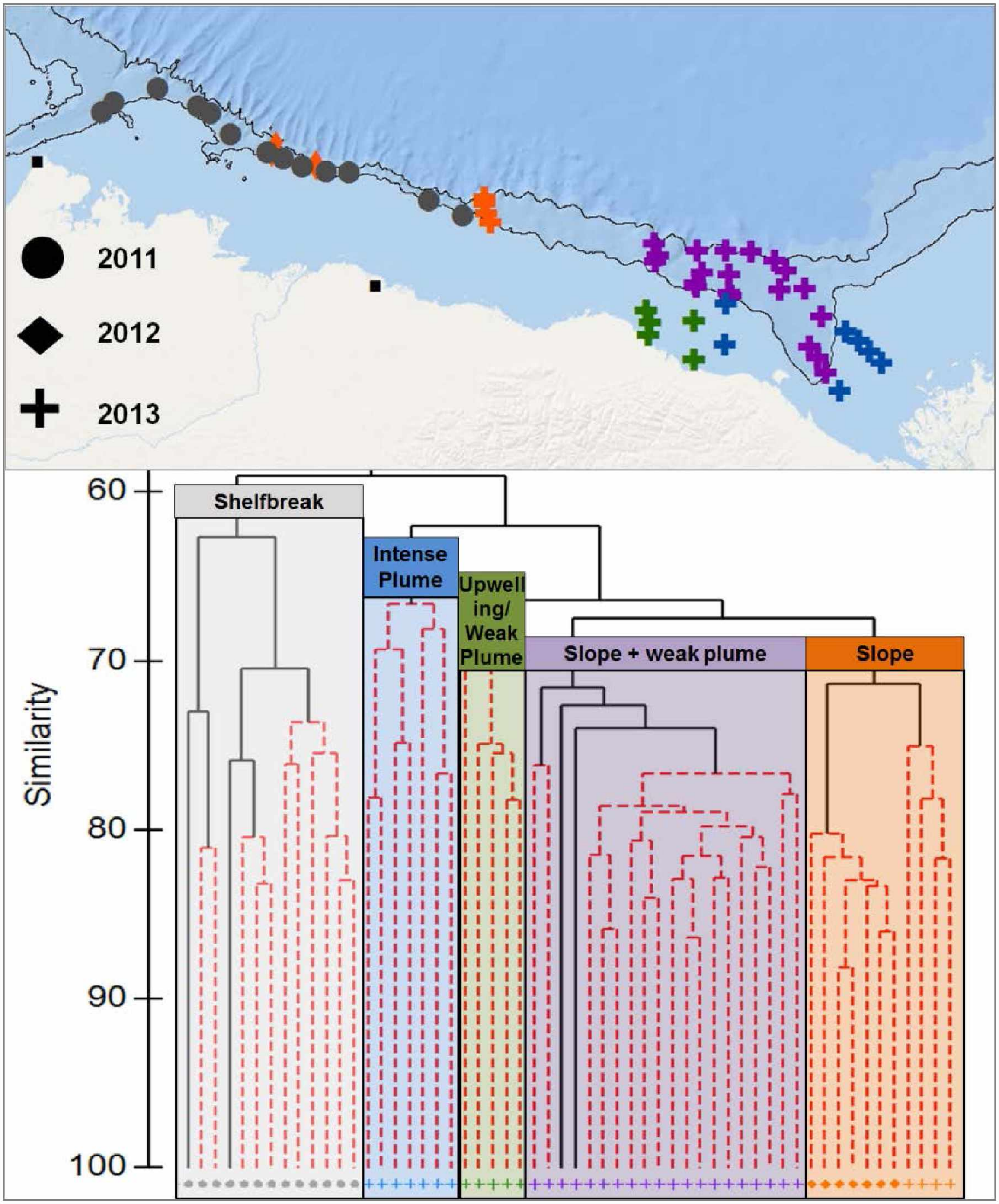

Figure 1.11. Beaufort Sea zooplankton community structure within Group 4 for 150-µm net abundances from 2010-13. Upper panel shows spatial distribution of clusters depicted in lower panel

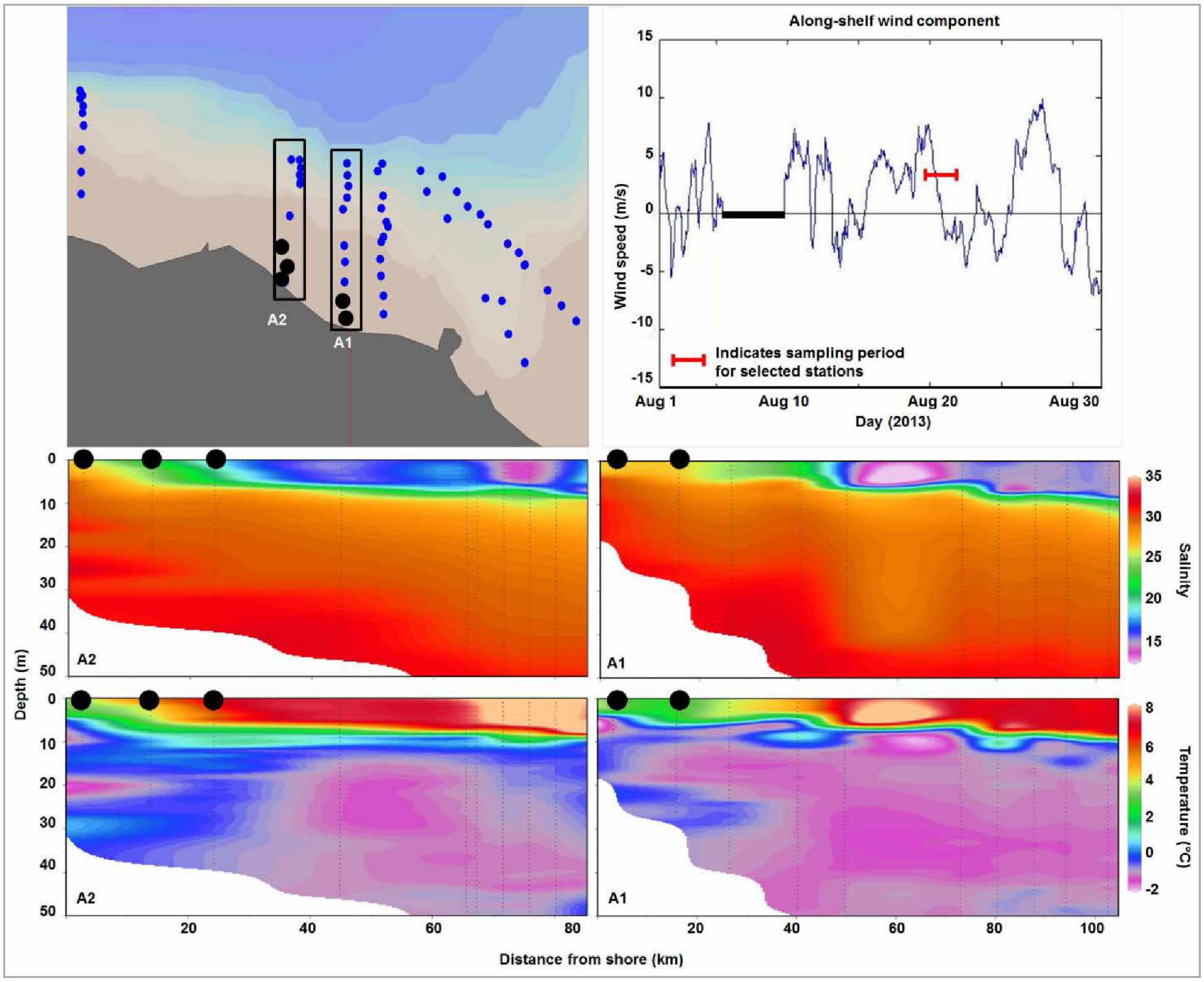

Figure 1.12. Environmental conditions at Lines A1 and A2 within Faunal Group 4 in the Beaufort Sea during August 2013. Upper left: Station map for 2013 sampling. Stations of interest are enlarged. Upper right: alongshore component of wind velocity during August 2013 survey. Data source: NOAA/ESRL/GMD Baseline Observatories, National Oceanic and Atmospheric Administration, Oceanic and Atmospheric Research Earth System Research Laboratory, Global Monitoring Division (Barrow Meteorological Station). Black bar indicates wind data are not available. Lower panel: Oceanographic conditions (T, S) along Lines A1 and A2.

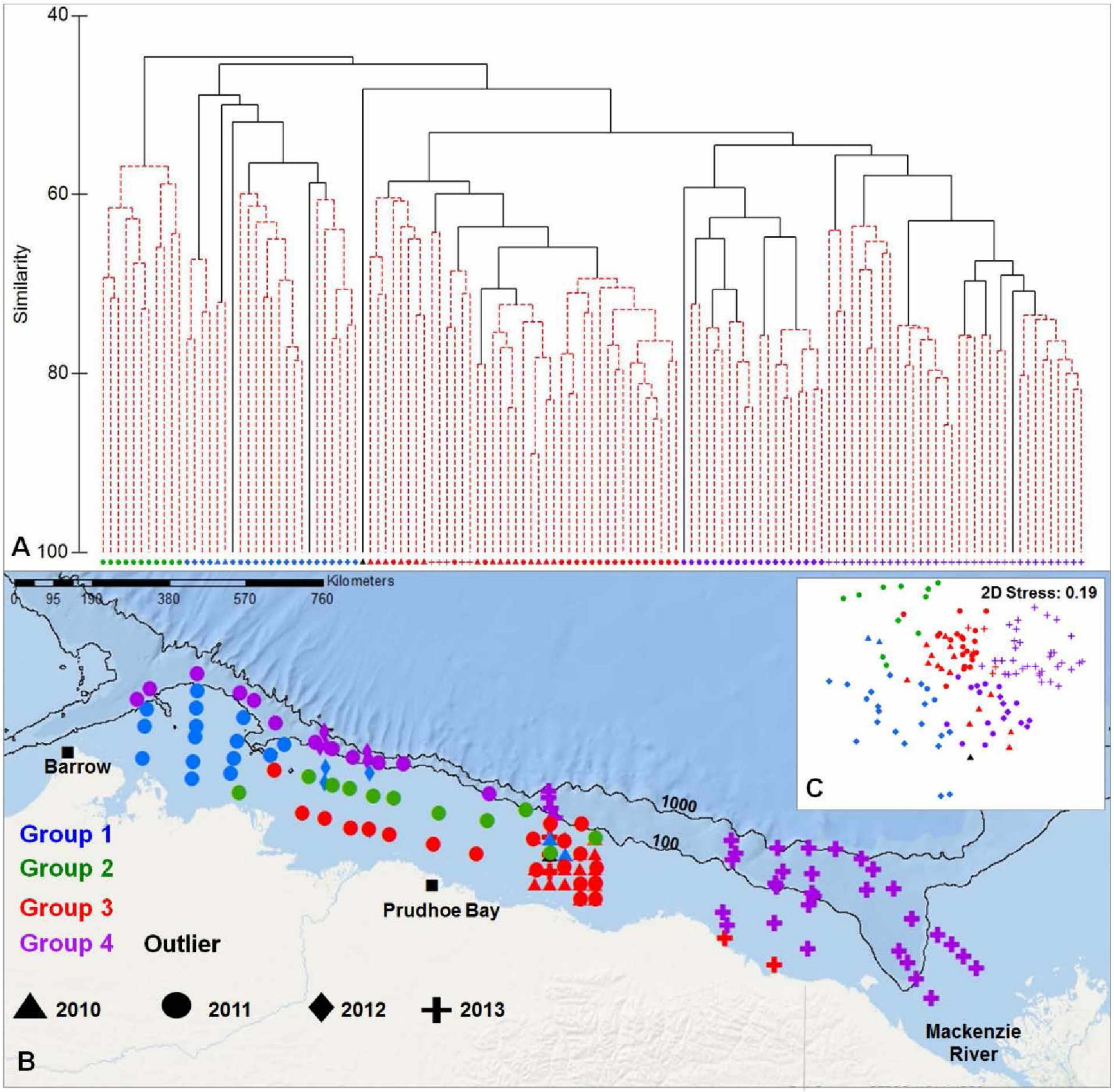

Figure 1.13. Beaufort zooplankton community structure for the 150-µm net biomass data from 2010-13. Shapes indicate year. Colors indicate faunal grouping. A) Bray-Curtis sample similarity as determined by hierarchical clustering. Dotted red lines connect samples that are not statistically unique (SIMPROF, $p < 0.05$). B) Spatial distribution of observed community groups. C) Non-parametric Multidimensional Scaling (nMDS) of zooplankton community overlain with observed groupings.

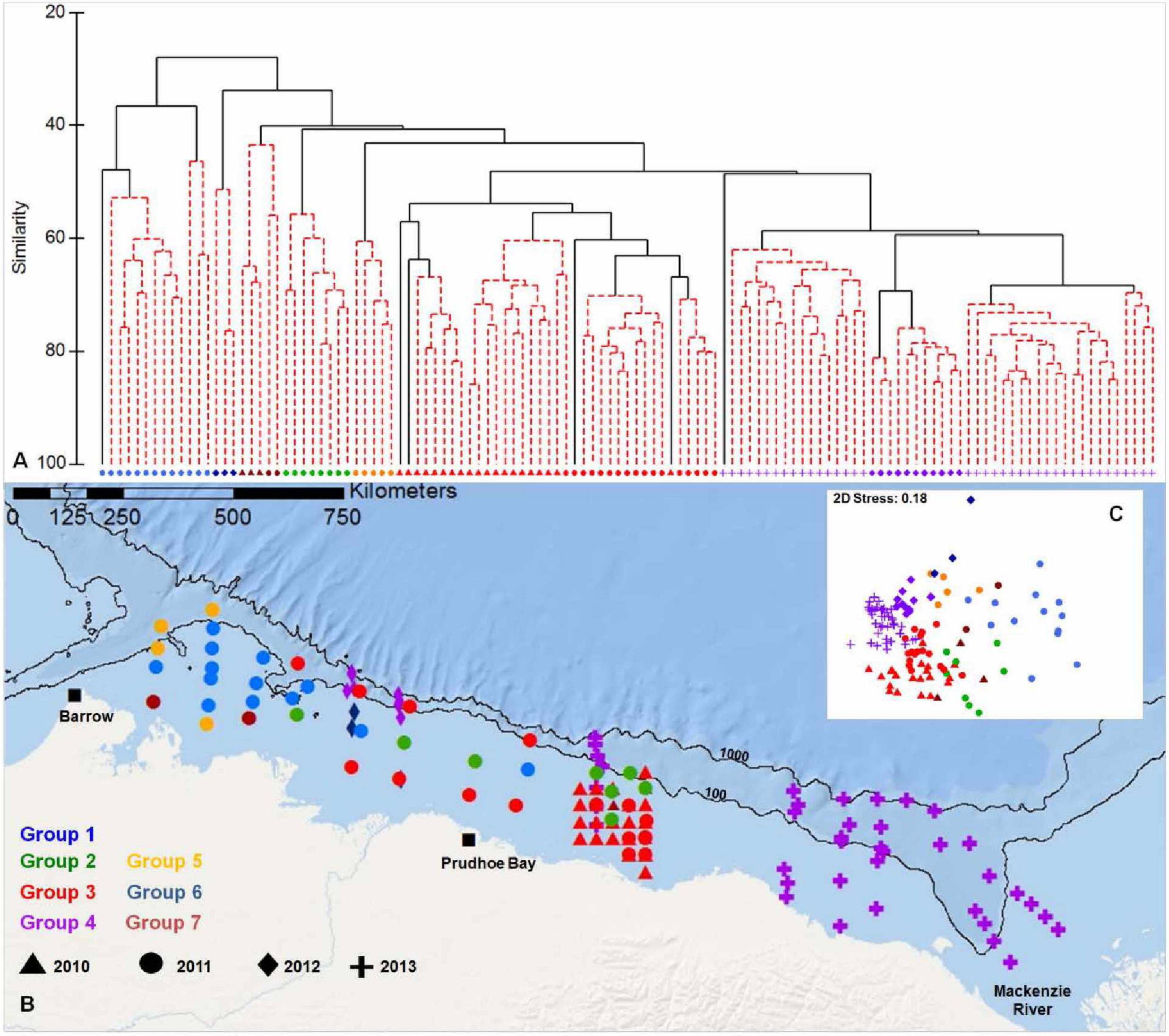

Figure 1.14. Beaufort zooplankton community structure for the 505-µm net abundance data from 2010-13. Shapes indicate year. Colors indicate faunal grouping. A) Bray-Curtis sample similarity as determined by hierarchical clustering. Dotted red lines connect samples that are not statistically unique (SIMPROF, $p < 0.05$). B) Spatial distribution of observed community groups. C) Non-parametric Multidimensional Scaling (nMDS) of zooplankton community overlain with observed groupings.

