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Abundance, biomass and community structure of epipelagic zooplankton in the Canada Basin

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Changing environmental conditions such as decreasing sea ice cover impact Arctic zooplankton. In the Canada Basin, zooplankton surveys have seldom been done due to its traditionally thick, year-round ice cover. Here, we describe the zooplankton community of the Canada Basin before the two recent sea ice minima (2007 and 2012). Zooplankton were sampled from the upper 100 m during August and September of the years 2003–2006 using a 150- μ m mesh net to determine species composition, abundance and biomass. To describe the zooplankton community and its relation to the environment, we used Bray–Curtis similarity, and then applied hierarchical clustering, non-parametric multidimensional scaling and the BEST BIO-ENV routine. The most abundant zooplankton species in all years were smaller copepods such as *Oithona similis* and *Microcalanus pygmaeus*. Biomass was dominated by larger copepod species such as *Calanus hyperboreus* and *Calanus glacialis*. For the non-copepod zooplankton, the pteropod *Limacina helicina* and the larvacean *Fritillaria borealis* were typically the most abundant species. The non-copepod biomass was dominated by the chaetognath *Eukrohnia hamata* and *L. helicina*, while *F. borealis* contributed relatively little to the overall biomass despite its high numbers. Zooplankton communities differed between shelf/slope and basin stations. We found no obvious interannual changes in community structure over our short 4-year observation period, with community structure influenced to a small degree by environmental factors.

KEYWORDS: Arctic; Canada Basin; mesozooplankton; abundance; biomass

INTRODUCTION

The Canada Basin is a deep, ice-covered basin located in the central Arctic Ocean. Zooplankton within the Arctic basins are intricately tuned to the basin's primary

production cycle (Smith and Schnack-Schiel, 1990). While the Canada Basin was historically been covered year-round by thick multiyear ice, sea ice extent and concentration have declined rapidly within the past decades, reaching a record minimum during summer 2007

only to have it exceeded recently during summer 2012 (Comiso, 2012; Parkinson and Comiso, 2013). The sea ice meltwater represents the major freshwater influx to the Arctic that is supplemented by river discharge, with both sources increasing over time (Yamamoto-Kawai *et al.*, 2009). Water temperatures in the Canada Basin already showed a warming trend from 1993 to 2008 (Jackson *et al.*, 2010) while freshening of the Beaufort Gyre, as well as a deepening of the nutricline and chlorophyll maximum, have also been observed between the years 2003 and 2009 (McLaughlin and Carmack, 2010). Such detectable changes in the environmental conditions typically have an impact on zooplankton communities (Richardson, 2008), and this may be particularly true in the Arctic (Gradinger *et al.*, 2010; Nelson *et al.*, 2014).

Zooplankton in the Canada Basin has been studied only sporadically due to its traditionally thick, year-round ice cover. Studies during the last century established rudimentary community composition and seasonal cycles but were seldom synoptic or repeated (Johnson, 1963; Pautzke, 1979; Thibault *et al.*, 1999; Ashjian *et al.*, 2003). In contrast, the Beaufort Sea slope region experienced more extensive activities often related to oil and gas exploration (Hufford *et al.*, 1974; Horner and Murphy, 1985; Hopky *et al.*, 1994a, b, c). Even the more recent studies have been concentrated in the more coastal Beaufort Sea and shelf areas (Darnis *et al.*, 2008; Lane *et al.*, 2008; Walkusz *et al.*, 2008, 2010, 2013; Smoot and Hopcroft, 2017a), with less focus on the central Canada Basin (Hopcroft *et al.*, 2005; Kosobokova and Hopcroft, 2010; Hunt *et al.*, 2014).

At present, indications are that many species are shared between the Arctic's major basins (Kosobokova *et al.*, 2011). The fauna contains a mixture of endemic Arctic species, viable species shared with other ocean basins and species that are advected from the Pacific such as *Eucalanus bungii*, *Pseudocalanus newmani*, *Metridia pacifica* and *Neocalanus flemingeri* (Hopcroft *et al.*, 2005; Kosobokova and Hopcroft, 2010; Hunt *et al.*, 2014) that are not thought to be viable in the Arctic or have little reproductive success (Matsuno *et al.*, 2015; Wassmann *et al.*, 2015). The abundance and biomass within the epipelagic upper 100 m of the water column are typically dominated by copepods, whereby the smaller bodied species such as *Oithona similis*, *Microcalanus pygmaeus* and *Triconia borealis* make up the bulk of the abundance, while larger bodied endemic copepods such as *Calanus hyperboreus*, *Calanus glacialis*, *Metridia longa* and *Paraeuchaeta glacialis* dominate the biomass (Kosobokova and Hopcroft, 2010). Non-copepod abundance is frequently dominated by the larvaceans *Fritillaria borealis* and *Oikopleura vanhoeffeni* as well as the pteropod *Limacina helicina* that can at times

contribute a significant percentage to the biomass (Hopcroft *et al.*, 2005; Kosobokova and Hopcroft, 2010; Hunt *et al.*, 2014). Zooplankton species are also advected from the shelf into the basin within eddies (Carmack and Macdonald, 2002; Llinás *et al.*, 2009), and hence meroplankton typical for shelf communities, such as cirripedia cyprids and echinoderm larvae, can occasionally be found far into the basin (Hunt *et al.*, 2014).

A freshening and warming of the Canada Basin due to climate change has implications for the zooplankton community. The epipelagic large-bodied endemic copepods are probably at greatest risk of stress or competition from the advected subarctic species. Hunt *et al.*, (2014) suggested that there has already been a decrease in abundance of species that are typical for the Arctic and Subarctic, such as *O. similis*, *L. helicina*, *M. pygmaeus*, and *F. borealis* during 2007 and 2008. An earlier sea ice retreat and a shrinking sea ice extent combined with the freshening of the Beaufort Gyre (McLaughlin and Carmack, 2010) could potentially increase primary productivity (Arrigo and Van Dijken, 2015) and zooplankton biomass in the basins (Hunt *et al.*, 2014) as has already been demonstrated for the Chukchi Sea shelf (Ershova *et al.*, 2015).

Here we present new data describing the epipelagic zooplankton abundance, biomass and community structure in the Canada Basin for 2003 to 2006 to fill in spatial and temporal gaps. By describing the basin's zooplankton community before the two recent summer sea ice minima of 2007 and 2012, we hope to build a better foundation for comparison of zooplankton communities before and after major environmental changes to establish how they may be affected.

