Depth-stratified community structure of Beaufort Sea slope zooplankton and its relations to water masses

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Depth-stratified samples were collected along the Beaufort Sea slope during August and September 2012–2014 to characterize the vertical structure of zooplankton communities from 0 to 1000 m. We documented 95 holoplanktonic categories (88 species, 5 genera, 1 order and 1 phylum); greatest diversity was observed in the copepods (51 species and 1 genus), followed by the cnidarians (11 species and 1 genus) and amphipods (7 species and 3 genera). Distinct communities were associated with the main water masses in the study region: the Polar Mixed Layer (PML; 0–50 m), Arctic Halocline Water (50–200 m) and Atlantic Water (AW; 200–1000 m). Average abundance and biomass were highest in the PML (1230 ind. m^{-3} and 24.3 mg DW m^{-3}, respectively) and declined to a minimum in AW (22 ind. m^{-3} and 1.9 mg DW m^{-3}, respectively). Copepods dominated in the PML, with *Calanus* species, *Oithona similis*, *Metridia longa*, *Triconia borealis*, *Microcalanus pygmaeus* and *Pseudocalanus* spp. contributing more than 80% of copepod abundance and biomass. Mesopelagic copepods were important contributors to the AW community, which exhibited the highest species richness. Community structure was highly correlated with salinity and depth. We report similar species composition but higher biomass when compared with the interior basins, likely due to elevated coastal production.

KEYWORDS: Arctic; Beaufort Sea; mesopelagic

INTRODUCTION

In addition to their widely recognized role as trophic 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; Robinson *et al.,* 2010; Wilson *et al.,* 2010).

Omnivory and carnivory generally increase in importance with depth (Auel and 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 also on fish eggs and larvae (Yen, 1983, 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 and Hirche, 2000; Auel and Hagen, 2002, Hopcroft et al., 2005; Kosobokova and 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 and Fortier, 2014). These efforts have inventoried mesopelagic taxa and demonstrated distinct communities associated with different water masses (Auel and 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 and 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). 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 (Darnis et al., 2008; Lane et al., 2008; Walkusz et al., 2010) and used depth-stratified sampling techniques (Walkusz et al., 2013; Smoot and Hopcroft, in press), and also focus on the epipelagic realm. This study aims to characterize epipelagic and mesopelagic zooplankton communities of the Beaufort Sea slope, identify environmental variables that structure these communities, and examine species–water mass associations.

METHOD

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 and 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 and 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 into 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 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); the transition to AW occurs between 200 and 300 m (Codispoti et al., 2005).

Sample collection and processing

Physical, chemical and biological data were collected along cross-shelf transects at stations ranging from 20 to 1000 m in depth during August and September 2012–2014 as part of the US–Canada Transboundary Fish and Lower Trophic Levels project, a multi-year, interdisciplinary effort to characterize the physics and biology of the Beaufort Sea. Here, we focus on the Beaufort Sea slope (Fig. 1). Physical oceanographic data were collected with a Seabird SBE25 CTD to a depth of 600 m (2012 and 2013) or SBE911+ to a depth of 1000 m (2014) and averaged into 1 m vertical intervals.

Zooplankton were sampled with a vertically hauled HYDRO-BIOS Multiple Plankton Sampler MultiNet, type Midi (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 and 500–1000 m. Samples were preserved in 5% buffered formalin. During the laboratory processing, the samples were subsampled using a
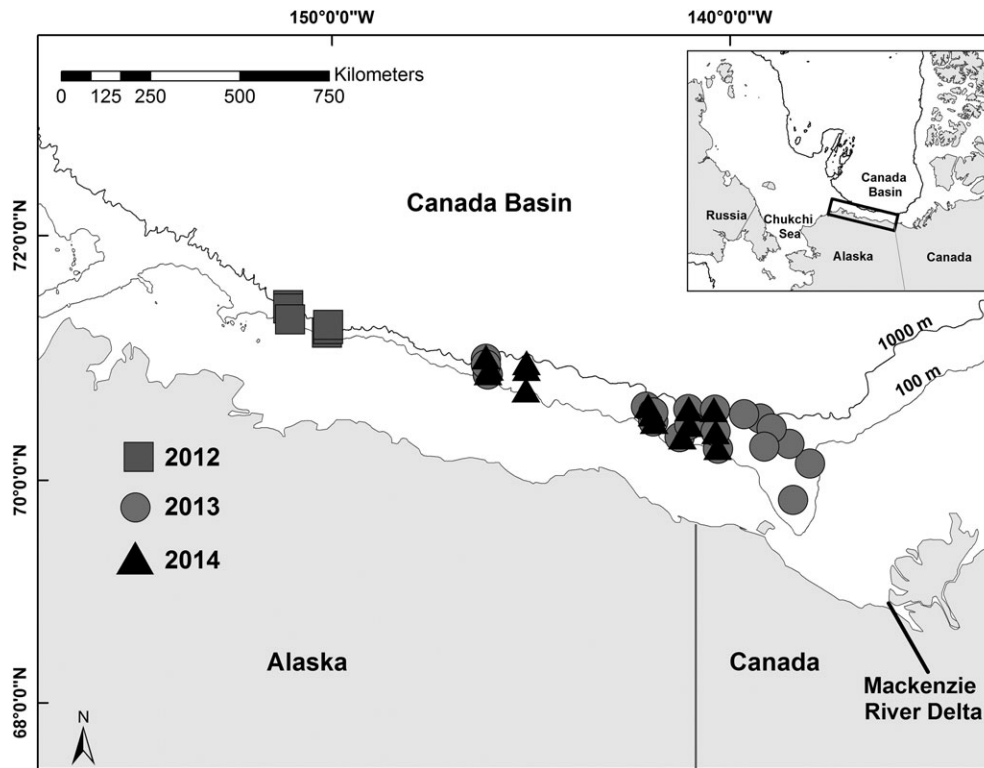
Fig. 1. Station locations for stratified zooplankton sampling in the Beaufort Sea during 2012–2014.

Folsom splitter until a given aliquot contained ~100 individuals of the most abundant taxa. Increasingly, larger fractions were examined for larger and less abundant taxa. Organisms were identified, enumerated and measured to determine community composition, abundance and biomass. Additionally, copepods were categorized according to the developmental stage (CIV, adult female and adult male). Measurements were completed using the ZoopBiom program (Roff and Hopcroft, 1986), a program that estimates the biomass of organisms based on species-specific length–dry weight (DW) relationships derived from the literature or from the 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 (CI–CIV) were grouped together.