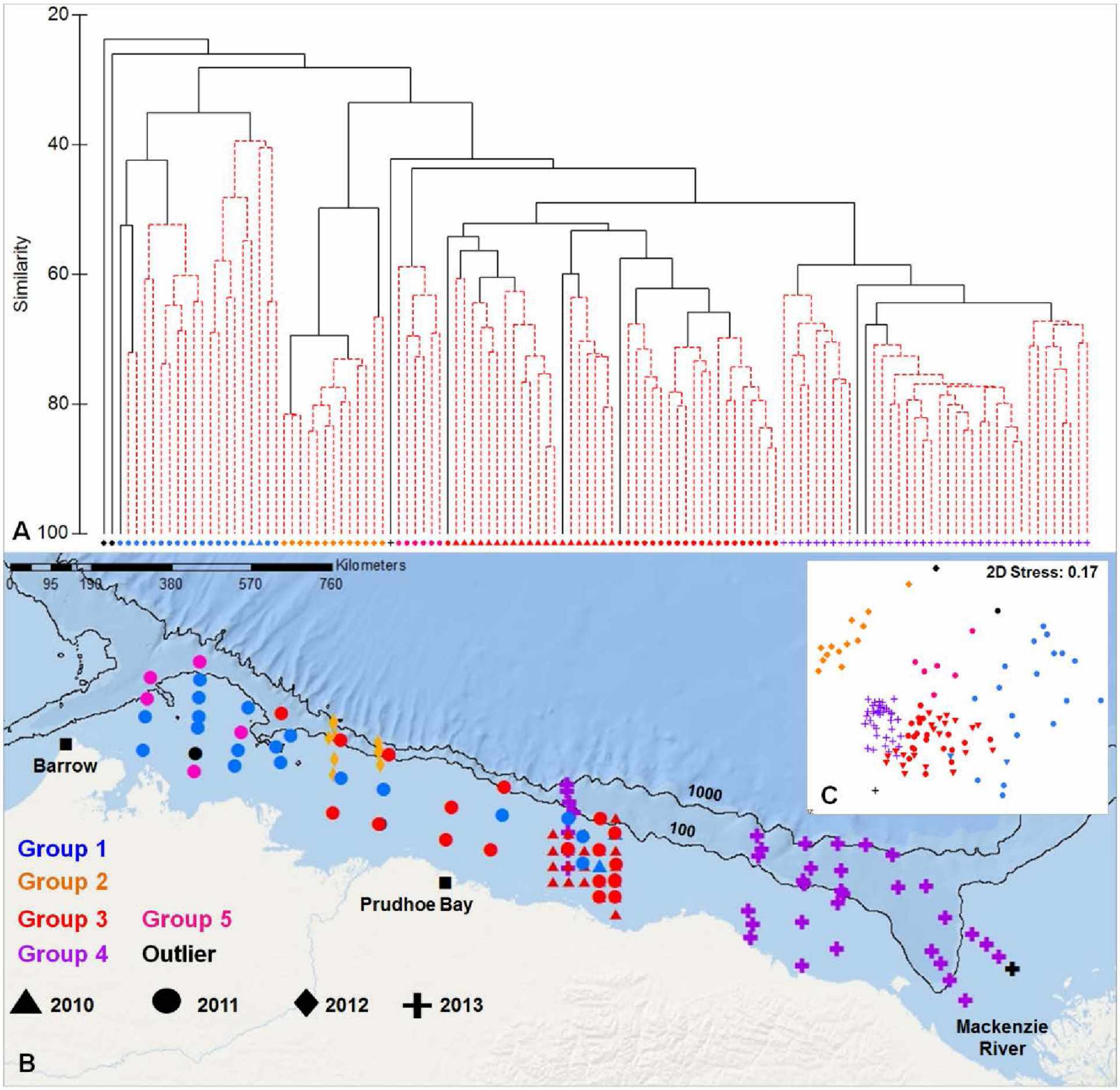

Figure 1.15. Beaufort zooplankton community structure for the 505-µm net biomass data from 2010-13. Shapes indicate year. Colors indicate faunal grouping. A) Bray-Curtis sample similarity as determined by hierarchical clustering. Dotted red lines connect samples that are not statistically unique (SIMPROF, $p < 0.05$). B) Spatial distribution of observed community groups. C) Non-parametric Multidimensional Scaling (nMDS) of zooplankton community overlain with observed groupings.

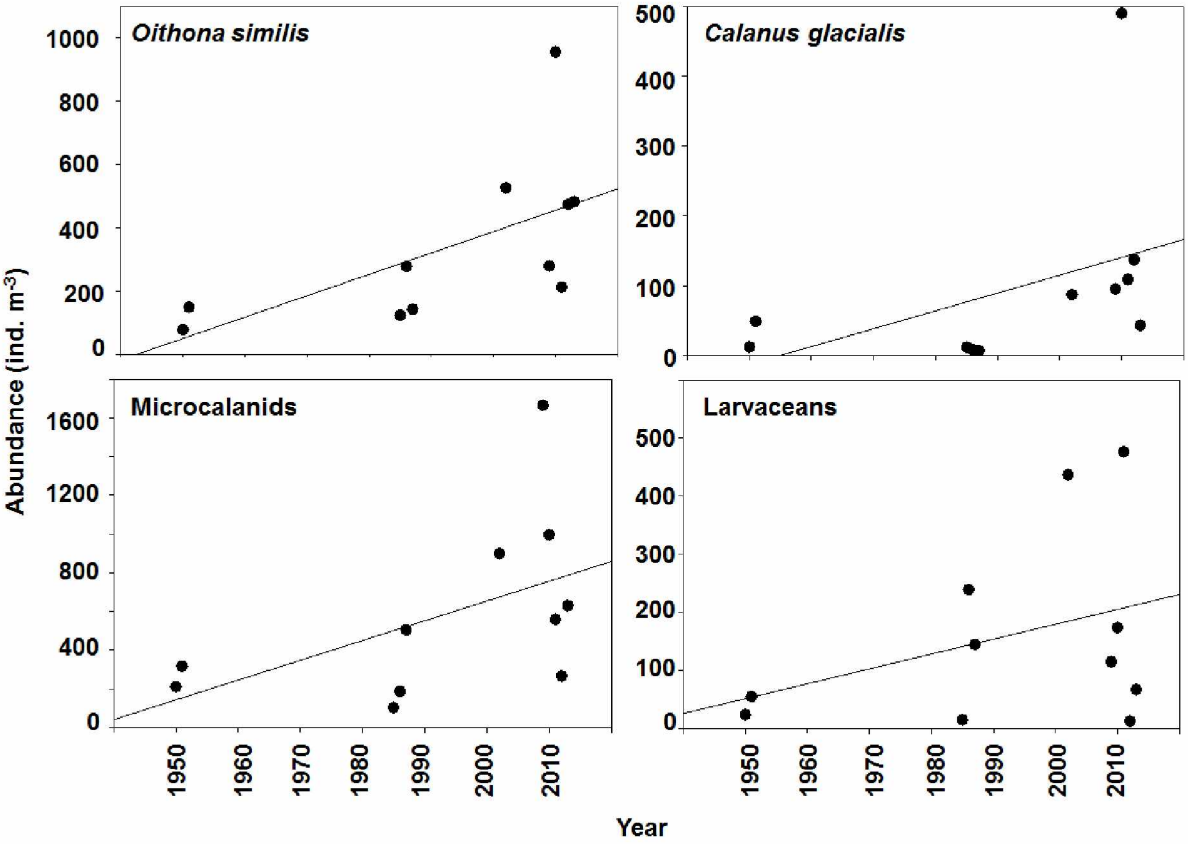

Figure 1.16. Comparison of average abundances (ind. m^{-3}) of select taxa in the Beaufort Sea region over the past 60 years. Trendlines are shown.

Data sources:

1950: USS *Burton Island*, 120 μm net, stations 3-11, 32, 33, 57, 58, 60, 62, 64, 66; Johnson, 1956

1951: USS *Burton Island*, 120 μm net, stations 1, 5-11, 17, 20, 22, 31, 32, 36, 37, 38, 63, 64; Johnson, 1956

1985-1987: NOGAP2, 85 μm net; Hopky *et al.*, 1994a,b,c

2002: SBI, 150 μm net; Lane *et al.*, 2006

2009: *Nahidik*, lower stratum 20-100m, 150 μm net; Walkusz *et al.*, 2013

2010: Camden Bay, 150 μm net; this study

2011: *Beaufish*, 150 μm net; this study

2012-13: *Transboundary*, 150 μm net; this study

Tables

Table 1.1. Mean holozooplankton abundance and biomass for each field season in the Beaufort Sea during 2010-2013.

Year	Survey Dates	No. Stations 150/505 µm	Avg. Abundance (Ind. m^{-3}) ± SE		Avg. Biomass (mg DW m^{-3}) ± SE	
			150 µm	505 µm	150 µm	505 µm
2010	09/22-09/28	22/22	3380 ± 857	214 ± 78	59.7 ± 20.8	17.5 ± 4.5
2011	08/16-09/03	59/45	1830 ± 338	47 ± 11	23.8 ± 3.6	13.9 ± 3.2
2012	09/21-09/30	11/14	1110 ± 124	196 ± 114	76.9 ± 11.7	57.6 ± 28.8
2013	08/13-08/31	39/39	1910 ± 187	47 ± 5	40.2 ± 4.9	25.6 ± 2.4

Table 1.2. Average abundance and biomass of Beaufort Sea zooplankton taxa captured by the 150-µm net during 2010-2013. * - indicates that a taxon was only observed in abundances < 0.01 ind. m^{-3}; biomass <0.01 mg DW m^{-3}. *NC* – indicates biomass was not calculated.

	Abundance (Ind. m^{-3})				Biomass (mg DW m^{-3})			
Calanoida	**2010**	**2011**	**2012**	**2013**	**2010**	**2011**	**2012**	**2013**
Aetideopsis minor	-	-	-	0.09	-	-	-	*
Acartia longiremis	6.00	1.57	4.06	6.53	0.03	0.01	0.02	0.03
Acartia bifilosa	-	*	-	1.65	-	-	-	0.03
***Acartia* spp. (copepodite)**	-	8.05	4.85	5.07	-	0.01	0.01	0.01
Augaptilus glacialis	-	-	-	*	-	-	-	*
Eurytemora herdmani	-	-	-	6.17	-	-	-	0.06
Eurytemora pacifica	-	*	-	-	-	*	-	-
Eurytemora richsingi	-	-	-	*	-	-	-	*
***Eurytemora* spp. (copepodite)**	1.12	0.18	-	62.92	*	*	-	0.22
Calanus glacialis	508.82	108.92	137.23	42.49	20.36	4.70	43.00	5.70
Calanus hyperboreus	17.36	9.62	0.68	15.11	12.03	9.01	1.98	15.05
Centropages abdominalis	*	-	-	0.40	*	-	-	0.01
Chiridius obtusifrons	-	*	0.36	0.31	-	*	0.07	0.04
Epilabidocera amphitrites	-	-	-	-	-	-	-	-
Eucalanus bungi	-	0.10	*	0.50	-	*	0.01	1.82
Gaetanus tenuispinus	-	-	-	0.02	-	-	-	*
***Gaetanus* spp.**	-	-	-	0.00	-	-	-	*
Heterorhabdus compactus	-	-	-	0.01	-	-	-	*
Heterorhabdus norvegicus	-	0.14	0.22	0.88	-	0.05	0.04	0.16
Jashnovia tolli	-	*	0.23	*	-	*	0.01	*
Limnocalanus macrurus	-	-	-	1.16	-	-	-	0.03
Metridia longa	1.47	1.48	17.73	7.87	0.23	0.24	1.55	1.25
Metridia pacifica	-	0.34	-	-	-	0.01	-	-
***Metridia* spp. (copepodite)**	15.65	2.30	3.98	1.47	0.07	0.01	0.03	0.01

Table 1.2, continued

Microcalanus pygmaeus	**11.07**	**13.14**	**13.99**	**47.52**	**0.01**	**0.02**	**0.02**	**0.06**
Neocalanus cristatus	-	*	*	*	-	0.03	0.33	1.87
Neocalanus flemingeri	-	*	0.10	*	-	0.01	0.05	*
Neocalanus plumchrus	-	*	-	-	-	0.01	-	-
Paraeuchaeta glacialis	0.15	0.63	1.55	2.08	0.09	0.61	1.11	1.82
Pseudocalanus acuspes	12.40	0.84	3.06	12.41	0.15	0.01	0.03	0.14
Pseudocalanus mimus	-	-	2.84	*	-	-	0.03	*
Pseudocalanus minutus	0.49	6.54	13.28	5.26	0.01	0.10	0.21	0.08
Pseudocalanus newmani	16.37	2.41	10.67	3.27	0.13	0.02	0.07	0.02
Pseudocalanus **spp. (male)**	5.78	2.75	6.40	3.47	0.03	0.02	0.03	0.02
Pseudocalanus **spp. (copepodite)**	1419.71	533.51	217.91	557.59	5.72	0.96	0.60	1.99
Scaphocalanus magnus	-	-	-	0.11	-	-	-	0.08
Scolecithricella minor	*	0.15	0.65	1.07	*	*	0.01	0.01
Spinocalanus magnus	-	-	-	0.47	-	-	-	*
Tortanus discaudatus	-	*	-	0.15	-	*	-	*
Cyclopoida								
Oithona similis	955.26	213.33	474.08	483.45	1.71	0.28	0.59	0.49
Poecilostomatoida								
Triconia borealis	103.81	23.57	27.53	88.40	0.16	0.05	0.05	0.14
Harpacticoida								
Harpacticoid unk.	-	0.17	-	0.15	-	*	-	*
Microsetella norvegica	-	0.61	1.57	1.82	-	*	0.01	0.01
Nauplii								
Harpacticoid nauplii	0.03	0.03	0.03	0.02	-	*	*	*
Calanoid nauplii	512.51	415.54	83.65	245.12	0.54	0.32	0.05	0.15
Cyclopoid nauplii	-	0.57	1.07	5.12	-	*	*	*
Appendicularia								
Oikopleura vanhoeffeni	132.14	64.15	5.67	18.29	2.37	0.86	0.02	0.08
Fritilaria borealis	36.01	412.54	7.18	48.87	*	0.01	*	0.00
Pteropoda								
Limacina helicina	58.78	13.19	9.20	5.66	0.49	0.62	0.01	0.05
Clione limacina	0.02	0.01	0.18	*	*	0.05	1.94	0.02
Chaetognatha								
Eukrohnia hamata	0.24	0.05	-	0.10	0.17	0.04	-	0.33
Pseudosagitta maxima	-	-	-	0.07	-	-	-	*
Parasagitta elegans	5.47	11.67	31.36	2.39	1.75	2.05	1.19	0.16
Cladocera								
Evadne nordmanni	-	-	-	2.88	-	-	-	0.07
Podon leuckarti	0.10	0.23	-	31.82	0.33	*	-	0.14
Ostracoda								
Boroecia maxima	-	0.02	0.14	1.51	-	*	0.01	0.14
Euphausiacea								
Euphausid nauplii	-	*	-	0.01	-	*	-	*
Euphausid calyptopis	-	0.33	-	-	-	*	-	-
Euphausid juvenile	0.06	0.27	-	-	*	0.03	-	-