METHOD

Zooplankton sampling and taxonomic analysis

Our study area encompassed much of the Canada Basin to as far north as 80°N latitude (Fig. 1). Samples were collected during August and September of 2003 to 2006 (day and night) aboard the Canadian Coast Guard vessel Louis S. St-Laurent. Bongo nets with a mouth diameter of 60 cm and 150- μ m mesh size were deployed vertically in the upper 100 m of the water column. During 2003 and 2004, the nets were equipped with General Oceanics flowmeters to measure the volume of filtered water, while during 2005 and 2006, OceanTest flowmeters were used. On three occasions, flowmeters iced-up and gave false readings. In these cases, a filtration efficiency of 100% was assumed because there was

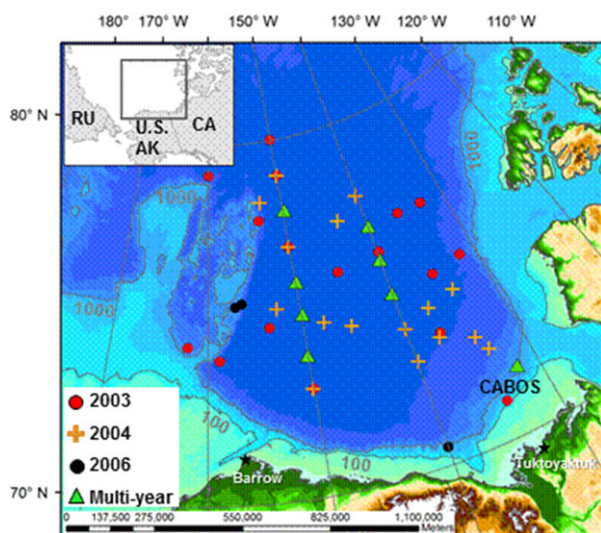


Fig. 1. Map of the study area in the Canada Basin. Multiyear stations include 2003, 2004, 2005 and 2006 stations, if applicable.

insufficient phytoplankton to impact filtration efficiency. A total of 60 samples were analyzed: 23 from 2003, 23 from 2004, only 4 from 2005 (due to wire-time constraints) and 10 from 2006. Upon collection, the samples were preserved in seawater with 4% formaldehyde.

In the lab, collections were subsampled using a Folsom splitter (Harris *et al.*, 2000), with smaller subsamples (e.g. 1/128th) used to identify very abundant species (such as *O. similis*) and larger subsamples used for the rarer species. The full sample was generally analyzed for cnidarians, amphipods, chaetognaths and larger copepods. Animals were enumerated and measured using the ZoopBiom software (Roff and Hopcroft, 1986). For the more prominent species, up to 100 individuals per species were measured with remaining individuals in the aliquot simply enumerated. The developmental stage of larger copepods and the sex of adults were also recorded. We used prosome length to differentiate between *C. glacialis* and *C. hyperboreus* during early developmental stages (copepodite stages CI–CIII). For individuals where early life stages could not be distinguished between species, they were grouped according to their genus. In order to calculate dry weights (DW), we applied length–weight relationships according to Hopcroft *et al.* (2005) that were species–specific or from morphologically similar species.

The ZoopBiom software employs subsample fractions and volume filtered to calculate both abundance and biomass, along with their size spectra, for each taxa. Here we used arithmetic bins of 50- μm width for creating the size spectra and summed the spectra for all copepod taxa within a sample. These sample–specific spectra

were then averaged for each study year. It is notable that samples from 2 years (2004 and 2006) of our study were collected concurrently with the work by Hunt *et al.*, (2014) that employed a coarser mesh size (256 μm).

Environmental data

Concurrent temperature ($^{\circ}\text{C}$), salinity (PSU) and oxygen (mL/L) data were obtained using a SBE 911 plus (Sea-Bird Electronics Inc.) (McLaughlin *et al.*, 2009). Means were calculated for 0–50 m and 0–100 m depth layers.

We derived the Euclidean distance to the coastline from World Vector Shoreline data from the National Oceanic and Atmospheric Administration (NOAA) by using ArcMap 10.1 and the Geospatial Modelling Environment (GME). The coastline was imported into ArcMap 10.1 and the “Euclidean distance tool” applied to derive a raster layer displaying the Euclidean distance to the coastline. After that, the “isectpnrst”-command in GME was applied to spatially correlate the stations with the corresponding Euclidean distance value.

Statistical analysis

Statistical analysis was conducted using the PRIMER (Version6) (Clarke and Warwick, 2001), R (Version 3.2.3) and ArcMap 10.1 software. Analysis was completed using all species within a sample unless stated otherwise. We applied a fourth–root transformation of abundance and biomass data and calculated the Bray–Curtis similarity index (Bray and Curtis, 1957). Differences and patterns in the zooplankton community between stations or years were detected using weighted average hierarchical cluster analysis and non-parametric multidimensional scaling (nMDS) based on the Bray–Curtis matrix. To take spatial variability into account, we applied a permutational multivariate analysis of variance (PERMANOVA) using the Adonis function in R (Vegan package) using 5000 permutations. We applied two factors to the function: year and region, whereby the region was split into sampling stations that had a bottom depth above 1100 m versus deeper stations. Species that showed up only once in the entire dataset were excluded from the PERMANOVA. For *Microcalanus*, *Metridia* and *Pseudocalanus*, the copepodites and adults were pooled as *Microcalanus* spp., *Metridia* spp. and *Pseudocalanus* spp., respectively for the hierarchical cluster analysis, nMDS and PERMANOVA. We used the SIMPER routine to define the similarity percentage between clusters, and which species were driving the grouping/clustering. For the SIMPER analysis, any species that contributed less than 70% to the within–group similarity was excluded.

We tested for a possible increase in mean community abundance and biomass from 2003 to 2006 using the Spearman's rank correlation coefficient (ρ ; "cor.test" command in R). To test for significant differences between the annual mean abundance and biomass on species level, the data were log-transformed and analysis of variance (ANOVA) was conducted in R. If applicable, Tukey tests were used to determine which years were significantly different. The year 2005 was excluded from these analyses because of the small sample size during that year.

To relate environmental data to community patterns, we employed Primer's BEST BIO-ENV routine after normalizing the physical variables.

RESULTS

Environmental conditions

Overall, 2003 and 2004 were more similar in their environmental conditions compared to 2005 and 2006. All years had a core of low salinity towards the center of the study area related to dynamics of the Beaufort Gyre. During 2003 and 2004, the northern stations were more saline than 2005 and 2006 (Fig. 2). A small tongue of elevated salinity occurred at the southern stations during 2003 and 2005.

The average temperature for the upper 100 m decreased with increasing latitude during all years. Overall, temperatures were colder further offshore, and in 2003 on the eastern and western edges. During 2003, 2005 and 2006, the core of the study area had temperatures between -1 and -0.5°C . This temperature range occurred further south for 2004 compared to 2003.

Oxygen concentrations during 2003 and 2004 were lower in the North relative to the core of the study area. The same pattern was observed during 2006, with the difference that the southern part of the study area showed a lower oxygen concentration compared to the other years. Oxygen concentration during 2005 was relatively high, with the highest concentration in the Northeast.

General abundance and biomass

In total, 50 taxonomic categories were found during 2003–2006, of which 27 were copepods (Supplementary Table SI). Of the other categories, three were euphausiids, four amphipods, four hydrozoans, two larvaceans, two pteropods, one ctenophore, an isopod, an annelid and then larvae of several different taxonomic groups.