Data processing and statistical analyses

Samples were collected primarily during the extended daylight hours of the Arctic summer; however, a subset of stations fell during the short dark period. The literature suggests that synchronized diel vertical migration (DVM) is less pronounced at this time of year (Cottier *et al.*, 2006; Wallace *et al.*, 2010). We compared day and night abundances for the 20 most abundant holoplanktonic taxa within each sampling interval (Wilcoxon test, $P < 0.05$). These analyses revealed no significant differences between day and night, with the exception of *Metridia longa* in the 200–300 m layer. Therefore, all data were pooled.

Analyses were performed separately for fourth root transformed abundance and biomass matrices (183 samples × 147 taxonomic categories). Community similarity was assessed using the Bray–Curtis similarity index (Bray and Curtis, 1957) and community structure was explored with a hierarchical clustering routine and nonparametric multidimensional scaling (nMDS) conducted in Primer (v6) (Clarke and Warwick, 2010). Statistical significance of clusters was assessed using the SIMPROF routine. The differences in the zooplankton community between water masses and depth layers 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 data sets (Anderson and Walsh, 2013). Indicator species were identified for each water mass using the Indicator Value (IndVal) function (Dufrene and Legendre, 1997) in R's labdsv software package. IndVal analysis identifies indicator species based on both the specificity and fidelity to

a given grouping; thus, the IndVal for a given species is maximized (1.0) when individuals of a species are observed at all sites of only one grouping. Significance of IndVals was assessed with Monte Carlo randomization using 10 000 permutations. We classified zooplankton taxa into trophic guilds based on the published literatures (Boxshall, 1985; Nishida and Ohtsuka, 1996; Mauchline *et al.*, 1998; Matsuura and Nishida, 2000; Turner *et al.*, 2001; Haro-Garay, 2003; Darnis *et al.*, 2008; Homma and 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 the developmental stages. Finally, we related the observed biotic community patterns to abiotic variables. A mean value for temperature and salinity was calculated at each station for each zooplankton sampling interval. Temperature and salinity values from 2014 were used for the deepest interval in 2012 and 2013. Primer's BEST bio-env routine was used to examine the relationship between the zooplankton community and hydrographic characteristics. The BEST routine relates matrices of multidimensional biological and environmental data using both forward-selection and backward-elimination techniques (Clarke and Warwick, 2010). Hereafter, "Arctic guild" refers to *Calanus hyperboreus*, *Calanus glacialis*, *M. longa*, *Oithona similis*, *Triconia borealis*, *Microcalanus pygmaeus* and *Pseudocalanus* spp. Although some of these taxa are pre-

sent outside of the Arctic, this group of copepods has long been recognized as dominant in surface waters of the Arctic (Grainger 1965).

RESULTS

Oceanographic conditions

The study region was characterized by three primary water masses in all surveys: the PML, AHW and AW (Fig. 2). The PML exhibited extreme ranges in temperature and salinity across the survey years, demonstrating the variable physical conditions that zooplankters within the surface layer experience. 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 in 2013, with surface salinies as low as 12. AHW was characterized by colder (<0°C) temperatures and salinity of ~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. nMDS of mean salinity and temperature in each of the zooplankton sampling intervals divided the samples 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 the intervals below 200 m were all within Atlantic origin water (Fig. 2).
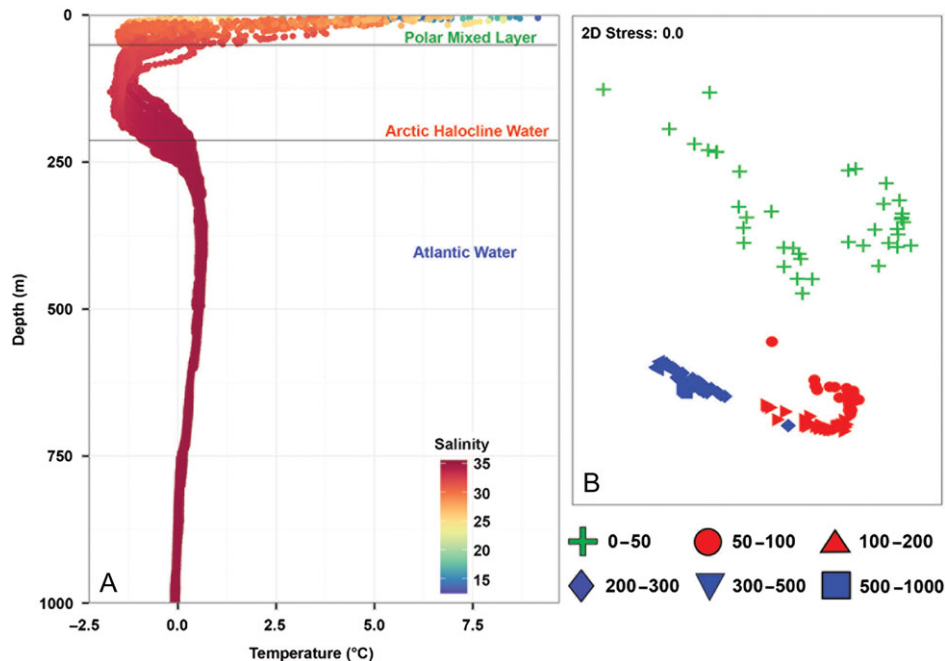
Fig. 2. Oceanographic profiles from Beaufort Sea slope stations 2012–2014. (**A**) Temperature and salinity profile and (**B**) nMDS plot of averaged *T*, *S* for each zooplankton sampling interval (m).

Table I: Mean abundance, biomass and species richness of the zooplankton community in each sampling strata for the Beaufort Sea 2012–2014

Water mass	Depth interval (m)	Mean abundance (ind. m^{-3}) ± SE	Mean biomass (mg DW m^{-3}) ± SE	Species richness
PML	0–50	1230 ± 84	24.3 ± 3.4	56
AHW	50–100	257 ± 35	12.8 ± 1.9	59
AHW	100–200	102 ± 9	8.3 ± 1.7	68
AW	200–300	104 ± 12	10.0 ± 1.2	61
AW	300–500	81 ± 11	7.1 ± 1.2	74
AW	500–1000	22 ± 6	1.9 ± 0.7	71

Water masses are noted.