Table 1.2, continued

Euphausid furcillia	-	**0.07**	-	-	-	**0.01**	-	-
Thysanoessa inermis	-	-	0.19	0.01	-	-	1.84	0.08
Thysanoessa longipes	-	-	-	*	-	-	-	0.02
Thysanoessa raschii	0.02	0.02	0.06	0.04	*	0.06	0.46	0.19
Mysidae								
Mysis spp.	-	0.02	-	0.01	-	0.30	-	0.01
Mysis oculata	0.02	-	-	*		-	-	0.01
Decapoda								
Hippolytidae	*	0.03	0.01	*	0.01	0.04	0.02	0.02
Pandalidae	-	0.01	*	0.01	-	*	0.01	-
Cumacea	0.03	-	-	0.00	0.03	-	-	*
Amphipoda								
Amphipod unk.	-	0.14	0.08	0.07	-	0.21	0.05	0.05
Apherusa glacialis	-	*	-	0.01	-	*	-	*
Gammarus wilkitzkii	-	-	0.01	-	-	-	*	-
Cyphocaris challengeri	-	-	-	0.01	-	-	-	0.04
Hyperia galba/medusarum	0.24	0.04	0.03	*	0.08	0.01	*	0.01
Hyperoche medusarum	*	-	-	-	0.01	-	-	-
Onisimus spp.	-	-	-	0.01	-	-	-	*
Themisto abyssorum	0.09	0.12	0.17	0.95	0.13	0.12	0.57	0.90
Themisto libellula	0.01	0.18	0.28	0.27	0.42	0.10	0.70	0.37
Isopoda	-	0.01	0.22	0.22	-	*	*	*
Siphonophora								
Dimophyes arctica	-	*	-	0.02	-	*	-	3.43
Hydrozoa								
Aeginopsis laurentii	1.00	0.28	*	0.21	0.51	0.13	*	0.09
Aglantha digitale	53.92	18.44	24.93	13.07	5.06	1.88	0.69	4.68
Catablema vesicarium	-	*	-	-	-	*	-	-
Cyanea capillata	*	-	-	-	1.92	-	-	-
Euphysa flammea	-	-	-	*	-	-	-	*
Halitholus cirratus	0.24	-	-	0.03	16.54	-	-	0.21
Melicertum octopunctata	-	0.01	-	-	-	0.01	-	0.04
Obelia longissima	-	0.17	-	0.24	-	0.01	-	0.09
Ptychogena lactea	-	0.05	-	0.07	-	*	-	*
Sarsia tubulosa	0.02	-	-	-	0.25	-	-	-
Tiaropsis multicirrata	-	*	-	-	-	0.01	-	-
Ctenophora								
Mertensia ovum	0.13	0.07	0.13	0.01	0.45	0.30	0.50	0.19
Polychaeta								
Tomopteris septentrionalis	-	-	-	0.01	-	-	-	0.03
Rotifera	-	-	-	73.91	-	-	-	NC
Meroplankton								
Barnacle cypris	14.89	9.33	0.23	0.06	0.22	0.22	*	*
Barnacle nauplii	2.30	2.36	0.05	0.47	*	*	-	*
Bipinaria	0.44	6.73	0.49	2.35	*	0.01	*	*

Table 1.2, continued

Bivalve larvae	**42.13**	**58.10**	**32.63**	**25.00**	**0.01**	**0.02**	**0.01**	**0.04**
Brachyuran zoea	0.12	0.16	0.01	*		0.03	0.01	*
Cyphonautes	-	-	0.57	0.36	-	-	*	0.10
Echinoderm larvae	2.28	50.38	1.38	1.64	*	*	*	*
Gastropod larvae	-	3.92	3.52	1.02	0.04	*	*	*
Megalopa	*	0.01	0.05	*	0.00	*	0.04	*
Ophiuroid larvae	*	2.60	-	-	*	*	-	-
Pagurid zoea	-	0.04	0.03	0.05	-	0.03	*	*
Polychaete larvae	55.17	39.38	4.67	99.32	0.57	0.13	0.02	0.23

Table 1.3. Average abundance and biomass of Beaufort Sea zooplankton taxa captured by the 505-µm net during 2010-2013. * - indicates that a taxon was only observed in abundances < 0.01 ind. m^{-3}; biomass <0.01 mg DW m^{-3}. *NC* – indicates biomass was not calculated.

	Abundance (Ind. m^{-3})				**Biomass (mg DW m^{-3})**			
	2010	**2011**	**2012**	**2013**	**2010**	**2011**	**2012**	**2013**
Calanoida								
Aetideopsis minor	-	-	-	*	-	-	-	*
Acartia longiremis	*	*	0.01	0.01	*	*	*	*
Acartia bifilosa	-	-	-	0.04	-	-	-	*
Calanus glacialis	166.54	21.43	179.95	21.74	10.21	3.38	45.71	4.90
Calanus hyperboreus	7.43	6.48	0.42	11.28	3.10	6.57	0.83	10.04
Chiridius obtusifrons	-	0.01	0.07	0.09	-	*	0.01	0.02
Epilabidocera amphitrites	-	*	-	-	-	*	-	-
Eucalanus bungi	-	*	*	*	-	*	*	*
Gaetanus brevispinus	-	-	-	*	-	-	-	*
Gaetanus tenuispinus	-	-	*	0.02	-	-	*	*
Heterorhabdus compactus	-	-	*	0.05	-	-		
Heterorhabdus norvegicus	-	-	0.03	0.23	-	-	*	0.04
Jashnovia tolli	*	-	*	0.01	*	-	*	*
Limnocalanus macrurus	-	*	-	1.86	-	*	-	0.05
Metridia longa	0.60	0.73	8.30	4.10	0.12	0.20	0.67	0.61
Metridia pacifica	-	0.17	-	*	-	0.01	-	*
***Metridia* spp.**	0.06	-	0.01	0.02	*	-	*	*
Neocalanus cristatus	-	0.00	0.04	0.01	-	0.02	0.22	0.10
Neocalanus flemingeri	-	0.03	-	-	-	0.02	-	-
Neocalanus plumchrus	-	-	*	*	-	-	*	0.01
Paraeuchaeta glacialis	0.09	0.35	0.52	1.22	0.09	0.43	0.26	0.60
Pseudocalanus acuspes	1.10	*	-	0.00	0.02	*	-	*
Pseudocalanus mimus	-	0.01	-	-	-	*	-	-
Pseudocalanus minutus	0.07	0.70	1.39	0.63	*	0.01	0.03	0.01
Pseudocalanus newmani	0.14	-	-	-	*	-	-	-
***Pseudocalanus* spp. (male)**	-	-	*	0.01	-	-	*	*
***Pseudocalanus* spp. (copepodite)**	0.62	0.28	0.07	0.43	0.01	0.01	*	0.01

Table 1.3, continued

Scaphocalanus magnus	-	-	-	**0.05**	-	-	-	**0.03**
Scolecithricella minor	*	*	0.01	0.04	*	*	*	*
Tortanus discaudatus	-	*	-	-	-	*	-	-
Appendicularia								
Oikopleura vanhoeffeni	14.19	11.39	0.03	0.65	0.55	0.71	-	0.02
Fritilaria borealis	0.80	1.23	-	0.05	*	*	-	-
Pteropoda								
Limacina helicina	1.64	0.39	0.08	0.28	0.02	0.01	0.87	1.75
Clione limacina	0.01	0.01	0.12	*	0.01	0.02	*	*
Chaetognatha								
Eukrohnia hamata	0.11	-	-	0.09	0.17	-	4.58	0.11
Pseudosagitta maxima	-	-	-	0.02	-	-	-	*
Parasagitta elegans	0.46	0.94	2.93	0.47	0.67	0.60	-	0.78
Cladocera								
Evadne nordmanni	0.01	-	-	*	*	-	-	*
Podon leuckarti	-	*	-	0.11	-	*	*	*
Ostracoda								
Boroecia maxima	*	*	0.02	0.43	*	*	-	0.08
Euphausiacea								
Juvenile euphausiids (all stages)	0.04	0.54	*	*	*	0.06	0.45	*
Meganyctiphanes norvegica	-	-	Trace	-	-	-	0.15	-
Thysanoessa inermis	*	*	0.10	0.06	*	*	1.24	0.64
Thysanoessa longipes	-	-	*	*	*	*	0.87	*
Thysanoessa raschii	*	0.10	0.18	0.10	*	0.39	0.01	0.83
Thysanoessa spinifera	-	-	-	0.02	-	-	-	0.15
Mysidae								
Boreomysis arctica	-	-	-	*	-	-	-	*
Mysis oculata	0.03	0.02	0.01	*	-	0.10	*	0.03
Decapoda								
Hippolytidae	0.08	0.01	*	0.01	0.74	0.01	-	0.01
Pandalidae	*	*	*	0.01	0.01	*	-	0.03
Eulas **spp.**	-	-	*	*	-	-	*	0.04
Sabinea septemcarinata	-	-	-	*	-	-	-	0.02
Cumacea	0.01	*	*	*	0.01	-	*	*
Amphipoda								
Amphipod unk.	0.01	*	*	0.01	0.01	-	*	0.01
Argissa hamatipes	-	-	-	*	-	-	-	*
Apherusa glacialis	*	*	*	0.01	-	*	-	0.02
Gammarus wilkitzkii	0.04	*	*	-	0.03	*	*	-
Eusirus holmi	-	-	-	*	-	-	-	*
Hyperia galba/medusarum	0.02	0.01	-	*	0.01	*	0.02	*
Hyperoche medusarum	0.01	*	-	*	0.16	*	-	*
Monoculoides schneideri	-	-	-	*	-	-	-	*
Onisimus **spp.**	*	*	*	*	*	*	-	*
Themisto abyssorum	0.05	0.11	0.05	0.57	0.11	0.08	-	1.11

Table 1.3, continued

Themisto libellula	**0.01**	**0.01**	**0.01**	**0.07**	**0.46**	**0.18**	**-**	**0.76**
Pardalisca cuspidata	-	-	-	*	-	-	-	*
Phoxocephalidae	-	-	-	*	-	-	-	0.01
***Syrrhoe* spp.**	-	-	-	*	-	-	-	*
Isopoda								
Munnopsis typica	-	-	-	*				
Siphonophora								
Dimophyes arctica	*	*	*	0.01	-	*	0.20	*
Hydrozoa								
Aeginopsis laurentii	0.08	0.20	0.01	0.10	0.08	0.35	-	0.09
Aglantha digitale	19.52	1.16	1.67	2.17	1.11	0.72	1.50	1.18
Bougainvillia superciliaris	0.01	-	-	0.00	-	-	-	*
Catablema vesicarium	-	*	-	0.01	0.12	*	-	0.13
Cyanea capillata	-	*	-	-				
Eumedusae birulai	-	-	-	*	-	-	-	*
Euphysa flammea	*	-	-	*				
Halitholus cirratus	*	*	-	0.05	*	*	-	0.39
Melicertum octopunctata	*	0.01	-	*	*	*	-	-
Obelia longissima	0.01	*	-	0.01	*	*	-	*
Ptychogena lactea	*	*	-	-	0.01	*	-	*
Sarsia princeps	-	-	-	*	-	-	-	0.01
Sarsia tubulosa	-	-	-	*	-	-	-	0.01
Tiaropsis multicirrata	*	-	-	*	*	-	-	*
Ctenophora								
Bolinopsis infundibulum	-	-	-	*	-	-	-	0.27
Beroe cucumis	0.01	*	*	*	0.13	0.02	-	0.06
Beroe abyssicola	-	-	-	*	-	-	-	0.02
Mertensia ovum	0.06	*	0.11	0.01	0.27	*	0.06	0.56
Polychaeta								
Tomopteris septentrionalis	-	-	-	*	-	-	-	*
Meroplankton								
Barnacle cypris	-	0.02	-	-	*	*	-	-
Barnacle nauplii	-	0.04	-	0.01	*	*	-	*
Echinoderm larvae	0.04	-	-	0.02	*	-	-	*
Megalopa	-	0.02	*	-	-	*	0.20	-
Ophiuroid larvae	-	0.01	-	-	-	-	-	-
Pagurid zoea	0.01	0.06	-	*	*	*	-	*
Polychaete larvae	0.01	0.02	0.01	0.06	*	*	*	*

Table 1.4. Key taxa and their contribution to the first 90% of community similarity for community groupings for the 150-µm net abundance data from 2010-13.

Group	Similarity (%)	Description	Taxa (% Contribution)		
1	64.4	Strong ACW	*Oithona similis* (11.96)	*Calanus glacialis* (6.29)	Gastropod larvae (3.21)
		(T ≥ 4°C)	*Pseudocalanus* spp. (11.08)	*Limacina helicina* (5.23)	Barnacle cypris (2.92)
			Calanoid nauplii (9.66)	*Aglantha digitale* (5.18)	*Triconia borealis* (2.32)
			Fritillaria borealis (8.43)	Polychaeta larvae (3.89)	*Acartia longiremis* (2.28)
			Bivalve larvae (7.58)	*Acartia* spp. (3.22)	Echinoderm larvae (1.61)
			Parasagitta elegans (6.35)		
2	70.9	Weak ACW	Calanoid nauplii (10.93)	*Pseudocalanus* spp. (6.19)	*Acartia* spp. (3.15)
		(T 3-4 °C)	*Fritillaria borealis* (10.6)	Bivalve larvae (5.28)	Bipinaria (3.01)
			Oikopleura vanhoeffeni (10)	*Calanus glacialis* (5.22)	*Aeginopsis laurentii* (2.56)
			Oithona similis (8.61)	*Triconia borealis* (4.53)	Barnacle cypris (1.89)
			Aglantha digitale (6.86)	*Limacina helicina* (3.96)	*Acartia longiremis* (1.62)
			Polychaeta larvae (6.56)		
3	68.6	Cool Waters	Calanoid nauplii (11.48)	*Calanus glacialis* (7.65)	*Limacina helicina* (3.92)
		(T 0-3°C)	*Oithona similis* (11.36)	Polychaeta larvae (6.98)	Bivalve larvae (3.67)
			Pseudocalanus spp. (9.54)	*Fritillaria borealis* (6.22)	*Microcalanus pygmaeus* (3.14)
			Oikopleura vanhoeffeni (8.95)	*Aglantha digitale* (4.62)	*Metridia longa* (2.45)
			Triconia borealis (7.7)	*Calanus hyperboreus* (3.94)	
4	64.9	Cool Waters	*Oithona similis*(9.6)	*Metridia longa*(3.22)	*Paraeuchaeta glacialis*(1.89)
		FW influence	*Pseudocalanus* spp. (9.45)	*Pseudocalanus minutus* (3.01)	*Synchaeta* spp. (1.69)
		(T 0-3°C)	Calanoid nauplii (7.81)	*Parasagitta elegans* (2.77)	*Eurytemora* spp. (1.59)
			Triconia borealis (6.21)	*Fritillaria borealis* (2.74)	*Themisto abyssorum* (1.52)
			Calanus glacialis (5.72)	*Oikopleura vanhoeffeni* (2.61)	*Pseudocalanus newmani* (1.44)
			Microcalanus pygmaeus (5.11)	Bivalve larvae (2.52)	*Podon leuckartii* (1.41)
			Polychaeta larvae (4.86)	*Limacina helicina* (2.42)	*Metridia* spp. (C1-3) (1.28)
			Calanus hyperboreus (3.63)	*Pseudocalanus* spp. (male) (2.17)	
			Aglantha digitale (3.6)	*Pseudocalanus acuspes* (1.93)	

Table 1.5. Relationship between 150-µm zooplankton and abiotic factors over different depth intervals during 2010-2013. Temperature (*T*) and salinity (*S*) averages, and station depth (m) (*D*). * Indicates best variable combination explaining observed zooplankton community structure.