The mean community abundance and biomass varied 1.5-fold across years, being highest in 2006 (Table I), but there was no significant difference between the years (P -value abundance = 0.207; P -value biomass = 0.411) and no correlation between the years, mean abundance and biomass (Spearman's rank correlation coefficient abundance: P -value = 0.27, $\rho = 0.15$; biomass: P -value = 0.65, $\rho = 0.06$). The PERMANOVA showed that there was no significant interaction between the factors year and region (Table II). Both factors were significant (year: $P = 0.0002$; region: $P = 0.015$) for abundance and for biomass, only the year was significant ($P = 0.0002$). Copepods dominated the abundance (Fig. 3) and biomass (Fig. 4) for all years. They made up around 90% of the abundance during 2003, 2005 and 2006, and 84% in 2004, contributing up to 88% (2003) of community biomass. The abundance of non-copepod zooplankton was dominated by larvaceans, mainly *F. borealis*, during 2003, 2004 and 2006 (6, 12 and 9%, respectively). For 2005, non-copepod zooplankton abundance was dominated by pteropods (8%), but since this observation was based on only four stations, it was not appropriate to compare it statistically to the abundance of other years. The category of "others" (Fig. 3) consisted of polychaete larvae, isopods, cnidarians, meroplankton, amphipods, euphausiids, chaetognaths and ostracods, each of them contributing $<0.5\%$ to the overall abundance. Non-copepod biomass was dominated by chaetognaths for all years (2003 = 7%, 2004 = 11%, 2005 = 8%, 2006 = 11%) (Fig. 4) with *Eukrohnia hamata* contributing much more than *Parasagitta elegans* except at the most nearshore sites. The other major invertebrate predator of zooplankton in this system was the medusa *Aglantha digitale*.

The size spectra of copepod abundance and biomass showed expected patterns with the smaller species being the most abundant, but biomass being highest for large copepods where a series of modes occurred largely dominated by *Calanus* stages (Fig. 5). The peak in abundance and biomass for the size of ~ 300 – $450\ \mu\text{m}$ was formed by *O. similis*, *M. copepodites* and *T. borealis*. The species that contributed most to the peak in abundance around $3000\ \mu\text{m}$ were *C. glacialis* and *C. hyperboreus*, where the latter was also responsible for the peaks around 5000 and $7000\ \mu\text{m}$. For the biomass size spectra, the species responsible for the $3000\ \mu\text{m}$ peak were *C. glacialis*, *C. hyperboreus*, *M. longa* and *P. glacialis*. For the $5000\ \mu\text{m}$ peak, *C. hyperboreus* and *P. glacialis* were the main drivers and only *C. hyperboreus* for the $7000\ \mu\text{m}$ peak. The size spectra were similar throughout all years, with the exception of a shift in the $3000\ \mu\text{m}$ and the $5000\ \mu\text{m}$ peaks in 2006, for which *C. glacialis* and *C. hyperboreus* were responsible.

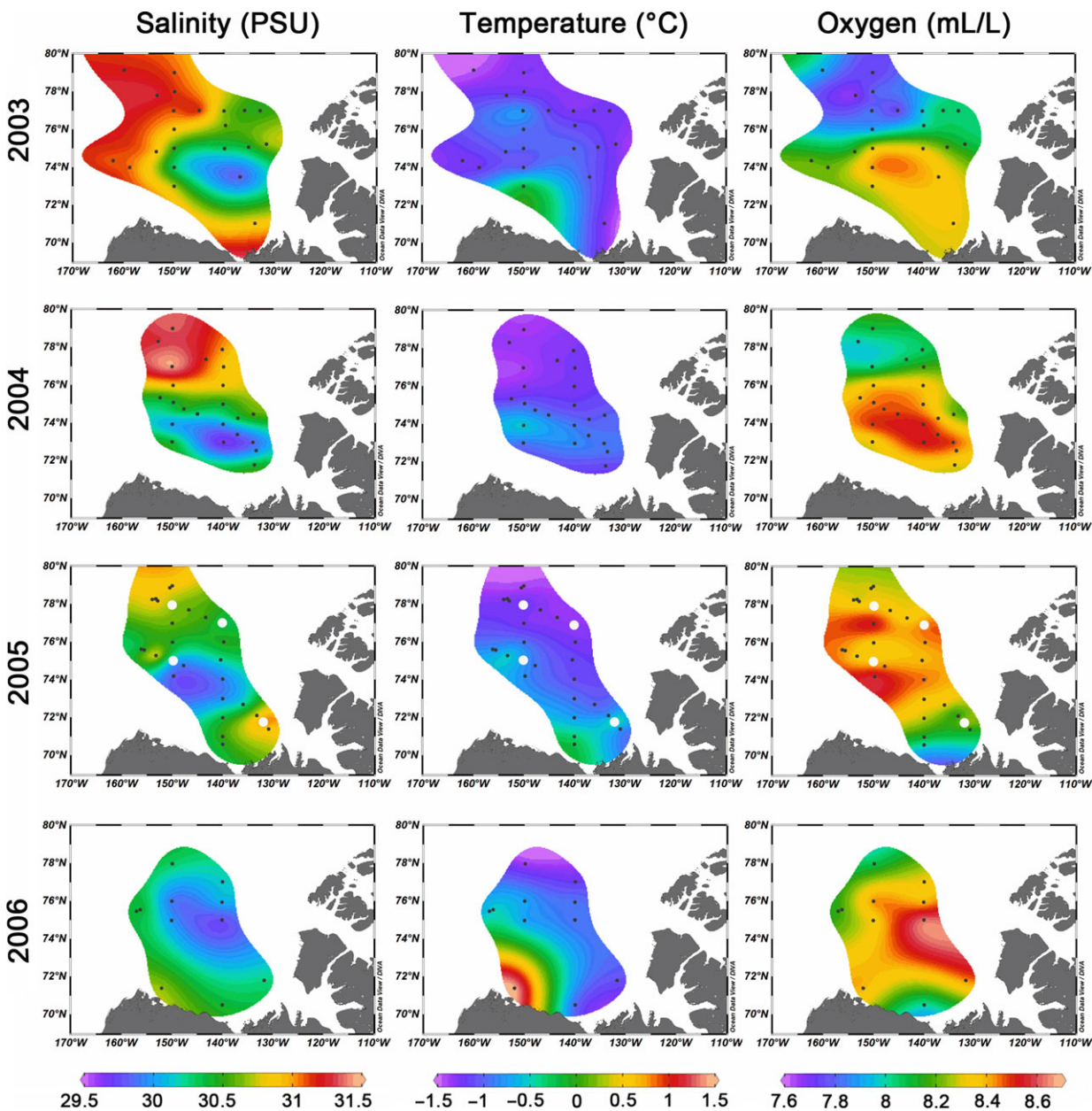


Fig. 2. Average (surface to 100 m) for salinity (PSU), temperature (°C) and oxygen (mL/L) plots for the years 2003–2006. Zooplankton sampling stations in 2005 indicated by white circles.