Zooplankton

General patterns

We observed 95 holoplanktonic categories (88 species, 5 genera, 1 order and 1 phylum), with the highest species richness in the copepods (51 species and 1 genus), followed by the hydromedusae (9 species and 1 genus) and the amphipods (7 species and 3 genera). We also observed numerous meroplanktonic categories (Supplementary Table S1); we documented various groups of meroplankton, the most common of which were polychaeta and bivalvia larvae. Average abundance and biomass declined with depth, with the exception of a slight increase in both community characteristics observed in the transition to AW (200–300 m). In contrast, species richness increased with depth, with a maximum in the 300–500 m layer (Table I). In addition to the dominant Arctic guild of copepods, we also observed 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. 3). The zooplankton community separated according to water mass (Fig. 4); each water mass hosted a significantly different zooplankton communities (PERMANOVA; $P < 0.001$), regardless of whether abundance or biomass was used in the analysis. In addition, each sampling stratum also hosted significantly different zooplankton communities, indicating additional biological structure within both the AHW and AW. Community structure was most highly correlated with salinity and depth, whether considered in terms of abundance (BEST Routine; Spearman correlation (ρ): 0.76, $P < 0.01$) or biomass ($\rho = 0.67$, $P < 0.01$). The addition of temperature did not improve the model (Table II).
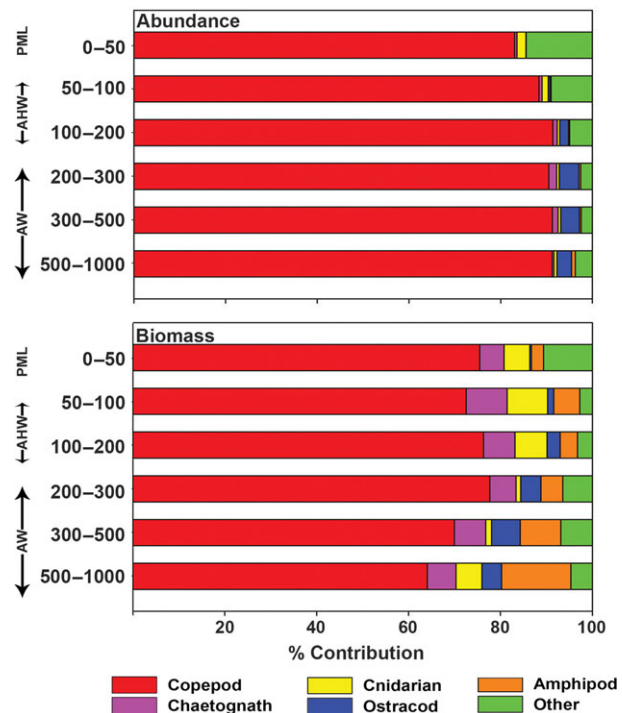

Fig. 3. Contribution of major taxonomic groups to abundance and biomass of the zooplankton community within each sampling interval (m). Water masses are noted.

Water mass communities

Average abundance and biomass in the PML (0–50 m) were 1230 ind. m^{-3} and 24.3 mg DW m^{-3}, respectively. We observed 56 taxa in the PML; of these taxa, 7 were restricted to this layer and reflect the heavily freshened nature of the surface waters in 2013. These taxa include *Acartia bifilosa*, *Eurytemora herdmani*, *Eurytemora richingsi*, *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. *Oithona similis* (IndVal: 0.90, $P < 0.01$) and *Pseudocalanus* spp.
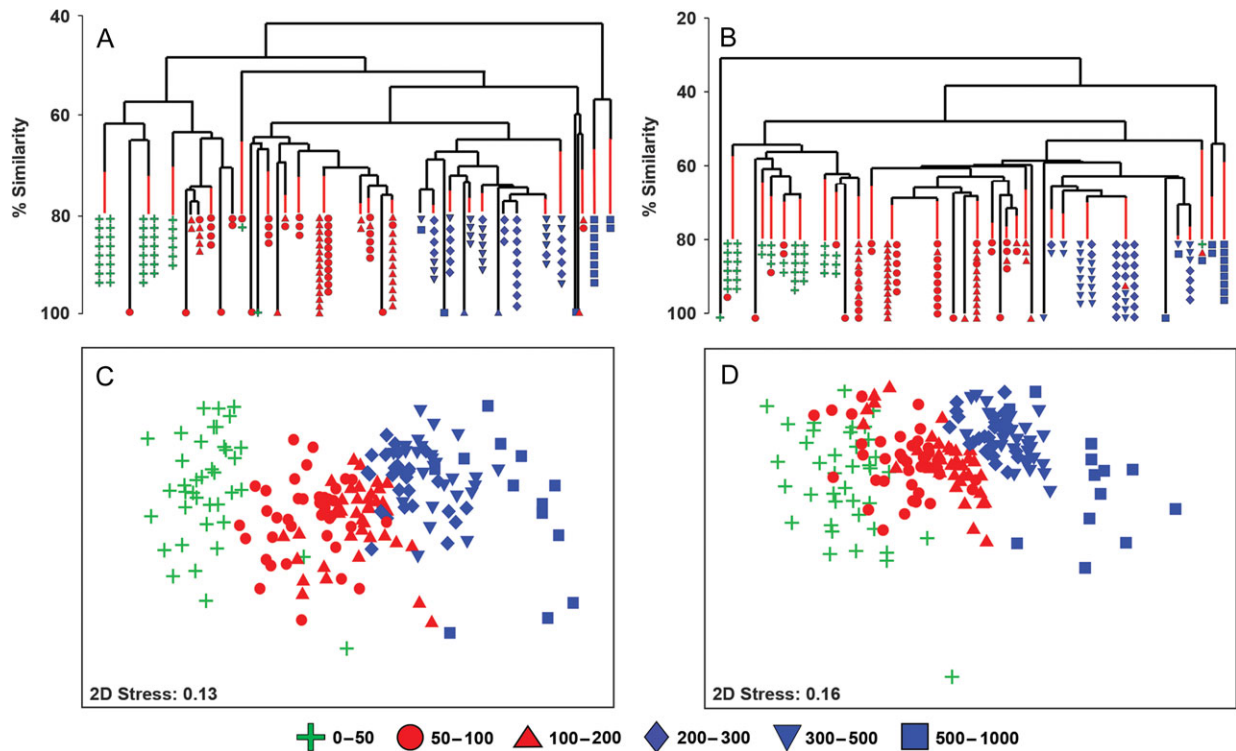
Fig. 4. Top panel: Hierarchical clustering of Bray–Curtis sample similarity using abundance (**A**) and biomass (**B**). Black lines indicate statistically distinct (SIMPROF, $P < 0.05$) clusters; red lines indicate intervals where clusters are not yet distinct. Clusters with similarity >80% or lack of statistical distinction are not shown; the number of samples clustering below this level is represented by depth-coded symbols. Statistically distinct samples failing to cluster are extended to the axis. Bottom panel: nMDS of abundance (**C**) and biomass (**D**) overlain with observed clusters.

