

RESEARCH ARTICLE

10.1002/2013JC009156

Special Section:

Canada's Three Oceans Project, A Canada's International Polar Year Initiative

Key Points:

- Mesoscale distribution of Arctic zooplankton communities
- Climate change impacts on Arctic zooplankton
- Allochthonous versus autochthonous production in the Canada Basin

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Citation:

Hunt, B. P. V., R. John Nelson, B. Williams, F. A. McLaughlin, K. Young, K. A. Brown, S. Vagle, and E. C. Carmack (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, doi:10.1002/2013JC009156.

Received 27 MAY 2013

Accepted 21 MAR 2014

Accepted article online 25 MAR 2014

Published online 22 APR 2014

Zooplankton community structure and dynamics in the Arctic Canada Basin during a period of intense environmental change (2004–2009)

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Abstract Mesozooplankton were sampled in the Canada Basin in the summers of 2004, 2006, 2007, 2008, and fall 2009. Six taxa (*Calanus hyperboreus*, *Calanus glacialis*, *Oithona similis*, *Limacina helicina*, *Microcalanus pygmaeus*, and *Pseudocalanus* spp.) accounted for 77–91% of the abundance in all years, and 70–80% of biomass in 2004–2008. The biomass of *C. hyperboreus* and *C. glacialis* was reduced in 2009, likely due to seasonal migration below the sampling depth. Mean abundance was consistent across surveys while biomass increased from 18.92 to 32.56 mg dry weight m⁻²³ between 2004 and 2008. Multivariate analysis identified a clear separation between shelf and deep basin (>1000 m) assemblages. Within the deep basin abundance and biomass were higher in the west, associated with a higher chlorophyll maximum. In 2007 and 2008 considerable heterogeneity developed in the assemblage structure, associated with variability in the contribution of the short-lived (<1 year) copepod species *O. similis* and *M. pygmaeus*. Conversely, the long lived (≥2 years) *C. hyperboreus* and *C. glacialis* showed an increasingly consistent spatial distribution of high biomass from 2004 to 2008. We propose that a greater dependence on autochthonous basin production by the short-lived species resulted in their decreased secondary production in the freshening Beaufort Gyre in 2007 and 2008. Conversely, long-lived species were supported by high allochthonous production on the Beaufort and Chukchi shelves and lipid stores accumulated from this source enabled them to persist in the low chlorophyll a biomass conditions of the Canada Basin.

1. Introduction

The Arctic Ocean is undergoing rapid and dramatic changes in response to climate forcing, perhaps most palpably evident in the decline in the September sea-ice minimum. Since the advent of satellite observations in 1979, September sea-ice extent has decreased by ~12% per decade [Comiso et al., 2008; Stroeve et al., 2012]. The period 2007–2010 recorded the four lowest minima on record [Stroeve et al., 2012], due to the positive feedback between reduced sea-ice albedo and increased upper ocean heat uptake [Perovich et al., 2007]. These and other changes outlined below are expected to have multiple and far reaching consequences for the Arctic's pelagic ecosystems. Due to their short life histories and sensitivity to environmental change [Reid and Edwards, 2001], the zooplankton are expected to be amongst the first organisms to show a response.

One of the most strongly impacted Arctic regions is the Beaufort Sea of the Canada Basin which, along with the Chukchi Sea, has experienced increases in heat uptake of up to 4% per year between 1979 and 2005 [Perovich et al., 2007]. Within the Beaufort Gyre, the near-surface summer temperature maximum has been observed to shoal and expand in areal extent between 1993 and 2008 [Jackson et al., 2010], while the temperature of the Pacific summer water [Shimada et al., 2006] and Atlantic water core has increased [McLaughlin et al., 2009]. Surface warming has increased sea-ice melt in the Canada Basin, and the resultant freshwater input has decreased salinities there [Yamamoto-Kawai et al., 2009b]. This increased melt, together with an increase in Ekman convergence that has brought additional riverine discharge to the region, has contributed to the interannual freshening of the upper water column of the Beaufort Gyre [McLaughlin and Carmack, 2010; Yamamoto-Kawai et al., 2009b].