Table I: Average abundance and biomass of zooplankton in the Canada Basin from 2003 to 2006

Year	Dates	# of samples	Abundance (ind. m ⁻³) ± SE	Biomass (mg DW m ⁻³) ± SE
2003	08/11–09/02	23	687 ± 62	13 ± 1.1
2004	08/09–08/30	23	736 ± 91	11 ± 1
2005	08/03–08/25	4	834 ± 263	12 ± 1.6
2006	08/10–09/8	10	1010 ± 202	17 ± 2.5

Values rounded to the nearest whole number. SE, standard error

Table II: PERMANOVA output for abundance (ab) and biomass (bm) using the factors year and region

	df	SS ab	MS ab	R ² ab	P ab	SS bm	MS bm	R ² bm	P bm
Year	2	0.14	0.07	0.1	0.0002	0.26	0.13	0.14	0.0002
Region	1	0.05	0.05	0.04	0.02	0.04	0.04	0.02	0.24
Year:region	2	0.02	0.02	0.01	0.54	0.03	0.03	0.02	0.4
Residuals	51	1.21	0.02	0.84		1.59	0.03	0.8	

Table shows degrees of freedom (df), sum of squares (SS), mean squares (MS), R² and P-value (P).

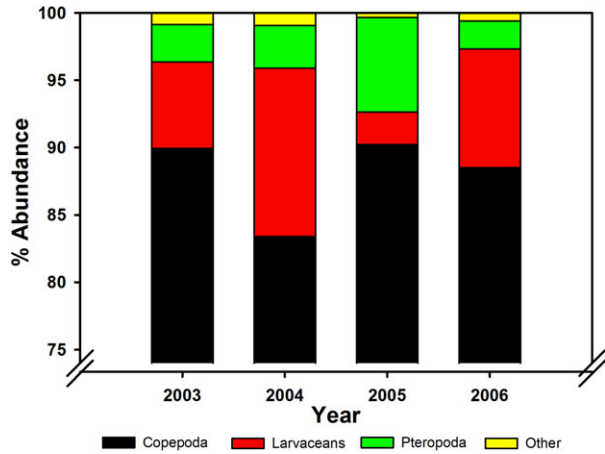


Fig. 3. Relative abundance (ind. m⁻³) of major zooplankton groups in the Canada Basin for 2003–2006. Lower panel range is trimmed to increase resolution.

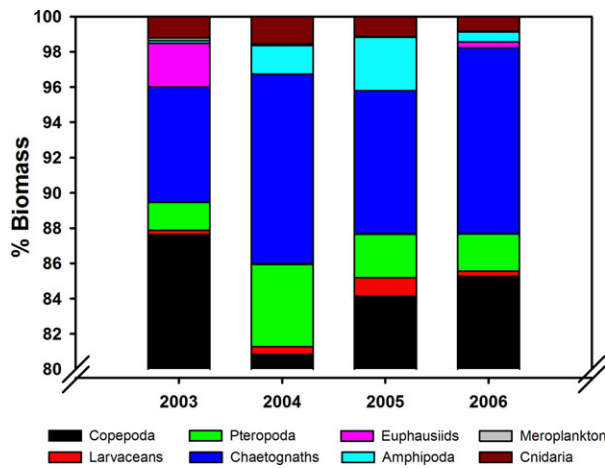


Fig. 4. Relative biomass (mg DW m⁻³) of zooplankton groups in the Canada Basin for 2003–2006. Lower panel range is trimmed to increase resolution.

Species-specific abundance

The zooplankton community for most stations consisted mostly of species common to the Arctic such as *C. hyperboreus*, *C. glacialis*, *M. longa*, *T. borealis*, *O. similis*, *M. pygmaeus*, *P. glacialis* and *F. borealis*, with *O. similis* and *M.*

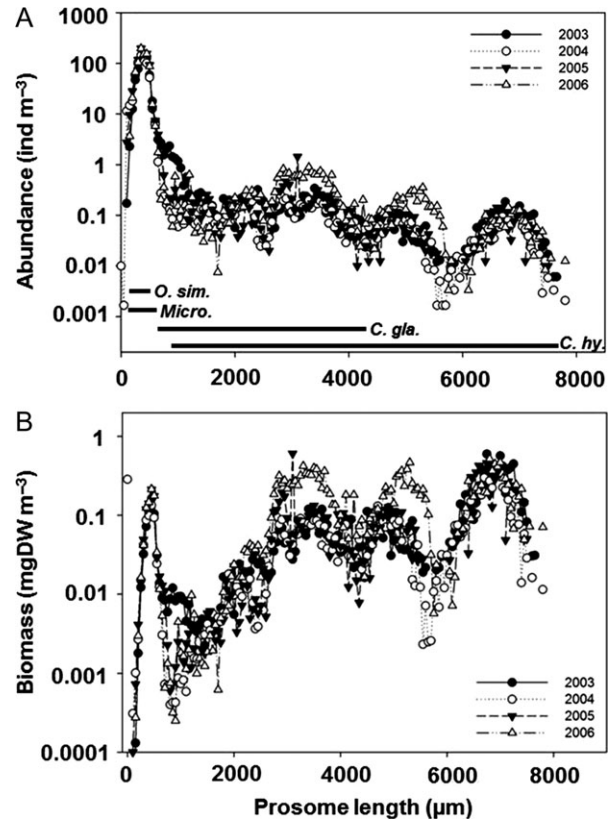


Fig. 5. Size spectra of copepod prosome length (μm) for abundance (A) and biomass (B) in the Canada Basin during 2003–2006 with prosome length ranges for *O. similis* (*O. sim.*), *Microcalanus* sp. (*Micro.*), *C. glacialis* (*C. gla.*) and *C. hyperboreus* (*C. hy.*).

pygmaeus the most abundant in all years (Supplementary Table SI and Fig. 6). The species *C. glacialis*, *M. longa*, *M. pygmaeus*, *O. similis*, *Scolecithricella minor*, *Paraheterorhabdus norvegicus*, *Pseudocalanus* sp. *copepodite*, *Eukrohnia hamata*, *Themisto libellula*, *T. abyssorum* and *A. digitale* were significantly different (P -value ≤ 0.05) between some years (Supplementary Table SI). Pacific species that were advected to the Canada Basin, such as *Eucalanus bungii* and *Neocalanus flemingeri*, were observed sporadically, typically with only one or two specimens per sample.

Microcalanus pygmaeus showed a pattern with higher abundance in the basin than towards the coast. *Calanus*

hyperboreus also generally displayed larger numbers in the basin than towards the coast. For 2003, 2004 and 2006, the lower abundances of *C. hyperboreus*, *C. glacialis* and *M. longa* coincided with the region of lower salinity and higher oxygen concentration within the Beaufort Gyre (Figs 2 and 6). For 2003, 2005 and 2006, *M. longa* displayed higher abundances towards the shelf than in the

Basin, while during 2004, abundances tended to be lower at a cluster of stations toward the north central basin.