*Table II: Relationship between zooplankton community structure and environmental variables, as revealed by BEST analysis for temperature (*T*), salinity (*S*) and depth (*D*)*

No. variables	BEST variable combinations (Spearman rank correlation)		
Abundance			
2	*S, D*	*S, T*	*T, D*
	0.76[a]	0.61	0.56
3	*S,D,T*		
	0.73		
Biomass			
2	*S, D*	*T, D*	*S, T*
	0.67[a]	0.56	0.52
3	*S, T, D*		
	0.66		

[a]Best variable combination explaining observed zooplankton community structure.

(IndVal: 0.90, $P < 0.01$) were the two top indicator taxa for the PML (Fig. 5). Herbivory and omnivory were the dominant feeding modes of the holozooplankton in the PML; omnivorous *O. similis* dominated numerically, while large-bodied *Calanus* species dominated herbivorous biomass.

AHWs (50–100 and 100–200 m) were characterized by marked decreases in average abundance (257 and 102 ind. m^{-3}) and biomass (12.8 and 8.3 mg DW m^{-3}) when compared with the overlying PML. We observed 59 taxa in the 50–100 m layer and 68 taxa in the 100–200 m layer. Three taxa were found exclusively in these layers; these taxa included the amphipods *Cyphocaris challengeri* and *Hyperia* sp., and the copepod *M. 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*, *M. pygmaeus* and *M. longa* when compared with the PML. *Microcalanus pygmaeus* (IndVal: 0.44, $P < 0.01$) and *P. glacialis* (IndVal: 0.41, $P < 0.01$) were identified as indicator species for AHW (Fig. 5). The biomass of predatory zooplankton increased in AHW, driven largely by the chaetognath *Parasagitta elegans*. The mesopelagic copepod *Spinocalanus antarcticus* emerged within this layer in low numbers.
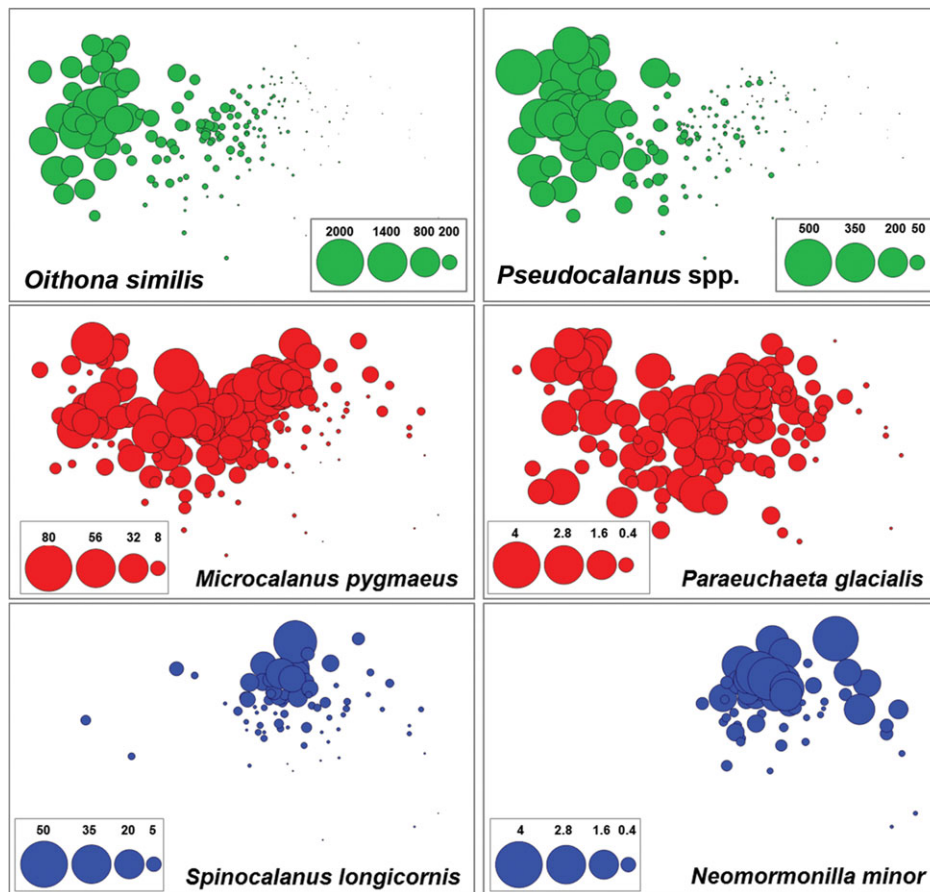
Fig. 5. Abundance (ind. m^{-3}) of top two indicator species for each water mass superimposed on nMDS abundance plot (see Fig. 4C) decomposed by water masses: PML (top), AHW (middle) and AW (bottom). Bubble size is proportional to species abundance. Therefore, if the indicator taxon was not present in a given sample, the corresponding point is not represented on the nMDS plot.

Average abundance and biomass were lowest in the Atlantic layer (200–300, 300–500 and 500–1000 m), where the abundance values ranged from 103 ind. m^{-3} in the 200–300 m layer to 22 ind. m^{-3} in the 500–1000 m layer. Biomass ranged from 10.0 mg DW m^{-3} in the 200–300 m layer to 1.9 mg DW m^{-3} in the 500–1000 m layer. The Atlantic layer exhibited the highest species richness, with 61, 74 and 71 taxa found in the 200–300, 300–500 and 500–1000 m layers, respectively. Seventeen taxa were observed exclusively in the Atlantic layer, including the copepods *Scaphocalanus brevicornis* and *Neomormonilla minor*, and the decapod *Hymenodora glacialis*. *Spinocalanus longicornis* (IndVal: 0.95, $P < 0.01$) and *N. minor* (IndVal: 0.85, $P < 0.01$) were identified as the top two indicator species for the Atlantic layer (Fig. 5). 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. Predatory biomass in the Atlantic layer was dominated by the

chaetognath *Eukrohnia hamata* and cnidarians, including both siphonophores and hydrozoan medusae. In addition, the large decapod *H. glacialis* contributed to high predatory biomass in AW. Contributions from omnivores, including copepods well adapted to utilize refractory material such as *T. borealis* and *Spinocalanus* spp., were also important in AW.