Associated with increased sea-ice melt, undersaturation ($X < 1$) of aragonite has been observed in Beaufort Sea surface waters [Yamamoto-Kawai et al., 2009a]. At these X levels aragonite shelled organisms, such as

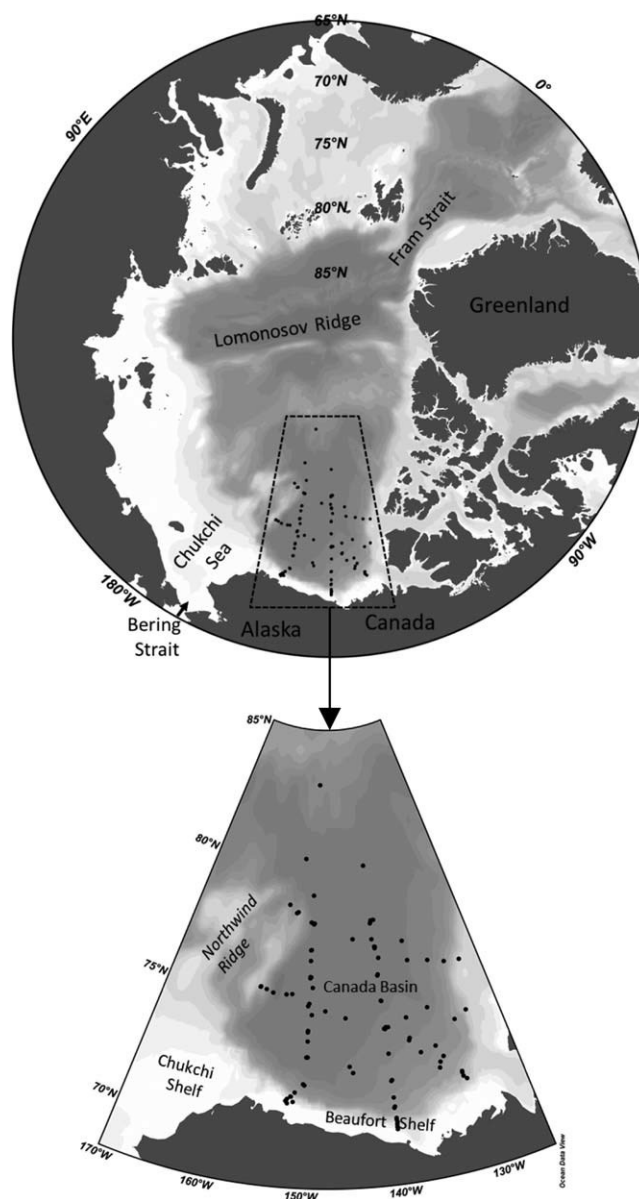


Figure 1. Map of the Arctic Ocean with the study area in the Canada Basin indicated by a polygon. All stations sampled during this study (2004, 2006, 2007, 2008, and 2009) are indicated. Figures 4 and 7 show the distributions of stations for individual years.

Canada Basin was mainly limited to the shelf areas and margins [e.g., Grainger, 1965], and sporadic drifting ice stations in the deep basin. The latter include the T-3 (1965–1966) ice islands [Hopkins, 1969], the NP-22 (1975–1976) Russian drifting station [Melnikov and Kolosova, 2001], and most recently the SHEBA (1997–1998) US/Canada ship drifting station [Melnikov and Kolosova, 2001; Ashjian et al., 2003]. Summer sampling from ice-breakers has contributed to filling data gaps in the northern Canada Basin [Kosobokova and Hirche, 2000; Thibault et al., 1999], while sampling programs in the 2000s provided additional data from shelf and shelf-break environments [Darnis et al., 2008; Lane et al., 2008; Llinas et al., 2009; Walkusz et al., 2010]. However, zooplankton sampling from the central Canada Basin remains sparse [Hopcroft et al., 2005; Kosobokova and Hopcroft, 2010], and to date no study of the interannual variation in zooplankton communities has been reported. In conjunction with the oceanographic surveys conducted during the Canada/US Beaufort Gyre Exploration Project, mesoscale zooplankton surveys were carried out in the Canada Basin in 2004 and 2006–2009. In this paper, we use this sample set to conduct an analysis of interannual variation in

the arctic pteropod *Limacina helicina*, are vulnerable to dissolution [Bednaršek et al., 2012; Comeau et al., 2010]. The retreat of the ice edge away from the Beaufort Shelf is expected to result in enhanced wind-driven upwelling of deep nutrient rich but aragonite undersaturated water [Carmack and Chapman, 2003], which may both exacerbate acidification [Yamamoto-Kawai et al., 2009a] and enhance shelf primary production through nutrient addition [Carmack and Chapman, 2003].