While *C. hyperboreus*, *C. glacialis* and *M. longa* had higher abundances towards the western Beaufort Sea (especially in 2004), *O. similis* and *M. pygmaeus* had elevated abundances towards the eastern Beaufort Sea, where the water was fresher due to the Beaufort Gyre.

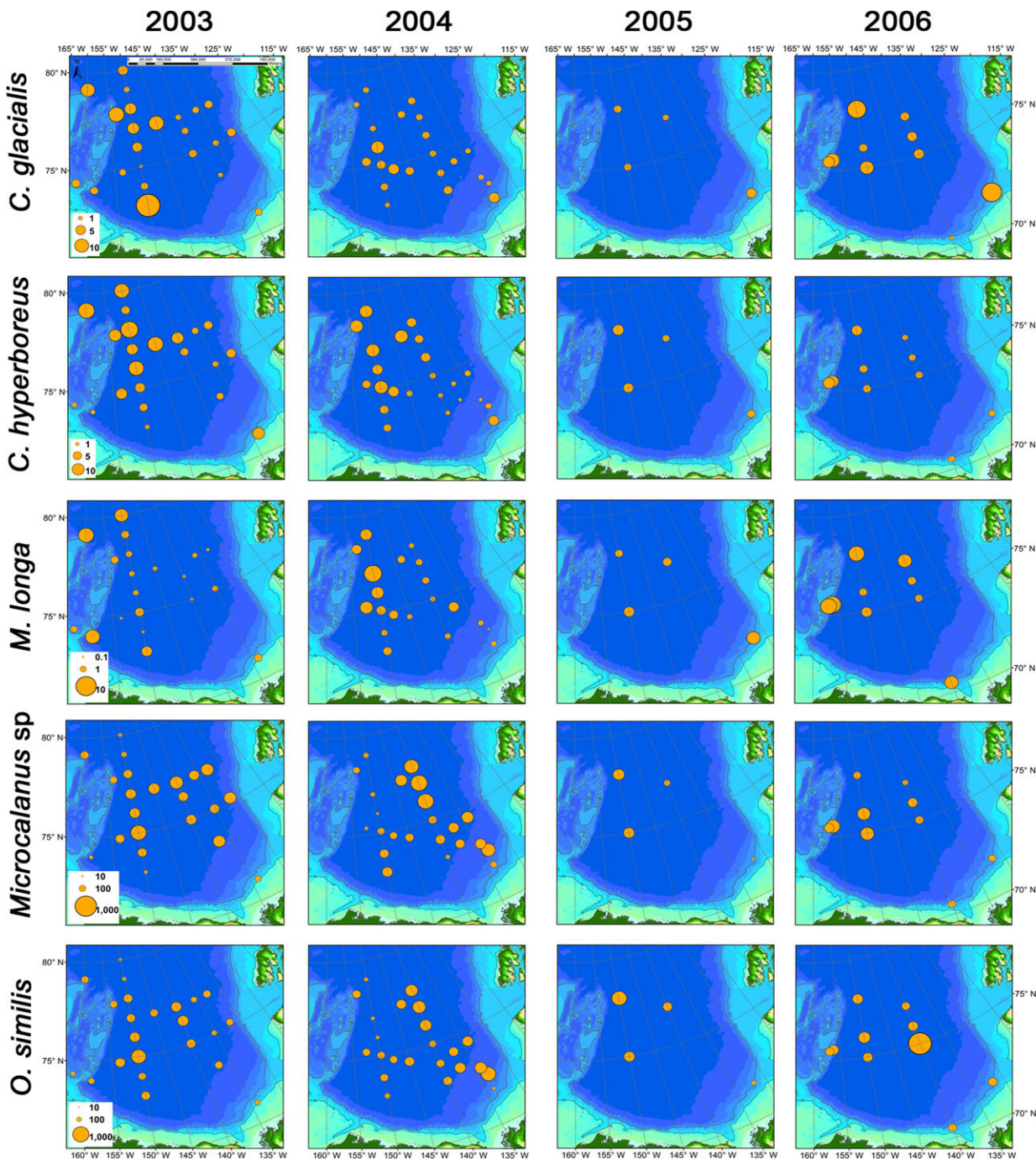


Fig. 6. Proportional abundance plots (ind. m⁻³) of copepods in the Canada Basin 2003–2006. *Microcalanus* copepodites and adults combined.

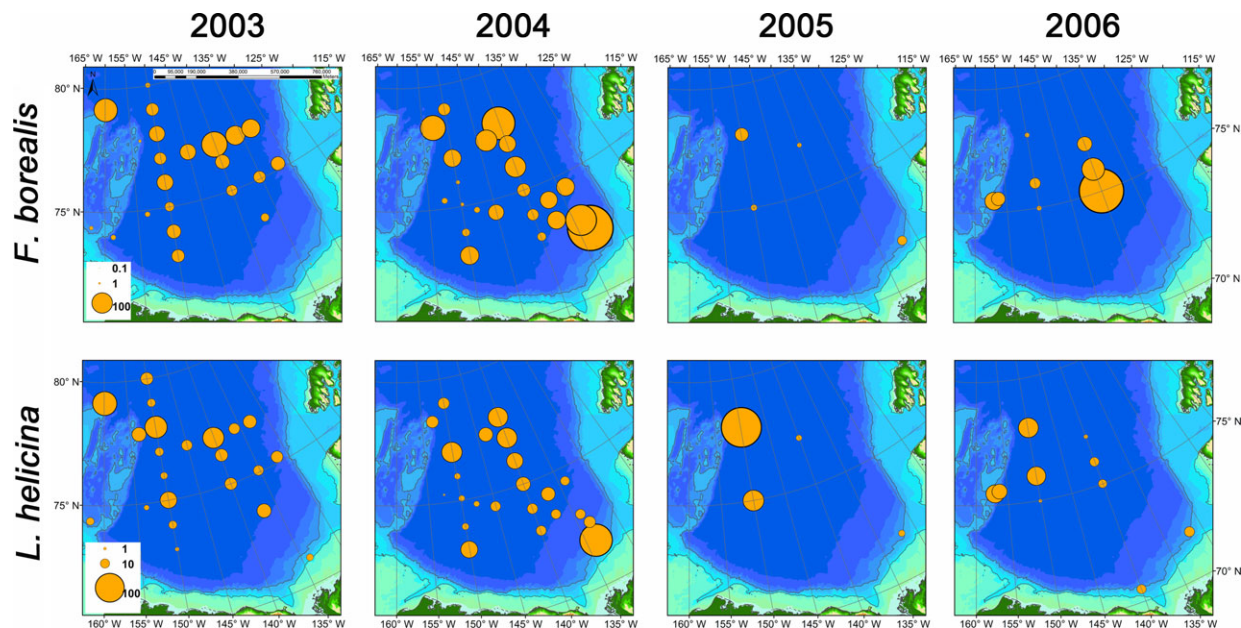


Fig. 7. Proportional abundance plots (ind. m^{-3}) of *F. borealis* and *L. helicina* in the Canada Basin 2003–2006.