	Abundance				Biomass			
Bottom	**# Var.**				**# Var.**			
	2	***T,S***	***D,T***	***D,S***	2	***T,S***	***D,T***	***D,S***
		0.45	0.31	0.15		0.44	0.31	0.18
	3	***D,T,S***			3	***D,T,S***		
		0.35				0.35		
200m average								
	2	***T,S***	***D,T***	***D,S***	2	***T,S***	***D,T***	***D,S***
		0.5	0.37	0.15		0.47	0.35	0.19
	3	**D,T,S**			3	**D,T,S**		
		0.41				0.4		
100m average								
	2	***T,S***	***D,T***	***D,S***	2	***T,S***	***D,T***	***D,S***
		0.53*	0.36	0.17		0.49*	0.34	0.2
	3	***D,T,S***			3	***D,T,S***		
		0.43				0.4		
50m average								
	2	***T,S***	***D,T***	***D,S***	2	***T,S***	***D,T***	***D,S***
		0.51	0.31	0.21		0.45	0.29	0.23
	3	***D,T,S***			3	***D,T,S***		
		0.39				0.36		
Surface								
	2	***T,S***	***D,S***	***D,T***	2	***T,S***	***D,S***	***D,T***
		0.35	0.22	0.15		0.31	0.25	0.14
	3	***D,T,S***			3	***D,T,S***		
		0.27				0.26		

Table 1.6. Key taxa and their contribution to the first 90% of community similarity groupings for the 505-µm net abundance data from 2010-13.

Group	Similarity (%)	Description	Taxon (% Contribution)		
1	49.5	ACW	*Aglantha digitale* (17.21)	Pagurid zoea (7.02)	*Pseudocalanus minutus* (3.59)
		(T ≥ 4°C)	*Calanus glacialis* (16.44)	Megalopa (6.28)	*Limacina helicina* (2.54)
			Decapod larvae (13.97)	*Parasagitta elegans* (5.6)	Euphausiid juveniles (2.52)
			Fritillaria borealis (10.21)	*Paraeuchaeta glacialis* (9.51)	*Calanus hyperboreus* (6.47)
2	61.8	ACW	*Aglantha digitale* (20.97)	*Aeginopsis laurentii* (9.36)	*Metridia longa* (3.96)
		(T ≥ 4°C)	*Oikopleura vanhoeffeni* (18.22)	*Clione limacina* (4.44)	*Themisto abyssorum* (3.89)
			Fritillaria borealis (9.86)	*Calanus glacialis* (8.3)	Barnacle cypris (1.91)
3	58.9	Cool Waters	*Calanus glacialis* (20.05)	*Parasagitta elegans* (5.59)	*Paraeuchaeta glacialis* (2.66)
		(T 0-3°C)	*Oikopleura vanhoeffeni* (15.99)	*Metridia longa* (4.98)	*Limacina helicina* (2.19)
			Calanus hyperboreus (12.72)	*Aeginopsis laurentii* (4.61)	
			Aglantha digitale (12.42)	*Fritillaria borealis* (3.98)	
4	62.5	Cool Waters	*Calanus glacialis* (16.27)	*Themisto abyssorum* (5.18)	*Oikopleura vanhoeffeni* (2.03)
		(T 0-3°C)	*Metridia longa* (10.72)	*Pseudocalanus minutus* (4.47)	*Thysanoessa inermis* (1.96)
		Freshwater	*Calanus hyperboreus* (10.36)	*Limacina helicina* (3.35)	*Heterorhabdus norvegicus* (1.85)
			Aglantha digitale (7.96)	*Themisto libellula* (3.35)	*Limnocalanus macrurus* (1.52)
			Paraeuchaeta glacialis (7.13)	*Thysanoessa raschii* (3.31)	*Pseudocalanus* spp. (1.51)
			Parasagitta elegans (6.16)	*Boroecia maxima* (2.06)	*Neocalanus cristatus* (1.22)
5	65.8	ACW	*Calanus glacialis* (17.14)	Pagurid zoea (4.11)	*Thysanoessa raschii* (2.65)
		(T ≥ 4°C)	*Parasagitta elegans* (12.26)	*Aglantha digitale* (4.61)	Barnacle cyprus (2.22)
			Pseudocalanus minutus (9.19)	*Metridia pacifica* (4.37)	Decapod larvae (1.94)
			Euphausiid juvenile (8.09)	Megalopa (3.41)	*Limacina helicina* (1.92)
			Calanus hyperboreus (6.15)	*Themisto libellula* (3.39)	*Melicertum octocostatum* (1.75)
			Pseudocalanus spp. (5.43)	Barnacle nauplii (3.00)	
6	59.7	ACW (T ≥ 4°C)	*Calanus glacialis* (50.39)	*Aeginopsis laurentii* (11.69)	*Parasagitta elegans* (8.13)
		Shelfbreak	*Mertensia ovum* (11.81)	*Pseudocalanus* spp. (11.03)	Megalopa (7.9)
7	55.9	Shelf	*Calanus glacialis* (21.9)	*Clione limacina* (11.06)	*Themisto libellula* (7.9)
			Calanus hyperboreus (11.81)	*Themisto abyssorum* (9.93)	
			Aglantha digitale (large) (11.71)	*Aglantha digitale* (9.93)	

Table 1.7. Relationship between 505-µm zooplankton and abiotic factors over different depth intervals during 2010-2013. Temperature (*T*) and salinity (*S*) averages, and station depth (m) (*D*). * Indicates best variable combination explaining observed zooplankton community structure.

		Abundance				Biomass		
Bottom	**# Var**				**# Var.**			
	1	***T***	***S***	***D***	1	***T***	***S***	***D***
		0.43	0.13	-0.01		0.43	0.13	-0.01
	2	***T,S***	***D,T***	***D,S***	2	***T,S***	***D,T***	***D,S***
		0.46	0.33	0.03		0.46	0.33	0.03
	3	***D,T,S***			3	***D,T,S***		
		0.32				0.32		
200 m average								
	1	***T***	***S***	***D***	1	***T***	***S***	***D***
		0.57*	-0.01	-0.01		0.50*	0.06	0.04
	2	***T,S***	***D,T***	***D,S***	2	***T,S***	***D,T***	***D,S***
		0.44	0.37	-.04		0.42	0.36	0.01
	3	***D,T,S***			3	***D,T,S***		
		0.31				0.31		
100 m average								
	1	***T***	***S***	***D***	1	***T***	***D***	***S***
		0.56	0.01	-0.01		0.49	0.04	-0.02
	2	***T,S***	***D,T***	***D,S***	2	***T,S***	***D,T***	***D,S***
		0.48	0.37	-0.02		0.42	0.36	0.01
	3	***D,T,S***			3	***D,T,S***		
		0.34				0.31		
50 m average								
	1	***T***	***S***	***D***	1	***T***	***S***	***D***
		0.45	0.18	-0.01		0.47	0.12	0.04
	2	***T,S***	***D,T***	***D,S***	2	***T,S***	***D,T***	***D,S***
		0.49	0.316	0.05		0.38	0.33	0.05
	3	***D,T,S***			3	***D,T,S***		
		0.33				0.28		
Surface								
	1	***T***	***S***	***D***	1	***S***	***T***	***D***
		0.17	0.12	-0.03		0.11	0.06	0.04
	2	***T,S***	***D,T***	***D,S***	2	***T,S***	***D,T***	***D,S***
		0.23	0.08	0.03		0.11	0.05	0.04
	3	***D,T,S***			3	***D,T,S***		
		0.13				0.07		

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2. The vertical distribution of Beaufort Sea zooplankton in relation to water masses[2]

Abstract

We collected stratified zooplankton samples at stations along the Beaufort Sea slope during August 2013 to characterize the vertical structure of zooplankton communities from the surface to 1000 meters depth. We documented 93 taxonomic categories; the greatest diversity was observed in the copepods (48 species), followed by the cnidarians (9 species) and amphipods (8 species). Distinct zooplankton communities were associated with the three main water masses in the study region: the Polar Mixed Layer (PML), Arctic Halocline Water (AHW), and Atlantic Water (AW). Average abundance and biomass were highest (1160 ind. m^{-3} and 30.6 mg DW m^{-3}, respectively) in the PML, where the community was dominated by Arctic copepods. Arctic copepods, including *Calanus glacialis*, *Calanus hyperboreus*, *Oithona similis*, *Metridia longa, Triconia borealis*, *Microcalanus pygmaeus*, and the *Pseudocalanus* species complex, contributed upwards of 90% of copepod abundance and biomass in the PML. The AHW (50-100 and 100-200 m) communities were also dominated by Arctic copepods, but exhibited markedly lower average abundances (218 and 102 ind. m^{-3}) and biomasses (8.6 and 5.1 mg DW m^{-3}). The AW (200-300, 300-500, 500-1000 m) communities exhibited the lowest average abundances and biomasses: average abundance ranged from 127 ind. m^{-3} in the 200-300 m layer to 15 ind. m^{-3} in the 500-1000 m layer. Average biomass was 8.0 and 0.6 mg DW m^{-3} in the 200-300 and 500-1000 m layers, respectively. Mesopelagic copepods, including the spinocalanids and aetideids, were important contributors in the Atlantic layer, which exhibited the highest species richness of the three water masses. Community structure was highly correlated with salinity and depth, both in terms of abundance (Spearman correlation (ρ): 0.84, $p < 0.01$) and biomass ($\rho = 0.81, p < 0.01$). We report similar species composition but higher biomass when compared to corresponding depth intervals in the interior basins, likely due to elevated coastal production compared to the deep basins

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[2] Smoot, C. and Hopcroft, R.R. The vertical distribution of Beaufort Sea zooplankton in relation to water masses. Prepared for submission in Journal of Plankton Research.

Introduction

In addition to their widely recognized role as tropic intermediaries, zooplankton play an important role in processing and repackaging organic material as it sinks through the water column. Mesopelagic zooplankton fragment and aggregate particles via feeding and fecal pellet production; these modifications can influence remineralization and sinking rates, thereby impacting deeper waters and benthic communities (Dilling *et al.*, 1998; Wilson *et al.*, 2010; Robinson *et al.*, 2010). Omnivory and carnivory generally increase in importance with depth (Auel & Hagen, 2002; Yamaguchi *et al.*, 2002; Blachowiak-Samolyk *et al.*, 2007; Darnis *et al.*, 2008; Wilson *et al.*, 2010). Aetideids in the Greenland Sea can consume upwards of 40% of vertical carbon flux (Auel, 1999), and although the simplified classical food chain depicts zooplankton as a uniform group, extensive trophic interactions take place between zooplankters. Euchaetidae are known to be voracious carnivores, exerting predation pressure not only on other copepods, but on fish eggs and larvae as well (Yen, 1983; Yen, 1987; Auel, 1999). Therefore, zooplankton interactions may influence the flux and remineralization of organic matter, as well as trophic transfer.

Despite their important ecological and biogeochemical roles, mesopelagic communities are less studied than their epipelagic counterparts due to the inherent logistical demands and costs associated with deep-water sample collection and multi-layer sample processing. Vertical examinations of zooplankton communities have been done in the Arctic's basins (e.g., Hopkins, 1969; Mumm, 1991; Kosobokova & Hirche, 2000; Auel & Hagen, 2002, Hopcroft *et al.*, 2005; Kosobokova & Hopcroft, 2010), Fram Strait and the Greenland Sea (Blachowiak-Samolyk *et al.*, 2007; Laakmann *et al.*, 2009), and for key copepods in the Amundsen Gulf (Darnis & Fortier, 2014). These efforts have inventoried mesopelagic taxa and demonstrated distinct communities associated with different water masses (Auel & Hagen, 2002; Kosobokova *et al.*, 2011; Kosobokova, 2012), as well as vertical partitioning of the water column by congeners (Auel, 1999; Laakmann *et al.*, 2009; Kosobokova & Hopcroft, 2010). Depth-stratified examinations of zooplankton communities have been carried out for other marginal Arctic seas (Eilertsen *et al.*, 1989; Kosobokova *et al.*, 1998; Arashkevich *et al.*, 2002) but only with a coarse two-layer resolution of the epipelagic realm for two transects in the Canadian Beaufort Sea (Walkusz *et al.*, 2013).

Historical efforts to document zooplankton in the Beaufort Sea are fragmented and hampered by gear biases (e.g. Johnson, 1956; McConnell, 1977), and focus on the epipelagic waters of the shelf. More recent efforts in the Alaskan and Canadian Beaufort have documented the influence of physical processes on zooplankton communities (Lane *et al.*, 2008; Darnis *et al.*, 2008; Walkusz *et al.*, 2010; Walkusz *et al.*, 2013), but also focus on the epipelagic realm. This study focuses on the mesopelagic realm of the Beaufort slope.

Methods

Study region

The Beaufort Sea is a seasonally ice-covered marginal shelf sea of the Arctic Ocean, characterized by a relatively narrow shelf and an extremely abrupt and steep continental slope. Complex physical oceanographic processes, including upwelling, eddy formation, and river plumes shape the water masses present on the shelf and slope (e.g., Carmack *et al.*, 1989; Williams & Carmack, 2008; Williams *et al.*, 2008). Distinct vertical layering of Arctic water masses is nonetheless apparent. The Polar Mixed Layer (PML) extends from the surface to between 25-50 m and is modified by freshwater input, atmospheric exchange, and freezing and melting processes (Carmack *et al.*, 1989; Lansard *et al.*, 2012). Large amounts of freshwater and terrestrial material enter the Beaufort Sea via the Mackenzie River plume, the extent and location of which is subject to physical forcing (MacDonald *et al.*, 1998; Mulligan *et al.*, 2010). The plume, along with meltwater, can form a buoyant freshwater lens that extends across much of the shelf and slope in summer months. Below the PML lies Arctic Halocline Water (AHW), extending from 50 to approximately 200 m. Additional structure within AHW is recognized and is often referred to as Bering Sea Summer Water and Bering Sea Winter Water (MacDonald *et al.*, 1989). Below the AHW is warmer and saltier Atlantic Water (AW) that begins between 200 and 300 m (Codispoti *et al.*, 2005).