Copepods
The copepods, dominant in all depth layers, were primarily composed of an Arctic guild of taxa that included *C. glacialis*, *C. hyperboreus*, *M. longa*, *O. similis*, *T. borealis*, *M. pygmaeus* and the *Pseudocalanus* spp. 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 50% of copepod abundance and biomass in all sampling
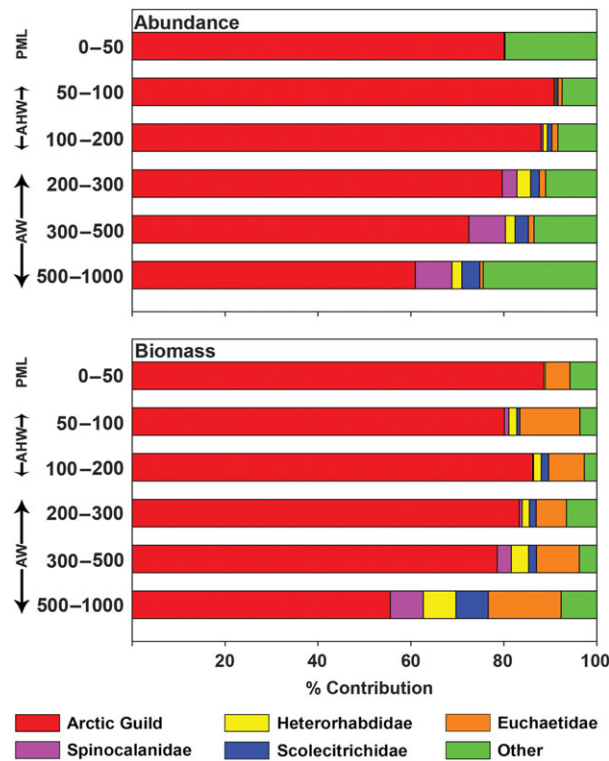
Fig. 6. Contribution of major copepod groups to abundance and biomass of the copepod community within each sampling interval (m). Water masses are noted.

intervals, although the relative contribution declined with depth (Fig. 6). Within the guild of Arctic copepods, small-bodied *O. similis*, *T. borealis*, *M. pygmaeus* and *Pseudocalanus* spp. dominated numerically. *Oithona similis* and *Pseudocalanus* spp. dominated the surface layer, giving way to *T. borealis* and *M. pygmaeus* with increasing depth. In terms of biomass, large-bodied *C. glacialis*, *M. longa* and *C. hyperboreus* dominated all sampling depths, peaking in the PML, AHW and AW, respectively.

Although present in lower abundances than the copepods of the dominant Arctic guild, mesopelagic copepod families, such as Aetideidae, Heterorhabdidae, Scolecitrichidae, Spinocalanidae and Euchaetidae, occurred in AHW and became important contributors in the Atlantic layer (Fig. 6). Within these families, congeners displayed different depth preferences, even within water masses (Fig. 7). Within the Aetideids, *Chiridius obtusifrons* exhibited a wide depth range, occurring in all sampling intervals. *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 also exhibited this pattern of vertical partitioning 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 and Hagen, 2002; Kosobokova and Hopcroft, 2010; Kosobokova *et al.*, 2011). Abundance and biomass were concentrated in the upper layer of the water column and decreased with depth, while species richness increased with depth as mesopelagic genera appeared. Our estimate of abundance in the PML (1230 ind. m^{-3}) is consistent with that reported for the Canada Basin by Kosobokova and Hopcroft (Kosobokova and Hopcroft, 2010) (1170 ind. m^{-3} for 0–25 m and 1310 ind. m^{-3} for 25–50 m). Biomass
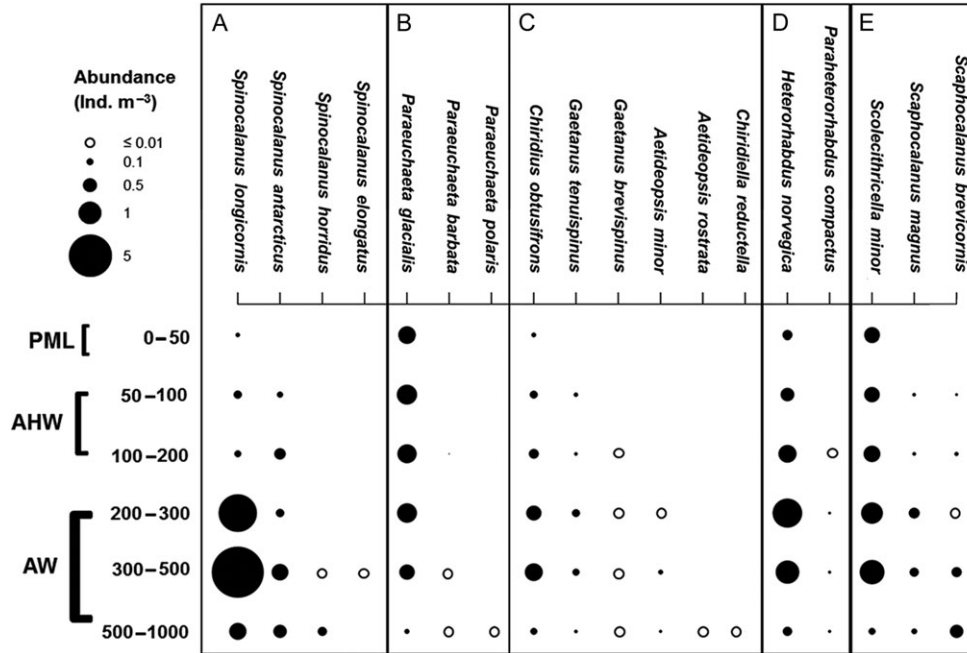
Fig. 7. Generalized vertical distribution of select copepod species in each sampling stratum (m) of the Beaufort Sea slope. Based on mean of all stations. (**A**) Spinocalanidae, (**B**) Euchaetidae, (**C**) Aetideidae, (**D**) Heterorhabdidae and (**E**) Scolecitrichidae.

Table III: *Comparison of mean biomass ($mg\,DW\,m^{-3}$) in zooplankton sampling intervals from the Beaufort Sea slope and the Arctic's basins*