During 2003, 2004 and 2006, *F. borealis* was less abundant in the south of our study area, towards the shelf break. Beyond that, no obvious spatial pattern of abundance was observed for *F. borealis* or *L. helicina* (Fig. 7). For most species, the distance to the coastline, bottom depth and mean salinity (surface to 100 m) each explained less than 8% of the variance (Table III). For *C. hyperboreus*, the distance to the coast explained 30% of the variance and salinity explained 36% of the variance. For *O. similis*, 21% of the variance was accounted for by salinity (Table III).

Table III: Relationship between zooplankton abundance and distance to coast, bottom depth and mean salinity for the upper 100 m of the Canada Basin from 2003 to 2006

Species	r^2 coast	r^2 depth	r^2 salinity
<i>Calanus glacialis</i>	0.05	0.01	0.02
<i>Calanus hyperboreus</i>	0.3	0.006	0.36
<i>Metridia longa</i>	0.11	0.02	0.08
<i>Microcalanus</i> sp.	0.0006	0.046	0.015
<i>Oithona similis</i>	0.00002	<0.001	0.21
<i>Fritillaria borealis</i>	0.04	0.14	0.002
<i>Limacina helicina</i>	0.08	0.0015	0.004

Abundance data were log-transformed.

Community structure

The hierarchical cluster analysis using abundance data showed one large group (group F: 37 samples) and five smaller groups (group A: 3 samples; group B: 2 samples; group C: 6 samples; group D: 2 samples; group E: 4 samples) and six single samples (hereafter called outliers except for station 28A) formed at 67–81% similarities. The large group F consisted of 17 samples from 2003, 14 samples from 2004, 5 samples from 2006 and 2 samples from 2005 (Fig. 8). The second largest group was group C with a total of six samples from all years except 2003. Most of the multiyear stations clustered together in groups C, D and F, indicating that community structure was fairly similar throughout the years for these stations (Fig. 8). However, some multiyear stations were by themselves as outliers or in separate groups. The nMDS

(2D stress: 0.22; 3D stress: 0.16) reinforced this pattern. SIMPER analysis revealed that most of the similarity within groups C and F was due to *O. similis*, *Microcalanus* and calanoid nauplii. Most of the dissimilarity between group C and F was due to *Triconia*, *O. similis* and *Microcalanus*.

The hierarchical cluster analysis of biomass showed seven groups that formed at 62–74% similarity. The majority of the samples were sorted into two larger groups (group B: 32 samples and group C: 21 samples), one smaller group (group A: 3 samples) and 4 samples that were by themselves (hereafter called outliers except for station 28A) (Fig. 9). This pattern was also presented in the nMDS (2D stress: 0.19; 3D stress: 0.14). Groups B and C contained samples from all years. The majority

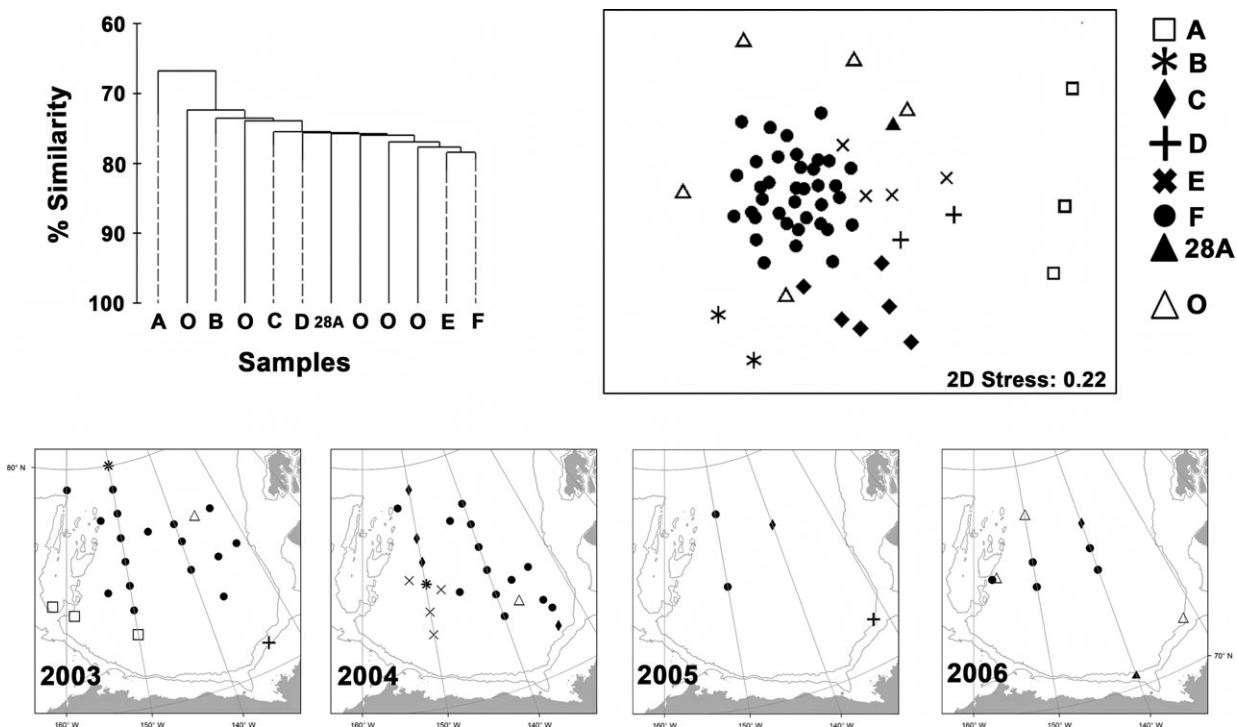


Fig. 8. Hierarchical clustering analysis of fourth-root transformed abundance (Bray–Curtis similarity in %, solid lines: outliers (O); broken lines: multiple stations), nMDS plot and spatial distribution of zooplankton abundance groups in the Canada Basin 2003–2006. Spatial maps with 100 and 1000 m depth contours.