Sample collection and processing

Physical, chemical and biological oceanographic data were collected along cross-shelf transects at stations ranging from 20 to 1000 m in depth during August 2013 as part of a multi-year, inter-disciplinary effort to characterize the physics and biology of the Beaufort Sea. Here we focus on the Beaufort slope (Fig. 2.1). Physical oceanographic data were sampled to a depth of 600 m with a Seabird SBE25 CTD, averaged into 1-m vertical intervals. An average value for each parameter (T, S) was calculated for each zooplankton sampling interval. Physical data (T, S) for water depths below 600 m were obtained from CTD casts conducted in the same region in 2014 with a Seabird SBE911 CTD. Water samples for chlorophyll-*a* and macro-nutrient analysis were collected with a 6-Niskin bottle SBE55 rosette attached to the CTD. Water samples were taken at the surface, 10, 20, 30, 40, and 50 m. Water for chlorophyll-*a* analysis was size-fractionated under low pressure onto Whatman GF/F filters and 20 µm polycarbonate filters, then frozen at -40 °C for post-cruise analysis following the methods of Parsons *et al.* (1984). Water for macro-nutrient analysis was filtered through 0.45 µm cellulose acetate filters and frozen immediately at -40°C for post-cruise analysis (Gordon *et al.*, 1993).

Zooplankton were sampled with a vertically-hauled Hydrobios Midi-Multinet (mouth aperture: 0.25 m^2) fitted with 150-µm mesh nets and programmed to collect stratified samples at the following depths: 0-50, 50-100, 100-200, 200-300, 300-500, 500-1000 m. Samples were preserved in 10% buffered formalin. During laboratory processing, samples were subsampled using a Folsom splitter until a given aliquot contained approximately 100 individuals of the most abundant taxa. Increasingly larger fractions were examined for larger and less abundant taxa. Organisms were identified, enumerated, measured, and staged (when appropriate) to determine community composition, abundance, and biomass. Measurements were completed using the ZoopBiom program (Roff & Hopcroft, 1986) with the biomass of organisms predicted from species-specific length-dry-weight (DW) relationships derived from the literature or from morphologically similar species (Questel *et al.*, 2013). Typically, 400-600 organisms were measured in each sample. Organisms were identified to species level when possible; indistinguishable early copepodite stages of congeneric species were grouped together.

Data processing and statistical analyses

Samples were collected primarily during the extended daylight hours of the Arctic summer; however, five stations fell during the short dark period. The literature suggests that synchronized diel vertical migration (DVM) is muted at this time of year (Cottier *et al.*, 2006; Wallace *et al.*, 2010). We compared day and night species abundances of individual species within each sampling interval (Wilcoxon test, $p < 0.05$). These analyses revealed no significant differences between day and night abundances of dominant species, with the exception of *Metridia longa* in the 0-50 m layer. Therefore, all data were pooled.

Analyses were performed separately for 4th root transformed abundance and biomass data. Community similarity was assessed using the Bray-Curtis similarity index (Bray & Curtis, 1957) and community structure was explored with a hierarchical clustering routine and Non-parametric Multi-Dimensional Scaling (nMDS) conducted in Primer (v6) (Clarke & Warwick, 2010). Statistical significance of clusters was assessed using the SIMPROF routine. Differences in the zooplankton community between water masses were assessed with a PERMANOVA using 10,000 unrestricted permutations of raw data; this method has been shown to be robust to heterogeneous dispersions and unbalanced designs that are often encountered in ecological datasets (Anderson & Walsh, 2013). Indicator species were identified for each community grouping using the Indicator Value (IndVal) function (Dufrene & Legendre, 1997) in R's labdsv software package (http://cran.r-project.org/web/packages/labdsv/index.html). Indicator Value analysis identifies indicator species based on both specificity and fidelity to a given grouping; thus the Indicator Value for a given species is maximized (1.0) when individuals of a species are observed at all sites of only one grouping. Significance of Indicator Values was assessed with Monte Carlo randomization using 10,000 permutations. We classified zooplankton taxa into trophic guilds based on published literature (Boxshall, 1985; Nishida & Ohtsuka, 1996; Mauchline *et al.*, 1998; Matsuura & Nishida, 2000; Turner *et al.*, 2001; Haro-Garay, 2003; Darnis *et al.*, 2008; Homma & Yamaguchi, 2010) to explore broadscale trophic patterns associated with depth; however, we acknowledge that feeding modes of zooplankters are quite flexible and often vary across developmental stages. Finally, we related the observed biotic community patterns to abiotic variables using Primer's BEST bio-env routine. The BEST routine relates matrices of multidimensional biological and environmental data using both forward-selection and backward-elimination techniques (Clarke & Warwick, 2010).

Results

Oceanographic conditions

The study region was highly stratified and characterized by three primary water masses: the Polar Mixed Layer (PML), Arctic Halocline Water (AHW), and Atlantic Water (AW). A thin (~10 m) and pronounced freshwater lens resulting from a mixture of Mackenzie River water and sea ice meltwater was present in the study region (Fig. 2.2a). Zooplankton samples did not resolve the freshwater lens and, therefore, represent the entire PML (0 – 50 m). The PML was characterized by a wide range of salinities (12-33) and temperatures (-1 to 9° C). AHW was characterized by colder (< 0° C) temperatures and salinity of approximately 33. At around 200 m, temperature and salinity increased, signaling the transition into waters of Atlantic origin. AW was characterized by high salinities and above-zero temperatures. Nonparametric multidimensional scaling of mean salinity and temperature in each of the zooplankton sampling intervals divided the intervals and stations by water mass type. The 0-50 m interval was characterized by the PML, the 50-100 and 100-200 m intervals were within AHW, and intervals below 200 m were all within Atlantic origin water (Fig 2.2b).

Chlorophyll-*a* and macro-nutrients

Inorganic macro-nutrients (silicate, nitrate, phosphate) were largely depleted in the upper water column during the survey period (Fig. 2.3). Silicate concentrations were elevated in surface waters at stations closest to the Mackenzie River. Nitrate was depleted in the upper 30 m, with highest concentrations observed at 40-50 m. Phosphate concentrations showed a similar pattern, exhibiting a subsurface maximum. Chlorophyll-*a* concentrations were generally low, both in the smaller (GFF) and larger (20 μm) size fractions. Overall, low macro-nutrient and chlorophyll-*a* concentrations indicate that sampling occurred after the seasonal phytoplankton bloom.

Zooplankton

General patterns

We observed 93 taxonomic categories, including 48 copepod species, 9 hydromedusae, 8 amphipod, 3 polychaete, 3 chaetognath, 2 cladoceran, 2 euphausiid, 2 ctenophore, 1 pteropod, and 1 siphonophore species (Table 2.1). We also documented various groups of meroplankton, the most common of which were polychaete and bivalve larvae. Average abundance and biomass declined with depth, with the exception of a slight increase in both parameters observed in the transition to Atlantic Water (200-300 m). In contrast, species richness increased with depth, with a maximum in the 300-500 and 500-1000 m layers (Table 2.2). Species composition was generally characteristic of Arctic waters, with the exception of several Pacific expatriates, including *Neocalanus cristatus*, *Eucalanus bungii*, *Metridia pacifica*, and *Pseudhaloptilus pacificus*. These taxa were present in extremely low abundances (< 1 ind. m^{-3}), but reflected the influence of Pacific-origin waters far into the Arctic. Copepods were dominant in all sampling intervals in terms of abundance and biomass, although their relative importance in terms of biomass declined with depth, as other groups, such as the ostracods, became important contributors (Fig. 2.4). The zooplankton community separated according to water mass (Fig. 2.5); each water mass hosted a significantly different zooplankton community (PERMANOVA; $p < 0.001$), regardless of whether abundance or biomass were used in analysis. Similarly, community structure was most highly correlated with salinity and depth, whether considered in terms of abundance (Spearman correlation (ρ): 0.84, $p < 0.01$) or biomass ($\rho = 0.81$, $p < 0.01$). The addition of temperature did not improve the model (Table 2.3).

Water mass communities

Average abundance and biomass in the PML (0-50 m) were 1150 individuals m^{-3} and 27.1 mg DW m^{-3}, respectively. We observed 42 taxa in the PML; of these taxa, seven were restricted to this layer and reflect the heavily freshened nature of the surface waters. These taxa include *Acartia bifilosa*, *Eurytemora herdmani*, *Eurytemora richsingi*, *Limnocalanus macrurus*, *Podon leuckartii*, *Evadne nordmanni*, and rotifers. Rotifers in the surface layer were largely of the genus *Synchaeta*; however, this group was under-sampled due to the mesh size used in this study. *Eurytemora* spp. was an indicator species (IndVal: 0.79, $p < 0.001$) of the freshwater influenced PML (Fig. 2.6a). Together, rotifers and cladocerans made significant numerical contributions to the community in the PML; however, their contribution to biomass was negligible. Herbivory and omnivory were the dominant feeding modes of the holozooplankton in the PML (Fig. 2.7); omnivorous *Oithona similis* dominated numerically, while large-bodied *Calanus* species dominated herbivorous biomass.

Arctic Halocline Waters (50-100 and 100-200 m) were characterized by marked decreases in average abundance (218 and 102 ind. m^{-3}) and biomass (8.6 and 5.1 mg DW m^{-3}) when compared to the overlying PML. We observed 47 taxa in the 50-100 m layer and 51 taxa in the 100-200 m layer. Three taxa were found exclusively in these layers; these taxa included the amphipods *Cyphocaris challengeri* and *Hyperia* spp., and the copepod *Metridia pacifica*. We note that these taxa, specifically the amphipods, may not actually be restricted to these layers but appear artificially scarce due to net avoidance. The community was characterized by higher abundances of the copepods *Paraeuchaeta glacialis*, *Microcalanus pygmaeus*, and *Metridia longa*. *Metridia longa* was identified as an indicator species (IndVal: 0.44, $p < 0.001$) for AHW (Fig 2.6b). Predatory biomass increased in AHW (Fig 2.7), driven largely by the chaetognath

Parasagitta elegans. The mesopelagic copepod *Spinocalanus antarcticus* emerged within this layer in low numbers.

Average abundance and biomass were lowest in the Atlantic layer (200-300, 300-500, 500-1000 m), where abundance values ranged from 127 ind. m^{-3} in the 200-300 m layer to 15 ind. m^{-3} in the 500-1000 m layer. Biomass ranged from 8.0 mg DW m^{-3} in the 200-300 m layer to 0.6 mg DW m^{-3} in the 500-1000 m layer. The Atlantic layer exhibited the highest species richness, at 49, 58, and 58 taxa found in the 200-300, 300-500, and 500-1000 m layers, respectively. Twenty-five taxa were observed exclusively in the Atlantic layer, including the copepods *Spinocalanus longicornis*, *Scaphocalanus brevicornis*, and *Neomormonilla minor*, and the decapod *Hymenodora glacialis*. *Spinocalanus longicornis* was identified as an indicator species (IndVal: 1.0, $p < 0.001$) for the Atlantic layer (Fig 2.6c). Mesopelagic copepods, including the species mentioned above and members of the Aetideidae, were important numerical contributors in this layer. Relative numerical contribution of predators peaked in AW (Fig. 2.7). Predatory biomass in the Atlantic layer was dominated by the chaetognath *Eukrohnia hamata* and cnidarians, including both siphonophores and hydrozoan medusae. Additionally, the large decapod *Hymenodora glacialis* contributed to high predatory biomass in AW. Contributions from omnivores, including copepods well adapted to utilize refractory material such as *Triconia borealis* and *Spinocalanus* spp., were also important in AW.

Arctic guild of copepods

The copepods, dominant in all depth layers, were primarily composed of an Arctic guild of taxa that included *Calanus glacialis*, *Calanus hyperboreus*, *Metridia longa*, *Oithona similis*, *Triconia borealis*, *Microcalanus pygmaeus*, and the *Pseudocalanus* species complex. This group has long been recognized as dominant in Arctic surface waters (e.g. Grainger, 1965) and is therefore referred to as the Arctic guild of copepods, despite the fact that some members are also present outside of the Arctic. This group accounted for upwards of 60% of copepod abundance and biomass in all sampling intervals, although relative contribution declined with depth. The relative contribution of this taxon guild to copepod abundance and biomass peaked in the 0-50 and 50-100 m layers, respectively (Fig. 2.8). Within the Arctic taxon guild, small-bodied *Oithona similis*, *Triconia borealis*, *Microcalanus pygmaeus*, and *Pseudocalanus* spp. dominated numerically. *Oithona similis* and *Pseudocalanus* spp. dominated the surface layer, giving way to *Triconia borealis* and *Microcalanus pygmaeus* with increasing depth. In terms of biomass, large-bodied *Calanus glacialis*, *Metridia longa*, and *Calanus hyperboreus* dominated all sampling depths, peaking in the PML, AHW, and AW, respectively (Fig. 2.9).

Mesopelagic copepods

Although present in lower abundances than the dominant guild of copepods, mesopelagic copepod families, such as Aetideidae, Heterorhabdidae, Scolecitrichidae, Spinocalanidae, and Euchaetidae, occurred in AHW and became important contributors in the Atlantic layer (Fig. 2.8). Within these families, congeners displayed different depth preferences, even within water masses (Fig. 2.10). Within the Aetideids, *Chiridius obtusifrons* exhibited a wide depth range, occurring in all sampling intervals below 50 m. *Aetideopsis* species occurred in sampling intervals below 200 m, and *Chiridiella reductella* was only encountered in the deepest sampling interval (500-1000 m). The two Heterorhabdid species observed in the study area exhibited vertical partitioning in the water column, with *Heterorhabdus norvegicus* peaking between 200 and 300 m, and *Paraheterorhabdus compactus* peaking in the 300-500 m interval. *Spinocalanus* and *Paraeuchaeta* species exhibited similar patterns within their respective genera.

Discussion

Depth-associated patterns and species inventory

Our results are consistent with the general depth-associated patterns of abundance, biomass, and species diversity observed in vertical examinations of zooplankton communities in the Arctic's basins (Hopkins, 1969; Mumm, 1991; Auel & Hagen, 2002; Kosobokova & Hopcroft, 2010; Kosobokova *et al.*, 2011). Abundance and biomass are concentrated in the upper layer of the water column and decrease with depth, while species richness increases with depth as mesopelagic genera appear. Our estimate of abundance in the PML (1150 ind. m^{-3}) is consistent with those reported for the Canada Basin by Kosobokova & Hopcroft (2010) (1170 ind. m^{-3} for 0-25 m and 1310 ind. m^{-3} for 25-50 m). Biomass estimates are also similar, with values of 27 mg DW m^{-3} (this study) and 21 and 38 mg DW m^{-3} for the 0-25 and 25-50 m intervals, respectively (Kosobokova & Hopcroft, 2010). These abundance estimates are higher than that reported in Auel & Hagen (2002) for the Nansen Basin (268 ind. m^{-3} in the 0-50 m layer), and likely reflect the fact that numerically important small-bodied taxa were less abundant in that region. We report higher average biomass values for mesopelagic layers between 100 and 500 m than reported for both the Canadian (Kosobokova & Hopcroft 2010) and Nansen basins

(Auel & Hagen 2002), consistent with the expectation that continental slopes are more productive than the deep basins (Ashjian *et al.*, 2003; Kosobokova & Hirche, 2009; Kosobokova & Hopcroft, 2010) (Table 2.4). In contrast, average biomass in the 500-1000 m interval was relatively similar across these studies. Finally, we observed a slight increase in abundance and biomass in the transition to Atlantic waters (200-300 m), as did Kosobokova and Hopcroft (2010) in the Canadian Basin. This is likely due to the fact that this layer represents a transitional zone and therefore is inhabited by the large-bodied *Calanus* species, as well as mesopelagic species, such as *Spinocalanus longicornis*.

The species composition of the Beaufort Sea slope is in agreement with studies from the Canada Basin (Kosobokova & Hopcroft, 2010; Hunt *et al.*, 2014); all confirm the dominance of a low diversity guild of Arctic copepod taxa in the epipelagic realm that gives way to increased contributions from mesopelagic taxa at depth. The presence of euryhaline taxa, such as *Eurytemora* spp. and rotifers, within the PML in our study represents an important departure from species inventories from the Arctic's basins. These euryhaline taxa reflect the dynamic nature of the shelf environment that can be profoundly influenced by seasonal freshwater inflow. The presence of rotifers in surface layers is characteristic of major river outflows, and is consistent with observations from the Laptev Sea, which is heavily influenced by numerous Siberian rivers (Abramova & Tuschling, 2005).