	Biomass ($mg\,DW\,m^{-3}$)		
Layer (m)	This study	Kosobokova and Hopcroft (Kosobokova and Hopcroft, 2010)	Auel and Hagen (Auel and Hagen, 2002)
Gear	(Multinet, 150 µm mesh)	(Multinet, 150 µm mesh)	(Multinet, 200 µm mesh)
Dates	13 August–30 September	29 June–25 July	20 August–21 September
0–25	24.3	21.0	20.9
25–50		38.0	
50–100	12.8	8.8	3.3
100–200	8.3	2.6	
200–300	10.0	3.8	0.6
300–500	7.1	2.2	
500–1000	1.9	0.8	0.5

estimates are also similar, with values of 24.3 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 and Hopcroft, 2010). These abundance estimates are higher than that reported by Auel and Hagen (Auel and 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 sampling intervals below 50 m than reported for both the Canadian (Kosobokova and Hopcroft, 2010) and Nansen (Auel and Hagen, 2002) basins, consistent with

the expectation that continental slopes are more productive than the deep basins (Ashjian *et al.*, 2003; Kosobokova and Hirche, 2009; Kosobokova and Hopcroft, 2010) (Table III). It should be noted that while these surveys used identical or similar gear, sampling took place between the end of June and September. Therefore, seasonal variability could be a factor influencing these observations. Finally, we observed a slight increase in abundance and biomass in the transition to AWs (200–300 m), as did Kosobokova and Hopcroft (Kosobokova and Hopcroft, 2010) in the Canadian basin. This is likely due to the fact that this

layer represents a transitional zone between water types and therefore is inhabited by the large-bodied *Calanus* species that are dominant in the PML and AHW, as well as mesopelagic taxa, such as *Spinocalanus* spp., that are more abundant in AW. The transitional nature of AHW is also reflected by lower IndVals of AHW indicator taxa, demonstrating that these taxa inhabited several water masses and were not tightly associated with AHW. This is in contrast to indicator taxa for the PML and AW, which had high IndVals and were therefore tightly associated with their respective water masses.

The species composition of the Beaufort Sea slope is characteristic of Arctic basin waters (Brodsky, 1950, 1957) and is in agreement with studies from the Canada basin (Kosobokova and 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. 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 and Tuschling, 2005). These euryhaline taxa reflect the dynamic nature of the shelf environment that can be profoundly influenced by seasonal freshwater inflow. The influence of the freshwater inflow (e.g. the Mackenzie River) in the Beaufort Sea varies both spatially and temporally; this is reflected in the species composition of the zooplankton community (Smoot and Hopcroft, in press). With respect to this study, euryhaline taxa in surface waters primarily occurred in 2013 when sampling took place near the Mackenzie River, and to a lesser extent in 2014.

We report a similar number of taxa to the 111 reported by Kosobokova and Hopcroft (Kosobokova and Hopcroft, 2010) in the Canada Basin. However, 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 and Hopcroft, 2010); our results demonstrate the penetration of these taxa into the eastern portion of the Alaskan Beaufort Sea. We also observed *P. pacificus*, a mesopelagic subarctic copepod, at a station near the Mackenzie River in the 300–500 m layer. Kosobokova and Hopcroft (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 expatriate copepods (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 and Hirche, 2000).

Community structure

We observed community structure similar to that observed in other depth-stratified examinations of zooplankton distribution in the Arctic, characterized by gross community separation according to water mass and additional internal structure within water masses (Auel and Hagen, 2002; Kosobokova and Hopcroft, 2010; Kosobokova *et al.*, 2011). The community in the PML 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.* (Carmack *et al.*, 1989) note that exchange between the shelf environment and the offshore environment occurs primarily in waters above the halocline (e.g. the PML). Contributions from euryhaline taxa in the PML highlight this phenomenon; the 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 and sampling location of different surveys. In addition, the 0–50 m layer showed the highest variability in abundance and biomass among stations, as has been observed in the Canada basin (Kosobokova and Hopcroft, 2010). Thus, a given depth interval is not necessarily homogenous, especially when considering the upper layers of the hydrographically dynamic shelf and slope region. Despite these nuances, the 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 are more pronounced than those associated with latitudinal or longitudinal changes (Auel and Hagen, 2002).

Below the variable PML, the traditional guild of Arctic copepods also dominated AHW; however, species richness increased as mesopelagic genera began to appear. The relative contribution of the dominant Arctic group of copepods reached a minimum in AW, where mesopelagic copepods became significant contributors to the community. This general pattern is consistent with previous depth-stratified examinations in the Arctic (Kosobokova and Hirche, 2000; Auel and Hagen, 2002; Kosobokova and 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 and Hopcroft, 2010; Kosobokova *et al.*, 2011). Kosobokova *et al.* (Kosobokova *et al.*, 2011) reported the 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 (Auel, 1999), Kosobokova and Hirche (Kosobokova and Hirche, 2000), Laakmann *et al.* (Laakmann *et al.*, 2009) and Kosobokova and Hopcroft (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 dynamic.

From the perspective of community composition, faunal differences associated with diel cycling are small compared with faunal differences associated with water mass (Rabindranath *et al.*, 2011); however, DVM and seasonal vertical migration (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 and 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.

CONCLUSION

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 that can vary depending on the degree of exchange between the shelf and slope. In addition, average biomass estimates in depth intervals below 50 m are higher than those reported from similar intervals in the basin, likely due to the proximity of our study area 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), will likely result in increased export production to the mesopelagic water layers of the Beaufort Sea. This would support higher mesopelagic zooplankton biomass and has implications for trophic interactions, particle flux and biogeochemical cycles.

SUPPLEMENTARY DATA

Supplementary data can be found online at *Journal of Plankton Research* online

REFERENCES

Abramova, E. and Tuschling, K. (2005) A 12-year study of the seasonal and interannual dynamics of mesozooplankton in the Laptev Sea: significance of salinity regime and life cycle patterns. *Glob. Planet. Change*, **48**, 141–164.

Anderson, M. J. and Walsh, D. C. I. (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? *Ecol. Monogr.*, **83**, 557–574.

Arashkevich, E., Wassmann, P., Pasternak, A. and Riser, C. W. (2002) Seasonal and spatial changes in biomass, structure, and development progress of the zooplankton community in the Barents Sea. *J. Mar. Syst.*, **38**, 125–145.

Arrigo, K. R., Van Dijken, G. and Pabi, S. (2008) Impact of a shrinking Arctic ice cover on marine primary production. *Geophys. Res. Lett.*, **35**, L19603.

Ashjian, C. J., Campbell, R. G., Welch, H. E., Butler, M. and Van Keuren, D. (2003) Annual cycle in abundance, distribution, and size in relation to hydrography of important copepod species in the western Arctic Ocean. *Deep Sea Res. Part I*, **50**, 1235–1261.

Auel, H. (1999) The ecology of Arctic deep-sea copepods (Euchaetidae and Aetideidae). Aspects of their distribution, trophodynamics and

effect on the carbon flux. *Berichte zur Polarforschung*, Vol. **319**. Alfred Wegener Institute, Bremerhaven, pp. 1–97.

Auel, H. and Hagen, W. (2002) Mesozooplankton community structure, abundance and biomass in the central Arctic Ocean. *Mar. Biol.*, **140**, 1013–1021.

Blachowiak-Samolyk, K., Kwasniewski, S., Dmoch, K., Hop, H. and Falk-Petersen, S. (2007) Trophic structure of zooplankton in the Fram Strait in spring and autumn 2003. *Deep Sea Res. Part I*, **54**, 2716–2728.