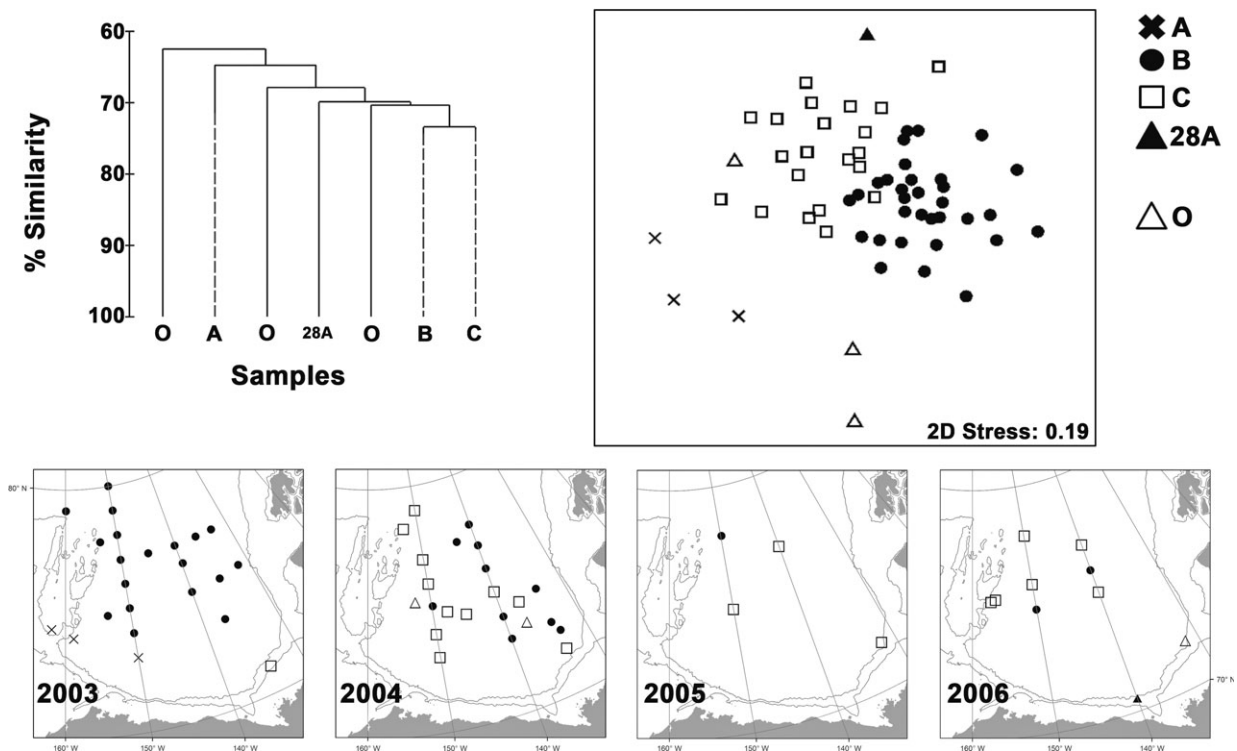


Fig. 9. Hierarchical clustering analysis of fourth-root transformed biomass (Bray–Curtis similarity %, solid lines: outliers (O); broken lines: multiple stations), nMDS plot and spatial distribution of zooplankton biomass groups in the Canada Basin 2003–2006. Spatial maps with 100 and 1000 m depth contour.

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Table IV: BEST BIO-ENV analysis of zooplankton community structure in the Canada Basin 2003–2006 to temperature (*T*), salinity (*S*), oxygen (*O*), distance to coastline (*C*) and bottom depth (*B*)

	Surface	0–50 m	0–100 m
Abundance	T (0.323)	B (0.2)	B (0.2)
	C, B (0.288)	T, B (0.297)	T, B (0.332)
	T, C, B (0.306)	T, C, B (0.342)	T, C, B (0.356)
	T, O, C, B (0.314)	T, S, C, B (0.354)	T, S, C, B, (0.351)
	T, S, O, C, B (0.315)	T, S, O, C, B (0.338)	T, S, O, C, B (0.318)
Biomass	T (0.293)	B (0.214)	B (0.214)
	T, B (0.249)	T, B (0.236)	T, B (0.267)
	T, O, B (0.253)	T, S, B (0.256)	T, C, B, (0.265)
	T, O, C, B (0.235)	T, S, C, B (0.252)	T, S, C, B (0.252)
	T, S, O, C, B (0.225)	T, S, O, C, B (0.242)	T, S, O, C, B (0.233)

Best combinations explaining clustering for abundance and biomass are in bold. ρ is given in parentheses.

of samples in group C were from 2004 (11 samples) followed by 2006 (6 samples), 2005 (3 samples) and only 1 sample was from 2003. The majority of samples in group B were from 2003 (19 samples), followed by 2004 (10 samples) and 2005 and 2006 only contributed 1 and 2 samples, respectively, to group B. Most of the Basin stations from 2003 to 2006 were within groups B and C. The main differences between these two groups were a lower mean biomass of *M. longa*, *T. libellula* and *Parasagitta elegans* in 2003 compared to 2004, but these differences were only significant for *M. longa* ($P \leq 0.001$; Supplementary Table SI). Group A consisted of three stations from 2003, all of which were located on the south-western part of the study area. Group A in the biomass analysis consists of the exact same samples as group A in the abundance analysis. The similarity in the abundance of these three samples was due to *Pseudocalanus*, *O. similis* and calanoid nauplii. The similarity for biomass was driven by *C. glacialis*, *E. hamata* and *C. hyperboreus*.

Sample 28A was displayed as a single sample in terms of biomass and abundance (Figs 8 and 9) and was located the closest to the mouth of the Mackenzie River, which influences the species composition and abundance. Compared to other groups, it had a very low abundance of *F. borealis* and *C. glacialis* and was the only station where the neritic *Centropages abdominalis* was observed. The sample CABOSs was also located closer to the shelf than most stations. It is notable that CABOSs was a multiyear station that was sampled during all years, and whereas the other three CABOS samples clustered in group C for biomass, the sample from 2006 was by itself. The CABOSs sample was one of only two samples where *E. bungii* was observed and *M. longa* and *T. libellula* were absent from the sample. The absence of *M. longa* and *T. libellula* during 2006 contributed the most to the dissimilarity between the CABOSs sample and group C according to the SIMPER analysis.

According to the BEST analysis, a combination of mean temperature for the upper 100 m, distance to coastline and bottom depth were the best environmental variables to explain the variance for community structure based on abundance ($\rho = 0.356$). Sea surface temperature was the best variable to explain the variance for biomass ($\rho = 0.293$) (Table IV). Adding salinity and oxygen to the models did not improve the relationships (Table IV).

DISCUSSION

Community structure, abundance and biomass

The zooplankton community in the Canada Basin consisted mostly of species characteristic for the Arctic such as *C. hyperboreus*, *C. glacialis*, *M. longa*, *O. similis*, *M. pygmaeus*, *F. borealis* and *L. helicina* (Johnson, 1956; Conover and Huntley, 1991; Auel and Hagen, 2002; Hopcroft *et al.*, 2005; Lane *et al.*, 2008), whereby small copepods dominated the abundance and larger bodied copepods dominated the biomass. These patterns are consistent with previous studies conducted in the Canada Basin and Beaufort Sea slope (Darnis *et al.*, 2008; Kosobokova and Hopcroft, 2010; Hunt *et al.*, 2014; Smoot and Hopcroft, 2017a) and were reflected in our copepod size spectra (Fig. 5), which displayed the pattern typical for Arctic basin copepods (Hopcroft *et al.*, 2005). Non-copepod abundance was dominated by larvaceans, except in 2005 when *L. helicina* dominated the non-copepod abundance. However, due to the small sample size in 2005, we cannot be certain whether pteropods were unusually dominant in the basin, although Kosobokova and Hopcroft (2010) also reported pteropods being more abundant than larvaceans slightly earlier in that same year. The major contribution of chaetognaths and hydrozoans to non-copepod biomass

is also consistent with previous studies (Hopcroft *et al.*, 2005; Kosobokova and Hopcroft, 2010).