We report fewer taxa (93) than the 111 reported by Kosobokova and Hopcroft (2010) in the Canada Basin, likely due to our more limited sampling depth, and the use of subsampling rather than processing 100% of every sample. Thus, we did not encounter the multiple *Lucicutia* and *Mimocalanus* species that are largely restricted to depths below 1000 m. Extremely low abundances of subarctic epipelagic copepods (e.g., *Neocalanus* spp.) have been documented across the Chukchi Plateau and into Central Basin (Hopcroft *et al.*, 2005; Kosobokova & Hopcroft, 2010); our results demonstrate the penetration of these taxa into the eastern portion of the Alaskan Beaufort Sea. We also observed *Pseudhaloptilus pacificus*, a mesopelagic subarctic copepod, at one station in our survey in the 300-500 m layer. Kosobokova and Hopcroft (2010) also observed this copepod in low numbers in the Canada Basin, noting that it is also likely a Pacific expatriate despite the lack of a mechanistic explanation for the transport of deep-water copepods through the shallow Bering Strait. In contrast, Atlantic expatriates (e.g., *Calanus* *finmarchicus*) were not observed in our study region, and have rarely been observed past the Lomonosov Ridge (Thibault *et al.*, 1999; Kosobokova & Hirche, 2000).

Community structure

We observed community structure similar to other depth stratified examinations in the Arctic, characterized by gross community separation according to water mass and additional internal structure within water masses (Auel & Hagen, 2002; Kosobokova & Hopcroft, 2010; Kosobokova *et al.*, 2011). The community in the Polar Mixed Layer was composed of a fairly low-diversity group of Arctic copepods, and in the case of our study area, numerical contributions of euryhaline taxa. Carmack *et al.* (1989) note that exchange between the shelf environment and the offshore environment occurs primarily in waters above the halocline. Contributions from euryhaline taxa in the PML highlight this phenomenon; abundance of euryhaline taxa, such as *Eurytemora* spp., varied across the upper layer of the survey area due to variations in the extent of the freshwater lens. Additionally, the 0-50 m layer showed the highest variability in abundance and biomass among stations (see Table 2.2.), as has been observed in the Canada Basin (Kosobokova & Hopcroft, 2010). Thus, a given depth interval is not necessarily homogenous, especially when considering the upper layers of the hydrographically-dynamic shelf and slope. Despite these nuances, differences in community composition along a depth gradient were generally more pronounced than differences between shelf-break and slope stations. This trend also holds true on the basin-level scale; depth related differences were pronounced than those associated with latitudinal or longitudinal changes (Auel & Hagen, 2002).

Below the variable PML, the traditional guild of Arctic copepods also dominated Arctic Halocline Water; however, species richness increased as mesopelagic genera started to appear. The relative contribution of the dominant Arctic group of copepods reached a minimum in Atlantic Water, where mesopelagic copepods became significant contributors to the community. This general pattern is consistent with previous depth stratified examinations in the Arctic (Kosobokova & Hirche, 2000; Auel & Hagen, 2002; Kosobokova & Hopcroft, 2010; Kosobokova *et al.*, 2011), as is the pattern of increased omnivory and carnivory with depth. Our results also mirror observations of increased contributions from cnidarians and amphipods with depth and a peak in ostracod contribution at intermediate depths (Kosobokova & Hopcroft, 2010; Kosobokova *et al.*, 2011). Kosobokova *et al.* (2011) report presence of amphipod taxa that are traditionally considered to be ice-associated within the pelagic realm; we also documented several of such species within the water column, such as *Apherusa glacialis* and *Eusirus holmi*, supporting the previous authors' conclusion that these species may be considered pelagic transients. We also observed vertical partitioning of the water column by congeneric species, contributing to additional community structure within water masses, as reported by Auel (1999), Kosobokova and Hirche (2000), Laakmann *et al.* (2009), and Kosobokova and Hopcroft (2010). Depth ranges for species observed here were largely consistent with those studies, with many species exhibiting vertical ranges that span multiple water masses. This is not surprising, given that water mass boundary depths are not absolute.

In summary, zooplankton communities of the Beaufort Sea slope are similar in species composition, structure, and diversity to the communities in the Arctic's interior basins, with the exception of increased contributions from euryhaline and neritic taxa in surface waters, which can vary depending on the degree of exchange between the shelf and slope. Additionally, average biomass in the sampled depth intervals between 100 and 500 m seems to be higher than those reported from similar intervals in the basin, likely due to the location of our study area relative to the more productive continental shelf. Expected increases in pelagic production on continental shelves due to reduced ice cover with ongoing climatic changes (e.g., Arrigo *et al.*, 2008), may result in increased export production to mesopelagic water layers of the Beaufort Sea. This, in turn, may support higher mesopelagic zooplankton biomass, and has implications for trophic interactions, particle flux, and biogeochemical cycles. Further studies are needed to solidify our understanding of these communities, their role in biogeochemical cycles, seasonal and inter-annual variability, and processes such as diel vertical migration (DVM) and seasonal vertical migration (SVM). At the community level, faunal differences associated with diel cycling are small compared to faunal differences associated with water mass (Rabindranath *et al.*, 2011); however, DVM and SVM of zooplankton species represent a significant movement of biomass through the water column. Thus, these movements have implications for upper trophic levels that utilize these animals as prey (Fortier *et al.*, 2001; Darnis & Fortier, 2014). Due to logistical constraints we were unable sample in a manner to document patterns of DVM or SVM. Given that DVM and SVM can vary not only in time and space (Daase *et al.*, 2013), but also at the level of the individual (Hays *et al.*, 2001), future studies examining DVM and SVM in the Alaskan Arctic would be warranted.

We provide a general characterization of vertical zooplankton community structure of the Beaufort Sea slope that may be used as a backdrop against which more nuanced changes in vertical distribution patterns may be viewed. Given that assessment of mesopelagic zooplankton communities in the Arctic is still relatively rare compared to the epipelagic realm, this work makes an important contribution to the emerging library of surveys of mesopelagic zooplankton throughout the Arctic Ocean.

Figures

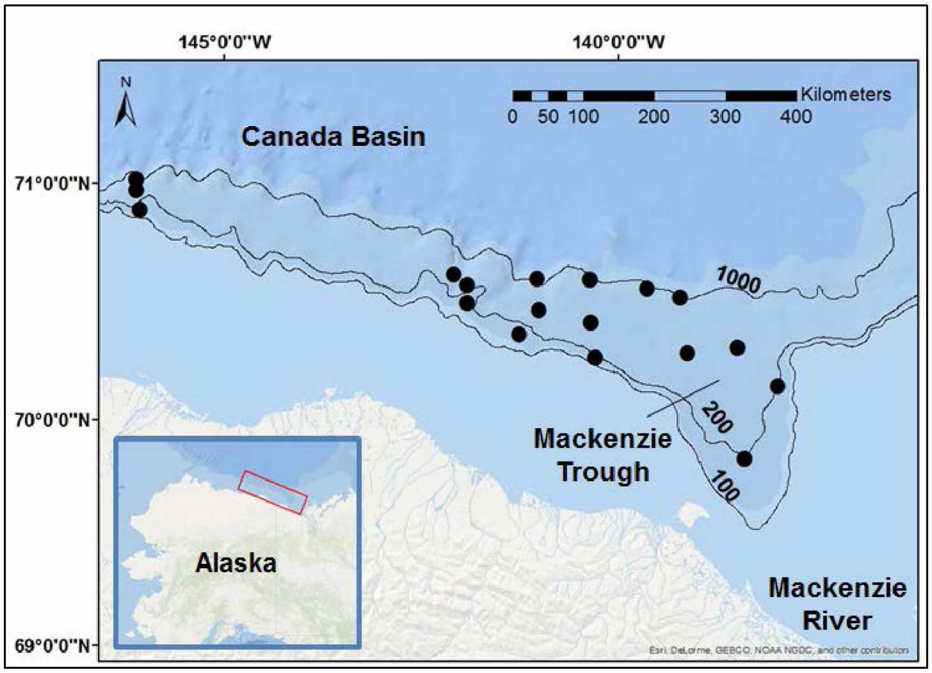

Figure 2.1. Station locations for 2013 Beaufort Sea stratified zooplankton sampling.

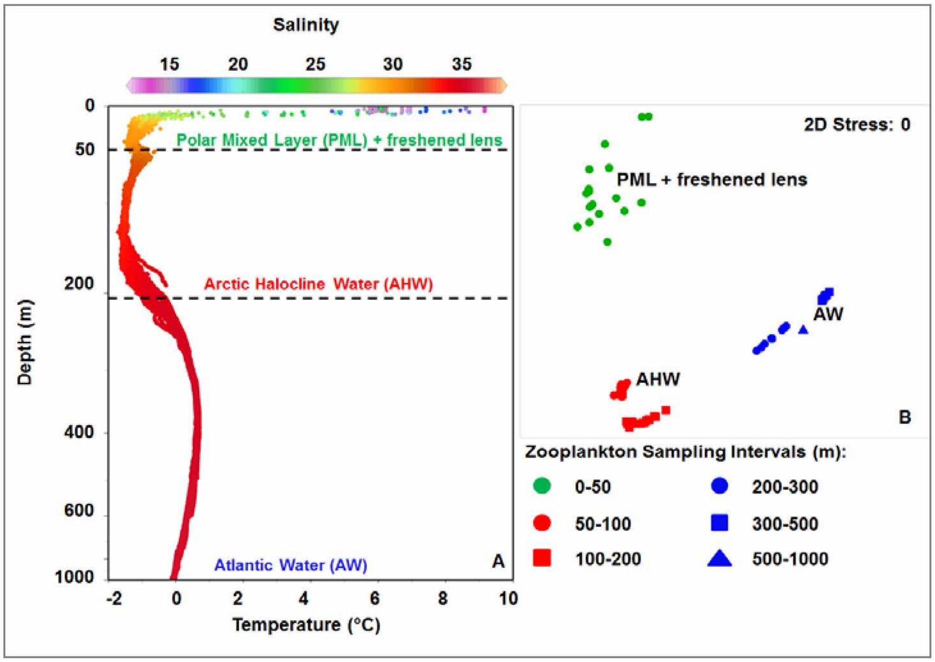

Figure 2.2. Oceanographic profiles from all 2013 Beaufort Sea slope stations. Depths below 600 m use data from 2014 cruise in same region, but show no apparent offset in value. A) Temperature and salinity profile for 2013 stations. B) Non-parametric Multidimensional Scaling (nMDS) plot of averaged T, S for each zooplankton sampling interval.

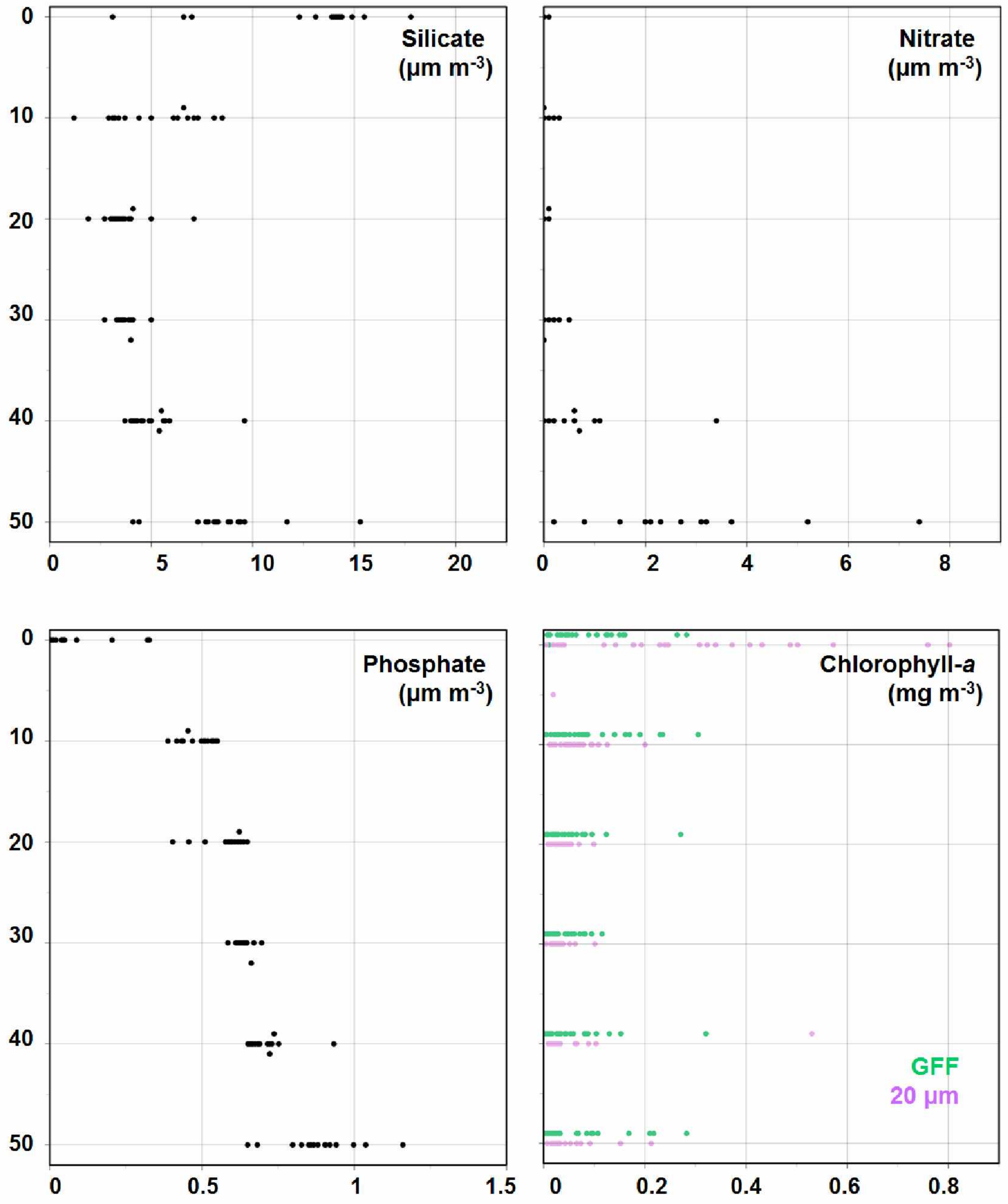

Figure 2.3. Inorganic nutrient (silicate, nitrate, phosphate) and chlorophyll-*a* concentrations in the upper 50 m of the Beaufort Sea August 2013. Chlorophyll size-fractions are offset 1 m to prevent overlap.