Boxshall, G. A. (1985) The comparative anatomy of 2 copepods, a predatory calanoid and a particle-feeding mormonilloid. *Philos. Trans. R. Soc. B*, **311**, 303–307.

Bray, J. R. and Curtis, J. T. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.*, **27**, 325–349.

Brodsky, K. A. (1950) Copepods (Calanoida) of the Far-Eastern Seas of the USSR and the Polar Basin. Zoological Institute of the Academy of Sciences of the USSR, Leningrad, in Russian.

Brodsky, K. A. (1957) The Copepod Fauna (Calanoida) and Zoogeographic Zonation of the North Pacific and Adjacent Waters. Izvestiya Akademii SSSR, Leningrad, in Russian.

Carmack, E. C., MacDonald, R. W. and Papadakis, J. E. (1989) Water mass structure and boundaries in the Mackenzie Shelf Estuary. *J. Geophys. Res. Oceans*, **94**, 18043–18055.

Clarke, K. R. and Warwick, R. M. (2010) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 2nd edn(PRIMER-E, Plymouth, United Kingdom, pp. 176.

Codispoti, L. A., Flagg, C., Kelly, V. and Swift, J. H. (2005) Hydrographic conditions during the 2002 SBI process experiments. *Deep Sea Res. Part I*, **52**, 3199–3226.

Cottier, F. R., Tarling, G. A., Wold, A. and Falk-Petersen, S. (2006) Unsynchronized and synchronized vertical migration of zooplankton in a high arctic fjord. *Limnol. Oceanogr.*, **51**, 2586–2599.

Daase, M., Falk-Petersen, S., Varpe, O., Darnis, G., Søreide, J. E., Wold, A., Leu, E., Berge, J. *et al* (2013) Timing of reproductive events in the marine copepod *Calanus glacialis*: a pan-Arctic perspective. *Can. J. Fish. Aquat. Sci.*, **70**, 871–884.

Darnis, G., Barber, D. G. and Fortier, L. (2008) Sea ice and the onshore–offshore gradient in pre-winter zooplankton assemblages in southeastern Beaufort Sea. *J. Mar. Syst.*, **74**, 994–1011.

Darnis, G. and Fortier, L. (2014) Temperature, food and the seasonal vertical migration of key arctic copepods in the thermally stratified Amundsen Gulf (Beaufort Sea, Arctic Ocean). *J. Plankton Res.*, **36**, 1092–1108.

Dilling, L., Wilson, J., Steinberg, D. and Alldredge, A. (1998) Feeding by the euphausiid *Euphausia pacifica* and the copepod *Calanus pacificus* on marine snow. *Mar. Ecol. Prog. Ser.*, **170**, 189–201.

Dufrene, M. and Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.*, **67**, 345–366.

Eilertsen, H. C., Tande, K. S. and Taasen, J. P. (1989) Vertical distributions of primary production and grazing by *Calanus glacialis* Jaschnov and *Calanus hyperboreus* Kroyer in Arctic waters (Barents Sea). *Polar. Biol.*, **9**, 253–260.

Fortier, M., Fortier, L., Hattori, H., Saito, H. and Legendre, L. (2001) Visual predators and the diel vertical migration of copepods under Arctic sea ice during the midnight sun. *J. Plankton Res.*, **23**, 1263–1278.

Grainger, E. H. (1965) Zooplankton from the Arctic Ocean and adjacent Canadian waters. *J. Fish. Res. Board Can.*, **22**, 543–564.

Haro-Garay, M. J. (2003) Diet and functional morphology of the mandible of two planktonic amphipods from the Strait of Georgia, British Columbia, *Themisto pacifica* (Stebbing, 1888) and *Cyphocaris challengeri* (Stebbing, 1888). *Crustaceana*, **76**, 1291–1312.

Hays, G. C., Kennedy, H. and Frost, B. W. (2001) Individual variability in diel vertical migration of a marine copepod: why some individuals remain at depth when others migrate. *Limnol. Oceanogr.*, **46**, 2050–2054.

Homma, T. and Yamaguchi, A. (2010) Vertical changes in abundance, biomass and community structure of copepods down to 3000 m in the southern Bering Sea. *Deep Sea Res. Part I*, **57**, 965–977.

Hopcroft, R. R., Clarke, C., Nelson, R. J. and Raskoff, K. A. (2005) Zooplankton communities of the Arctic's Canada Basin: the contribution by smaller taxa. *Polar. Biol.*, **28**, 198–206.

Hopkins, T. L. (1969) Zooplankton standing crop in the Arctic basin. *Limnol. Oceanogr.*, **14**, 80–85.

Hunt, B. P. V., Nelson, R. J., Williams, B., McLaughlin, F. A., Young, K. V., Brown, K. A., Vagle, S. and Carmack, E. C. (2014) Zooplankton community structure and dynamics in the Arctic Canada Basin during a period of intense environmental change (2004–2009). *J. Geophys. Res. Oceans*, **119**, 2518–2538.

Johnson, M. W. (1956) *The Plankton of the Beaufort and Chukchi Sea Areas of the Arctic and its Relation to the hydrography*. Arctic Institute of North America, Montreal, pp. 32.

Kosobokova, K. (2012) *Zooplankton of the Arctic Ocean. Community Structure, Ecology, Spatial Distribution*. GEOS, Moscow, pp. 272.

Kosobokova, K. and Hirche, H. J. (2000) Zooplankton distribution across the Lomonosov Ridge, Arctic Ocean: species inventory, biomass and vertical structure. *Deep Sea Res. Part I*, **47**, 2029–2060.

Kosobokova, K. and Hirche, H. J. (2009) Biomass of zooplankton in the eastern Arctic Ocean—a base line study. *Prog. Oceanogr.*, **82**, 265–280.

Kosobokova, K., Hopcroft, R. R. and Hirche, H. J. (2011) Patterns of zooplankton diversity through the depths of the Arctic's central basins. *Mar. Biodivers.*, **41**, 29–50.

Kosobokova, K. N., Hanssen, H., Hirche, H. J. and Knickmeier, K. (1998) Composition and distribution of zooplankton in the Laptev Sea and adjacent Nansen Basin during summer, 1993. *Polar. Biol.*, **19**, 63–76.

Kosobokova, K. N. and Hopcroft, R. R. (2010) Diversity and vertical distribution of mesozooplankton in the Arctic's Canada Basin. *Deep Sea Res. Part I*, **57**, 96–110.

Laakmann, S., Kochzius, M. and Auel, H. (2009) Ecological niches of Arctic deep-sea copepods: vertical partitioning, dietary preferences and different trophic levels minimize inter-specific competition. *Deep Sea Res. Part I*, **56**, 741–756.