The Canada Basin zooplankton community is very homogenous spatially and has an insignificant interannual variability during our observation window, possibly due to the relatively long life cycles of most predominant species like *C. hyperboreus* (2–4 years) (Hirche, 1997; Broms *et al.*, 2009), *C. glacialis* (2 years) (Kosobokova, 1999). The main patterns observed with the hierarchical clustering analysis and nMDS for abundance and biomass (Figs 8 and 9) confirm the observation of spatial homogeneity, with two large groups that incorporated samples from all years (mostly Basin samples). However, despite no statistical significant interannual differences in overall mean abundance and biomass, biomass cluster C consisted predominantly of 2004 samples and cluster B of samples from 2003. The PERMANOVA also revealed that the year has an effect on the zooplankton community. This could be due to a difference in sea ice concentration and the environmental conditions associated with it. During 2004, the ice edge was further north than during 2003 with a higher concentration of first-year ice observed in the southern Canada Basin and Beaufort Sea compared to 2004 (National Ice Center: Weekly chart products; <http://nsidc.org/data/bist/>). A sea ice retreat beyond the shelf break can lead to increased wind-driven upwelling at the shelf break (Carmack and Chapman, 2003), which brings nutrient-rich water into the surface layers and leads to increased production.

Besides observing the spatial homogeneity of the Canada Basin zooplankton community, we found the same distinctions between the shelf/slope and the basin stations as in Hunt *et al.* (2014). The BEST analysis supports the influence of station depth on differences between zooplankton communities, since the best models for abundance included bottom depth. The basin stations were characterized by the general absence of shelf taxa, although stations in the western basin had low numbers of meroplankton, which suggests some transport from the shelf into the basin by eddies (Llinás *et al.*, 2009). The clusters of shelf/slope stations (abundance: group A; biomass: group A) were defined by higher *Pseudocalanus* abundance and the presence of cirripedia nauplii and cyprids, which are all characteristics for water masses influenced by shelf/slope waters (Smoot and Hopcroft, 2017a). That station 28A was not included into the shelf/slope cluster, but displayed as a single sample for abundance as well as biomass likely reflects an influence by runoff from the Mackenzie River. This is further supported by the observation of the neritic copepod *Centropages abdominalis* and echinoderm larvae (Walkusz *et al.*, 2010; Smoot and Hopcroft, 2017a) in the sample.

The average abundance of *C. glacialis* and *C. hyperboreus* was of the same order of magnitude as previous observations in the same area (Hunt *et al.*, 2014), and those further towards the Chukchi Sea and central Arctic (Thibault *et al.*, 1999). While the abundance of *C. hyperboreus* and *M. longa* seemed to be impacted by the fresher water in the core of our study area, the abundance of *O. similis* did not appear to be substantially influenced. This may reflect the more euryhaline and eurythermic character of *O. similis* (Nishida, 1985; Nielsen *et al.*, 2002) compared to Arctic endemic species. *Oithona similis* showed a significant increase in mean abundance (P -value = 0.05) from 2003 to 2006. However, 4 years of observation is insufficient to convincingly establish whether these trends are persistent or not.

It is notable that we report higher mean abundance, but similar biomass and cluster structure, in both 2004 and 2006 than Hunt *et al.* (2014), who reported on samples collected concurrently in those years. This is a direct reflection of our finer mesh size of 150 μm (compared to their 236 μm) that catches earlier stages of smaller, abundant species such as *O. similis* and *M. pygmaeus* as well as copepod nauplii (Gallienne and Robins, 2001; Hopcroft *et al.*, 2005) that contribute little to community biomass. Our mean biomass for all years was slightly higher than the 9.6 mg m^{-3} (Hopcroft *et al.*, 2005) reported for 2002 using a similar methodological approach. The non-significant Spearman's rank correlation coefficients indicate that there is no significant change in abundance or biomass from 2003 to 2006, but if we combine our observation with those preceding (Hopcroft *et al.*, 2005) and partially overlapping (Hunt *et al.*, 2014) our observation period, it becomes clear that there has been an increasing trend in mean biomass from 2002 to 2008 (except in 2004).

Historic comparison

Historic datasets for comparison to our findings are limited for the Canada Basin due to the remoteness of the area as well as the ice cover. Most previous data come from ice-stations such as Drift Station Alpha (Johnson, 1963), T-3 ice islands (Scott, 1969), NP-22 and NP-23 (Kosobokova, 1982) and the Surface Heat Budget of the Arctic Ocean (SHEBA) (Ashjian *et al.*, 2003). The extremely low abundances suggested at Drift Station Alpha are most likely due to incomplete descriptions of methodology and shall be ignored. The T-3 ice island copepod mean abundance for August 1966 to 1969 were 105 ind. m^{-3} (mesh size 215- μm , sampling depth up to 100 m) (Scott, 1969), about 5–10-fold lower than our mean abundance, in part due to differences in collection mesh size. The mean abundance observed from

the ice-stations NP-22 and NP-23 during August and September 1975 and 1977 was 349 ind. m⁻³ (mesh size 180 µm). The NP-22 stations were located further north in the central Arctic compared to our study. Our data (811 ind. m⁻³ mean abundance for 2003, 2004 and 2006) were much closer to the mean abundance for the zooplankton community reported for SHEBA of 591 ind. m⁻³ (Ashjian *et al.*, 2003) for August and early September in 1998 (mesh size 150-µm, sampling depth: 100 m, lifestage “eggs” omitted) and that of Smoot and Hopcroft (2017b) of about 744 ind. m⁻³ along the Beaufort Slope for August and September 2012–2014 (mesh size 150 µm, sampling depth 100 m).

Overall, there is a suggestion of increasing mean abundance when comparing the historic and recent datasets. However, caution must be exercised comparing contemporary data to historical data due to differing sampling techniques, areas, as well as changing taxonomy (e.g. Johnson, (1956) reported *C. funmarchicus* instead of *C. glacialis*, since *C. glacialis* was not described by Jaschnov until 1955 (Jaschnov, 1955)). Nevertheless, increasing copepod biomass has also been suggested to occur in the adjoining Chukchi Sea (Ershova *et al.*, 2015). The lack of historic data that are comparable to our study, and the suggestion of increasing abundance and biomass highlight the need for the Canada Basin to be sampled more regularly and with consistent methods.

CONCLUSION

The epipelagic zooplankton communities of the Canada Basin are dominated by copepods both in number and in biomass. We found that there was no obvious inter-annual change in community structure over our short 4-year observation period, with community structure influenced to a small degree by environmental factors. When our observations are combined with contemporary studies (Hopcroft *et al.*, 2005; Hunt *et al.*, 2014) and historical data, both abundance and biomass have displayed increasing long-term trends.

SUPPLEMENTARY DATA

Supplementary material is available at *Journal of Plankton Research* online.

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DATA ARCHIVING

<https://arcticdata.io/catalog/#view/doi:10.18739/A27S4S>

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