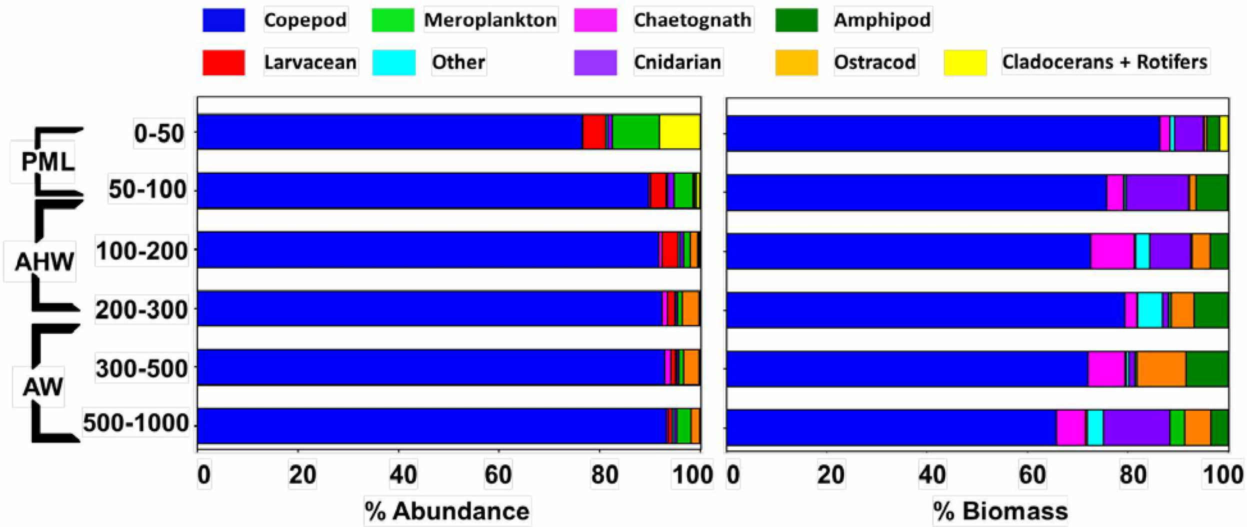

Figure 2.4. Contribution of major taxonomic groups to abundance and biomass of the zooplankton community within each sampling interval during August 2013. Water masses are noted.

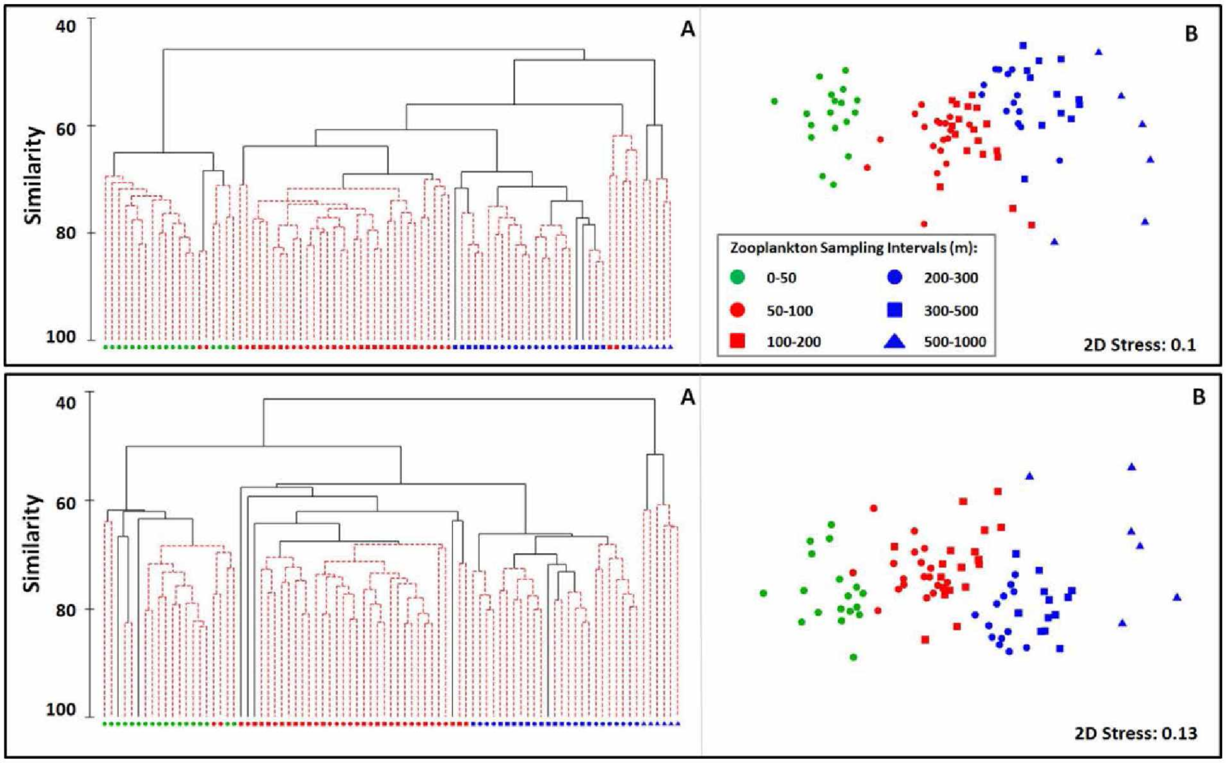

Figure 2.5. Zooplankton community structure in the Beaufort Sea during August 2013. Upper Panel is based on abundance; lower panel is based on biomass. A) Hierarchical clustering of Bray-Curtis sample similarity. Dotted lines connect samples that are not statistically unique (SIMPROF, $p<0.05$). B) Non-parametric Multidimensional Scaling (nMDS) of zooplankton community abundance overlain with observed clusters.

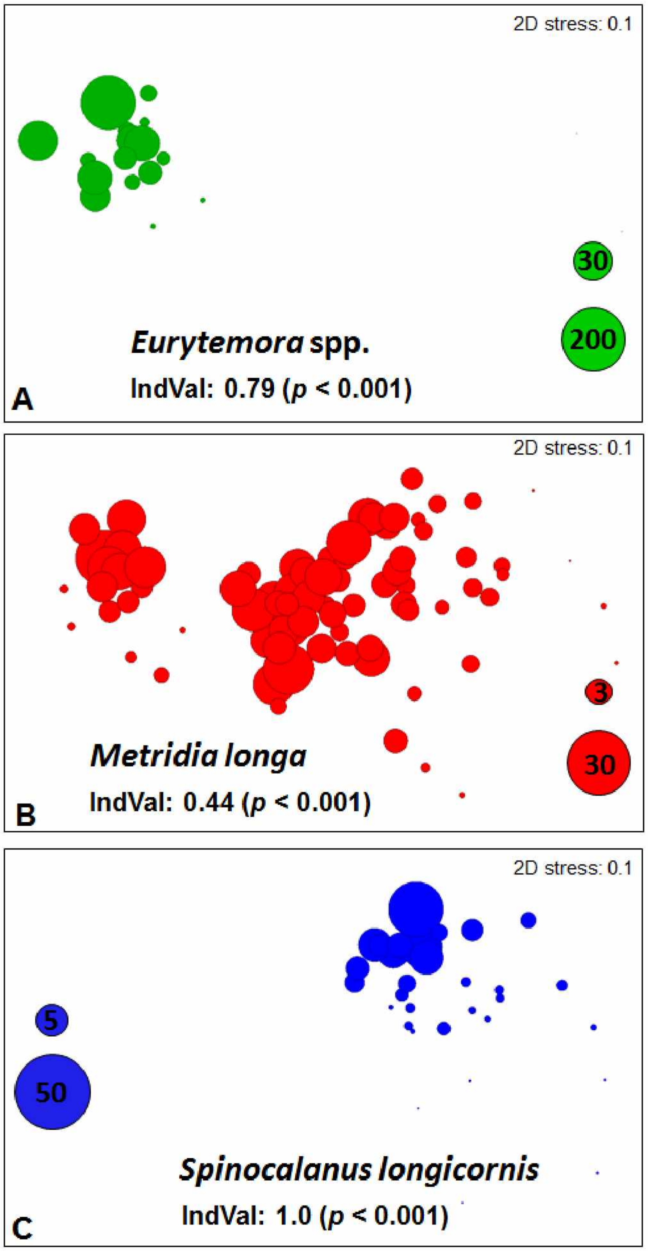

Figure 2.6. Abundance (ind. m^{-3}) of indicator species in the Beaufort Sea superimposed on nMDS plots decomposed by water masses for August 2013. A) PML B) AHW C) AW

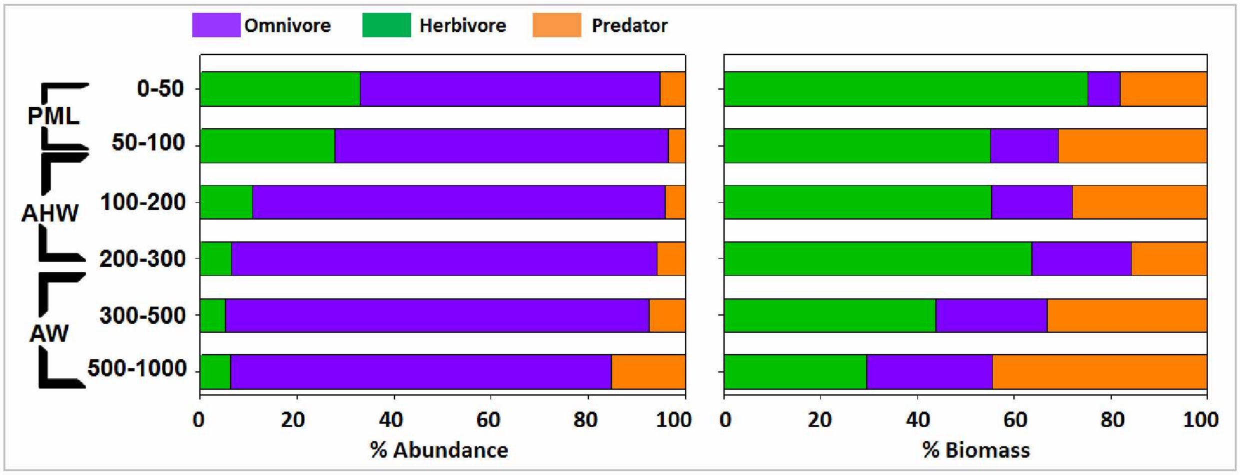

Figure 2.7. Contribution of holozooplankton trophic guilds to abundance and biomass within each sampling stratum for the Beaufort Sea during August 2013. Water masses are noted.

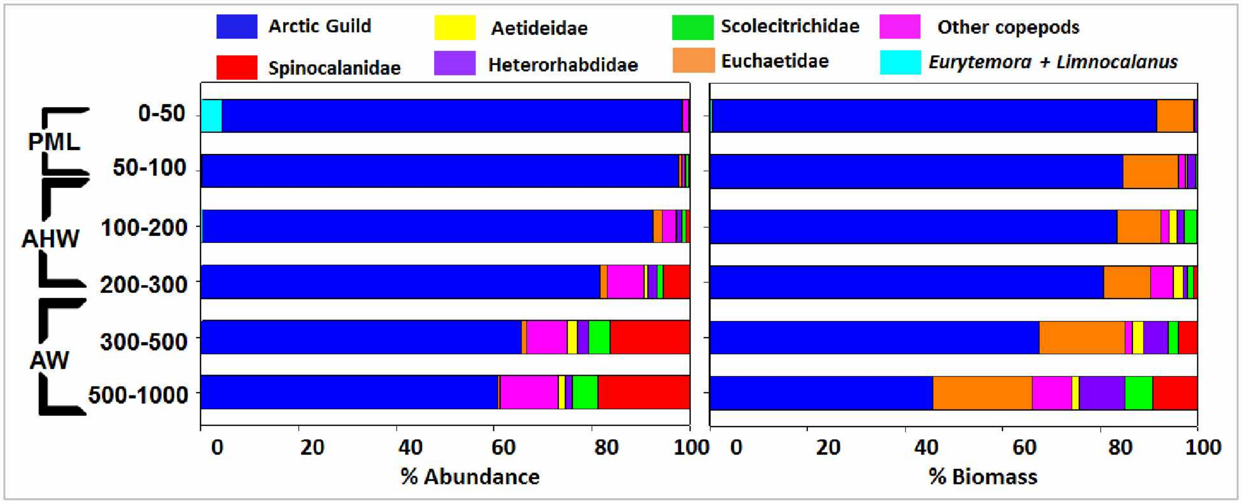

Figure 2.8. Contribution of major copepod groups to abundance and biomass within each sampling stratum interval for the Beaufort Sea during August 2013. Water masses are noted.

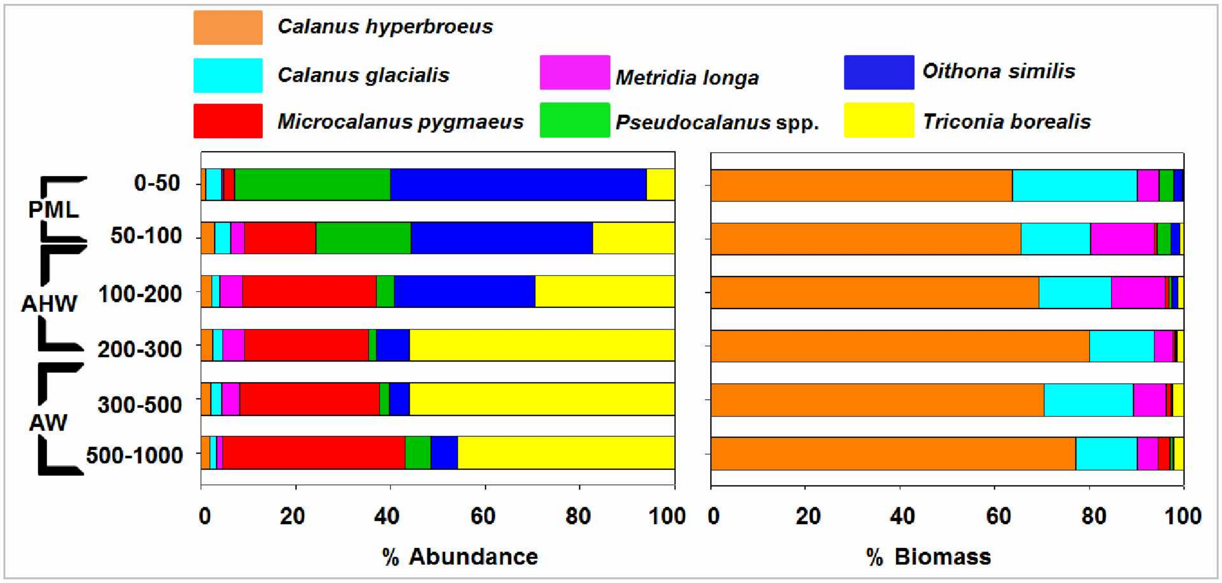

Figure 2.9. Contribution of dominant guilds of Arctic copepods to abundance and biomass within each sampling stratum for the Beaufort Sea during August 2013. Water masses are noted.