Lane, P. V. Z., Llinas, L., Smith, S. L. and Pilz, D. (2008) Zooplankton distribution in the western Arctic during summer 2002: hydrographic habitats and implications for food chain dynamics. *J. Mar. Syst.*, **70**, 97–133.

Lansard, B., Mucci, A., Miller, L. A., Macdonald, R. W. and Gratton, Y. (2012) Seasonal variability of water mass distribution in the southeastern Beaufort Sea determined by total alkalinity and delta O-18. *J. Geophys. Res. Oceans*, **117**, C03003.

MacDonald, R. W., Carmack, E. C., McLaughlin, F. A., Iseki, K., Macdonald, D. M. and Obrien, M. C. (1989) Composition and modification of water masses in the Mackenzie Shelf Estuary. *J. Geophys. Res. Oceans*, **94**, 18057–18070.

MacDonald, R. W., Solomon, S. M., Cranston, R. E., Welch, H. E., Yunker, M. B. and Gobeil, C. (1998) A sediment and organic

carbon budget for the Canadian Beaufort shelf. *Mar. Geol.*, **144**, 255–273.

Matsuura, H. and Nishida, S. (2000) Fine structure of the "button setae" in the deep-sea pelagic copepods of the genus *Euaugaptilus* (Calanoida : Augaptilidae). *Mar. Biol.*, **137**, 339–345.

Mauchline, J., Blaxter, J. H. S., Southward, A. J. and Tyler, P. A. (1998) *The Biology of Calanoid Copepods*. Academic Press, San Diego, CA, pp. 710.

McConnell, M. (1977) An analysis of the zooplankton community structure of the western Beaufort Sea (WEBSEC 1971). M.S. University of Rhode Island, Naragansett, p. 218.

Mulligan, R. P., Perrie, W. and Solomon, S. (2010) Dynamics of the Mackenzie River plume on the inner Beaufort shelf during an open water period in summer. *Estuar. Coast. Shelf Sci.*, **89**, 214–220.

Mumm, N. (1991) *On the Summerly Distribution of Mesozooplankton in the Nansen Basin, Arctic Ocean.* Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, pp. 174.

Nishida, S. and Ohtsuka, S. (1996) Specialized feeding mechanism in the pelagic copepod genus *Heterorhabdus* (Calanoida: Heterorhabdidae), with special reference to the mandibular tooth and labral glands. *Mar. Biol.*, **126**, 619–632.

Questel, J. M., Clarke, C. and Hopcroft, R. R. (2013) Seasonal and interannual variation in the planktonic communities of the northeastern Chukchi Sea during the summer and early fall. *Cont. Shelf Res.*, **67**, 23–41.

Rabindranath, A., Daase, M., Falk-Petersen, S., Wold, A., Wallace, M. I., Berge, J. and Brierley, A. S. (2011) Seasonal and diel vertical migration of zooplankton in the High Arctic during the autumn midnight sun of 2008. *Mar. Biodivers.*, **41**, 365–382.

Robinson, C., Steinberg, D. K., Anderson, T. R., Aristegui, J., Carlson, C. A., Frost, J. R., Ghiglione, J. F., Hernandez-Leon, S. *et al* (2010) Mesopelagic zone ecology and biogeochemistry – a synthesis. *Deep Sea Res. Part I*, **57**, 1504–1518.

Roff, J. C. and Hopcroft, R. R. (1986) High-precision microcomputer based measuring system for ecological research. *Can. J. Fish. Aquat. Sci.*, **43**, 2044–2048.

Smoot, C. A. and Hopcroft, R. R. (in press) Cross-shelf gradients of epipelagic zooplankton communities of the Beaufort Sea and the influence of localized hydrographic features. *J. Plankton Res*. doi:10.1093/plankt/fbw080.

Thibault, D., Head, E. J. H. and Wheeler, P. A. (1999) Mesozooplankton in the Arctic Ocean in summer. *Deep Sea Res. Part I*, **46**, 1391–1415.

Turner, J. T., Levinsen, H., Nielsen, T. G. and Hansen, B. W. (2001) Zooplankton feeding ecology: grazing on phytoplankton and predation on protozoans by copepod and barnacle nauplii in Disko Bay, West Greenland. *Mar. Ecol. Prog. Ser.*, **221**, 209–219.

Walkusz, W., Paulic, J. E., Kwasniewski, S., Williams, W. J., Wong, S. and Papst, M. H. (2010) Distribution, diversity and biomass of summer zooplankton from the coastal Canadian Beaufort Sea. *Polar Biol.*, **33**, 321–335.

Walkusz, W., Williams, W. J. and Kwasniewski, S. (2013) Vertical distribution of mesozooplankton in the coastal Canadian Beaufort Sea in summer. *J. Mar. Syst.*, **127**, 26–35.

Wallace, M. I., Cottier, F. R., Berge, J., Tarling, G. A., Griffiths, C. and Brierley, A. S. (2010) Comparison of zooplankton vertical migration in an ice-free and a seasonally ice-covered Arctic fjord: an insight into the influence of sea ice cover on zooplankton behavior. *Limnol. Oceanogr.*, **55**, 831–845.

Williams, W. J. and Carmack, E. C. (2008) Combined effect of wind-forcing and isobath divergence on upwelling at Cape Bathurst, Beaufort Sea. *J. Mar. Res.*, **66**, 645–663.

Williams, W. J., Melling, H., Carmack, E. C. and Ingram, R. G. (2008) Kugmallit Valley as a conduit for cross-shelf exchange on the Mackenzie shelf in the Beaufort Sea. *J. Geophys. Res. Oceans*, **113**, C02007.

Wilson, S. E., Steinberg, D. K., Chu, F. L. E. and Bishop, J. K. B. (2010) Feeding ecology of mesopelagic zooplankton of the subtropical and subarctic North Pacific Ocean determined with fatty acid biomarkers. *Deep Sea Res. Part I*, **57**, 1278–1294.

Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S., Ishizaka, J., Ikeda, T. *et al* (2002) Community and trophic structures of pelagic copepods down to greater depths in the western subarctic Pacific (WEST-COSMIC). *Deep Sea Res. Part I*, **49**, 1007–1025.

Yen, J. (1983) Effects of prey concentration, prey size, predator life stage, predator starvation, and season on predation rates of the carnivorous copepod *Euchaeta elongata. Mar. Biol.*, **75**, 69–77.

Yen, J. (1987) Predation by carnivorous marine copepod, *Euchaeta norvegica*, on eggs and larvae of the North Atlantic cod *Gadus morhua. J. Exp. Mar. Biol. Ecol.*, **112**, 283–296.