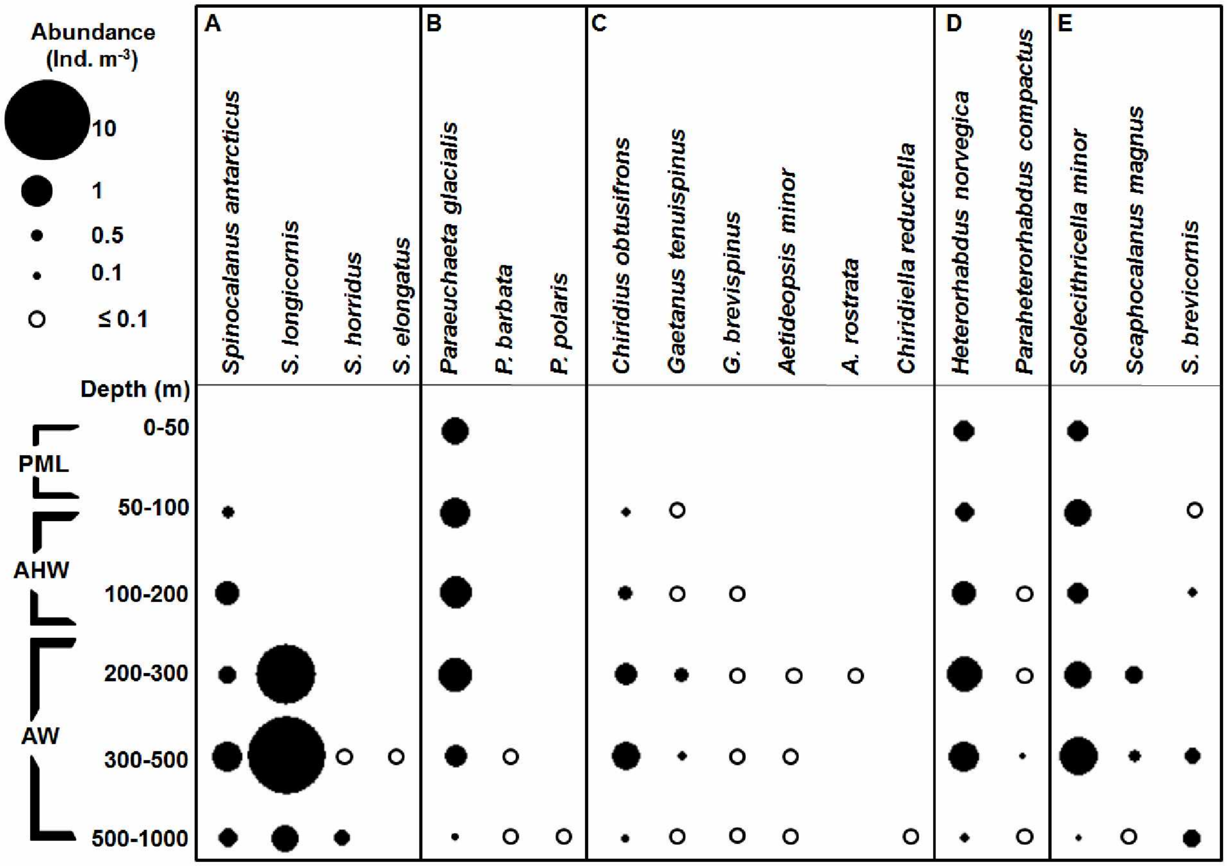

Figure 2.10. Generalized vertical distribution of select copepod species in each sampling stratum in the Beaufort Sea during August 2013. Based on mean of all stations. A) Spinocalanidae B) Euchaetidae C) Aetideidae D) Heterorhabdidae E) Scolecitrichidae

Tables

Table 2.1. Mean abundance and biomass over the entire water column for taxa observed at 2013 Beaufort Sea stations. Trophic guilds are indicated. *O* = omnivore, *P* = predator, *H* = herbivore. * indicates sampling interval where taxon was most abundant. Water masses and depth intervals (m) are noted. *Observed* indicates that taxon was encountered only a few times. – indicates average biomass <0.0001. *NC* indicates biomass was not calculated.

				PML	**AHW**		**AW**		
Guild	**Taxon**	**Avg. Abund. (ind. m^{-3})**	**Avg. Biomass (mg DW m^{-3})**	**0-50**	**50-100**	**100-200**	**200-300**	**300-500**	**500-1000**
	Calanoida								
O	*Acartia bifilosa*	0.034	0.0003	*					
O	*Acartia longiremis*	0.478	0.0028	*					
O	*Acartia* spp. (copepodite)	0.215	0.0003	*					
P	*Aetideopsis minor*	0.010	0.0011					*	
P	*Aetideopsis rostrata*	0.004	-				*		
O	*Augaptilus glacialis*	0.005	0.0024				*		
O	*Eurytemora herdmani*	0.368	0.0039	*					
O	*Eurytemora richsingi*	0.005	-	*					
O	*Eurytemora* spp. (copepodite)	5.943	0.0129	*					
H	*Calanus glacialis*	6.513	1.5557	*					
H	*Calanus hyperboreus*	3.363	5.0118	*					
P	*Chiridiella reductella*	Trace	-						*
O	*Chiridius obtusifrons*	0.414	0.0365					*	
H	*Eucalanus bungii*	Observed	-		*				
P	*Gaetanus brevispinus*	0.007	0.0029						*
P	*Gaetanus tenuispinus*	0.090	0.0139				*		
P	*Gaetanus* spp. (copepodite)	0.047	0.0007				*		
O	*Haloptilus acutifrons*	0.011	0.0010						
P	*Heterorhabdus norvegica*	0.960	0.1107					*	
H	*Jaschnovia tolli*	0.026	0.0016		*				
C	*Limnocalanus macrurus*	0.068	0.0019	*					
O	*Metridia longa*	3.702	0.4940		*				
O	*Metridia pacfica*	Observed	-						
O	*Metridia* spp. (copepodite)	2.639	0.0180			*			
O	*Microcalanus pygmaeus*	18.640	0.0215		*				
H	*Neocalanus cristatus*	0.012	0.0816				*		
P	*Paraeuchaeta glacialis*	1.135	0.5840			*			
P	*Paraeuchaeta barbata*	0.001	0.0066						*
P	*Paraeuchaeta polaris*	Observed	0.0005						*
P	*Paraheterorhabdus compactus*	0.024	0.0039					*	
H	*Pseudhaloptilus pacificus*	Observed	-						*

Table. 2.1, continued

H	***Pseudocalanus acuspes***	**0.514**	**0.0054**	*					
H	*Pseudocalanus newmani*	0.225	0.0012	*					
H	*Pseudocalanus mimus*	0.006	0.0001		*				
H	*Pseudocalanus minutus*	0.814	0.0119	*					
H	*Pseudocalanus* spp. (copepodite)	39.527	0.1350	*					
H	*Pseudocalanus* spp. (male)	0.427	0.0025	*					
O	*Scaphocalanus magnus*	0.181	0.0646				*		
O	*Scaphocalanus brevicornis*	0.106	0.0031						*
O	*Scolecithricella minor*	1.063	0.0058					*	
O	*Spinocalanus elongatus*	0.003	-					*	
O	*Spinocalanus horridus*	0.031	0.0010						*
O	*Spinocalanus longicornis*	2.552	0.0175					*	
O	*Spinocalanus antarcticus*	0.544	0.0149					*	
O	*Spinocalanus* spp. (copepodite)	0.046	0.0004					*	
O	*Tharybis groenlandica*	Observed	-						*
O	*Temorites brevis*	0.031	0.0007					*	
P	*Tortanus discaudata*	0.026	0.0014	*					
O	*Undinella oblonga*	0.001	0.0001					*	
	Monstrilloida								
Pa	*Monstrilla* spp.	Observed	-					*	
	Cyclopoida								
O	*Oithona similis*	87.520	0.0854	*					
	Poecilostomatoida								
	Atrophia glacialis	0.007	-						*
O	*Triconia borealis*	32.616	0.0497				*		
	Harpacticoida								
	Harpacticoid unk.	0.038	0.0001	*					
O	*Microsetella norvegica*	0.494	0.0017	*					
	Mormonilloida								
P	*Neomormonilla minor*	0.303	0.0020						*
	Copepod Nauplii								
H	*Calanoid nauplii*	56.426	0.0389	*					
H	*Cyclopoid nauplii*	1.467	0.0002	*					
	Appendicularia								
O	*Fritillaria borealis*	5.232	0.0002	*					
O	*Oikopleura vanhoeffeni*	1.131	0.0101	*					
	Chaetognatha								
P	*Eukrohnia hamata*	0.354	0.1120				*		
P	*Parasagitta elegans*	0.632	0.1492	*					
P	*Pseudosagitta maxima*	0.078	0.0052					*	
	Pteropoda								

Table 2.1, continued

H	***Limacina helicina***	**0.266**	**0.0303**	*					
	Cladocera								
P	*Evadne nordmanni*	0.069	0.0008	*					
P	*Podon leuckartii*	5.502	0.0203	*					
	Ostracoda								
O	*Boroecia maxima*	2.051	0.2398				*		
	Mysidae								
O	*Mysis spp.*	0.001	0.0064			*			
O	*Mysis oculata*	0.001	0.0190				*		
	Euphausiacea								
H	*Thysanoessa inermis*	0.003	0.0235	*					
H	*Thysanoessa raschii*	0.010	0.0154	*					
	Decapoda								
O	*Hymenodora glacialis*	0.001	0.0042						*
	Amphipoda								
	Amphipod unk.	0.043	0.0308						
O	*Apherusa glacialis*	0.001	0.0053					*	
P	*Cyphocaris challengeri*	0.002	0.0164			*			
P	*Eusirus holmi*	0.001	0.0590				*		
P	*Hyperia galba/medusarum*	0.001	0.0044			*			
H	*Onisimus* spp.	0.005	0.0004			*			
P	*Themisto abyssorum*	0.305	0.1255		*				
P	*Themisto libellula*	0.065	0.2073	*					
H	*Scina* spp.	Observed	-					*	
	Isopoda								
O	Isopoda (parasitic)	0.047	-		*				
	Siphonophora								
P	*Dimophyes arctica*	0.102	0.0169				*		
	Siphonophora unk.	0.009	0.0010				*		
	Ctenophora								
P	*Beroe cucumis*	0.001	0.0110		*				
P	*Mertensia ovum*	0.001	0.0035	*					
	Hydrozoa								
P	*Aglantha digitale*	1.649	0.5781	*					
P	*Obelia longissima*	0.036	0.0064	*					
P	*Aeginopsis laurentii*	0.014	0.0097			*			
P	*Sarsia tubulosa*	Observed	-						*
P	*Melicertum octopunctata*	0.001	-		*				
P	*Halitholus cirratus*	0.001	0.0028					*	
P	*Ptychogena* spp.	0.001	-		*				
P	*Sminthea arctica*	Observed	-						*

Table 2.1, continued

P	***Botrynema brucei***	**Observed**	-						*
	Annelida								
O	*Tomopteris septentrionalis*	0.012	0.0030						*
O	*Pelagobia longicirrata*	0.001	-						*
O	*Typhoscolex muelleri*	Observed	-						*
	Rotifera								
H	*Synchaeta* spp.	20.460	NC	*					
	Meroplankton								
	Gastropod larvae	0.087	0.0001	*					
	Cyphonautes	0.024	-	*					
	Polychaete larvae	7.908	0.0188	*					
	Echinoderm larvae	0.122	-	*					
	Bipinaria	0.277	0.0003	*					
	Megalopa	0.005	0.0069			*			
	Bivalve larvae	0.581	0.0002	*					
	Decapod zoea	0.028	0.0003		*				
	Barnacle cypris	0.028	0.0001		*				
	Barnacle nauplii	0.059	-		*				

Table 2.2. Mean abundance, biomass and species richness of the zooplankton community in each sampling strata for the Beaufort Sea during August 2013. Water masses are noted.

Water Mass	**Sampling Interval (m)**	**Average abundance (Ind. m^{-3})**	**Average biomass (mg DW m^{-3})**	**Species Richness**
PML	0-50	1150 ± 83	27.1 ± 3.0	42
AHW	50-100	218 ± 43	8.6 ±1.3	47
AHW	100-200	102 ± 14	5.1 ± 0.7	51
AW	200-300	127 ± 22	8.0 ± 1.2	49
AW	300-500	76 ± 20	3.3 ±0.5	58
AW	500-1000	15 ± 8	0.6 ± 0.1	58

Table 2.3. Relationship between zooplankton community structure and environmental variables during August 2013, as revealed by BEST analysis for Temperature (*T*), Salinity (*S*), and Depth (*D*). * Indicates best variable combination explaining observed zooplankton community structure.

No. Variables	BEST variable combinations (Spearman Rank Correlation)		
Abundance			
2	***S,D***	***S,T***	***T,D***
	0.84*	0.67	0.58
3	***S,D,T***		
	0.78		
Biomass			
2	***S, D***	***T,D***	***S,T***
	0.81*	0.62	0.62
3	***S, T, D***		
	0.77		

Table 2.4. Comparison of average biomass (mg DW m^{-3}) in zooplankton sampling intervals from the Beaufort slope and the Arctic's basins.

	Biomass (mg DW m^{-3})		
Layer (m)	**This study**	**Kosobokova & Hopcroft, 2010**	**Auel & Hagen, 1999**
0-25	27.1	21	20.9
25-50		38	
50-100	8.6	8.8	3.3
100-200	5.1	2.6	
200-300	8	3.8	0.6
300-500	3.3	2.2	
500-1000	0.6	0.8	0.5

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General Conclusion

Structure in pelagic marine communities is generated through a complex blending of abiotic and biotic variables that operate and interact on different spatial and temporal scales (Angel, 1993). Species pools are shaped by geological history, large-scale circulation regimes, and zoogeographical barriers. At a finer scale, species composition and diversity are influenced by these factors, as well as by more localized physical forcing factors, such as freshwater influence, depth, stratification, upwelling events, and other physical parameters. These factors combine to form ecological zones that are inhabited by a characteristic assemblage of species (e.g., Lane *et al.*, 2008; Walkusz *et al.*, 2010; Kosobokova *et al.*, 2011). Within these ecological zones, fine-scale community structure is influenced by complex biological interactions, including competition, predation, and partitioning of resources (e.g., Auel, 1999).

The findings herein present a shelf-scale examination of zooplankton communities of the Beaufort Sea and demonstrate that zooplankton communities are shaped by the distribution of water masses and their associated physical properties. Distinct zooplankton communities were associated with different epipelagic physical habitats produced by hydrographic conditions in the Beaufort Sea from 2010-13. A low-diversity guild of Arctic copepods dominated the community in all zones for all field years. The relative contribution of individual species within this guild, as well as other less abundant taxa, resulted in a zooplankton community whose faunal character reflected the underlying oceanography of its respective ecological zone. Generally, the western Beaufort around Point Barrow represents a transitional zone between the Pacific-affinity communities of the Chukchi Sea and the more Arctic faunal character of the Beaufort Sea. Moving eastward along the shelf, Pacific influence diminishes substantially. The eastern Beaufort is more estuarine in faunal character due to the influence of the Mackenzie River. These along-shelf gradients intersect across-shelf gradients transitioning from neritic environments dominated by *Pseudocalanus* spp., to more oceanic environments dominated by species such as *Calanus hyperboreus* and *Microcalanus pygmaeus*. The Mackenzie River causes additional across-shelf structure associated with the plume extent and the existence of plume-associated assemblages that include euryhaline and brackish species. These broad gradients can be disrupted on a more local scale by events such as upwelling or eddy formation.

Oceanic communities exhibited depth-associated community gradients, resulting in distinct zooplankton assemblages in the three vertically layered water masses in the Beaufort

Sea. The traditional guild of Arctic copepods dominates surface layers, giving way to contributions from mesopelagic genera at depth. Abundance and biomass were highest in surface layers; however, mesopelagic layers contained higher species diversity. Within a given water mass, zooplankton communities exhibited internal structure associated with species-specific depth preferences and vertical partitioning of the water column by congeners. Finally, depth-associated gradients intersect with both along- and across-shelf gradients, resulting in heterogeneous hydrography and biology within a given depth interval. This intersection is particularly pronounced in the upper portion of the water column where exchange between the inshore and offshore environments occurs (Carmack *et al*., 1989).

This work provides the most spatially comprehensive survey of epipelagic zooplankton communities of the Beaufort Sea to date; my results provide a modern reference point for community composition and magnitude, and may be compared with future community assessments as the Arctic continues to experience climate change and increased industrial activity. Additionally, these results provide the first detailed examination of mesopelagic communities of the Beaufort Sea slope ranging from the surface to 1000 m depth. This work highlights the complexity of the Beaufort Sea ecosystem, provides a framework from which future work to assess inter-annual variability and seasonal evolution in Beaufort Sea zooplankton communities may be viewed, and provides foundational information from which more process-oriented studies may be developed.

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