In the Canada Basin interior, the thinning of sea-ice was predicted to favor increased primary production through enhanced light availability in the surface ocean [Lee and Whittedge, 2005]. Satellite remote sensing has indeed shown an increase in production in the Arctic Ocean as a whole [Arrigo et al., 2008], although as yet, no increase has been observed in the Canada Basin [Grebmeier et al., 2010]. The latter observation is supported by in situ phytoplankton biomass measurements made during repeated oceanographic surveys between 2003 and 2009 [Li et al., 2009]. Water column profiles from these same surveys have demonstrated a deepening of the nutricline in the Beaufort Gyre due to freshwater input from meltwater, a corresponding deepening of the chlorophyll maximum [McLaughlin and Carmack, 2010], and a shift from nano to pico dominated phytoplankton communities [Li et al., 2009; Nishino et al., 2011].

Until the last decade, knowledge of the zooplankton communities of the

Table 1. Dates of Sampling and Number of Nets Tows Completed During Each of the Canada Basin Zooplankton Surveys Analyzed for This Study

	Survey Begin	Survey End	Number of Net Hauls
2004	6 Aug	28 Aug	25
2006	8 Aug	4 Sep	9
2007	28 Jul	24 Aug	20
2008	21 Jul	18 Aug	28
2009	18 Sep	7 Oct	25

zooplankton community composition, with the aim of investigating its response to the changing environment in the Canada Basin.

2. Methods

2.1. Sample Collection and Processing

Zooplankton net hauls were carried out in the Canada Basin in 2004, 2006, 2007, 2008, and 2009 (Figure 1). In all cases a bongo net was used, hauled vertically between 100 m and the surface. The nets had a 236 mm mesh and a mouth diameter of 60 cm. The number of net hauls was ≥ 20 in all years, with the exception of 2006 when nine were completed (Table 1). In all years sampling spanned the shelf and off-shelf regions (Figures 4 and 7). However, the majority of the stations (95) were in water deeper than 1000 m compared to five stations on the shelf-break in water 250–1000 m deep and seven stations on the shelf proper with depths < 250 m. The volume of seawater filtered was estimated from flow meter measurements, either a TSK or Seagear MF-315. In some instances, when the flow meter failed, the volume filtered was calculated assuming 100% filtration (tow depth $\times$ mouth area).

Zooplankton were examined under a dissecting microscope, identified to species where ever possible, to stage in the case of copepod species, and enumerated. Large species were enumerated from the entire sample. Densities of small and/or common taxa were determined from subsamples produced using a Motoda plankton splitter and ranged in size from 1/2 to 1/64. Zooplankton densities were expressed as individuals m^{-2} . In the case of noncopepod taxa, all specimens were categorized according to standardized size classes. These size classes were used for dry weight biomass estimation of noncopepod taxa according to species specific relationships established by the Department of Fisheries and Oceans Pacific Region zooplankton processing lab (D. Mackas, and M. Galbraith, unpublished data, 2012). In the case of copepods, biomass was estimated according to stage and species specific length-weight relationships (D. Mackas, and M. Galbraith, unpublished data, 2012). Biomass for all taxa was expressed as mg dry weight (DW) m^{-2} . *Calanus hyperboreus* included all specimens from Adult to Copepodite III; *Calanus glacialis* included Adult and Copepodite CV; the taxonomic grouping “*Calanus* copepodites” comprised all of the remaining copepodite stages of these two large calanoid copepod species, CI and CII in the case of *C. hyperboreus* and CI to CIV in the case of *C. glacialis*. *Paraeuchaeta* copepodite stages were not identified to species and all specimens in this genus were grouped as *Paraeuchaeta* spp. Based on adult species composition they were predominantly *Paraeuchaeta glacialis*.

Water column profiles were completed at each station with a Seabird CTD (SBE 911 plus) equipped with a fluorescence sensor. Temperature sensors were calibrated annually, while conductivity sensor data were calibrated with salinity bottle data following methods reported in McLaughlin et al. [2008]. Water samples were collected from the fluorescence maximum using niskin bottles and filtered through precombusted 0.7 mm Gelman glass fiber filters. Chlorophyll was then extracted from the filters in 90% acetone and measured using a Turner Designs fluorometer (Sunnyvale California) following the method of Parsons et al. [1984]. In some cases where no bottle samples were collected, the value of the chlorophyll a maximum was estimated from correlations established between fluorescence and chlorophyll a on each voyage (2004: $n = 210$, $R^2 = 0.88$; 2006: $n = 56$, $R^2 = 0.93$; 2007: $n = 183$, $R^2 = 0.71$; 2008: $n = 199$, $R^2 = 0.66$; 2009: $n = 102$, $R^2 = 0.64$).

Sea-ice concentration along the cruise track was obtained at 3.125 km resolution from the University of Bremen, Germany (www.seaice.de). Daily concentrations were determined from the Advanced Microwave Scanning Radiometer sensor (89 GHz frequency) on NASA's Earth Observing System satellite (AMSR-E) using

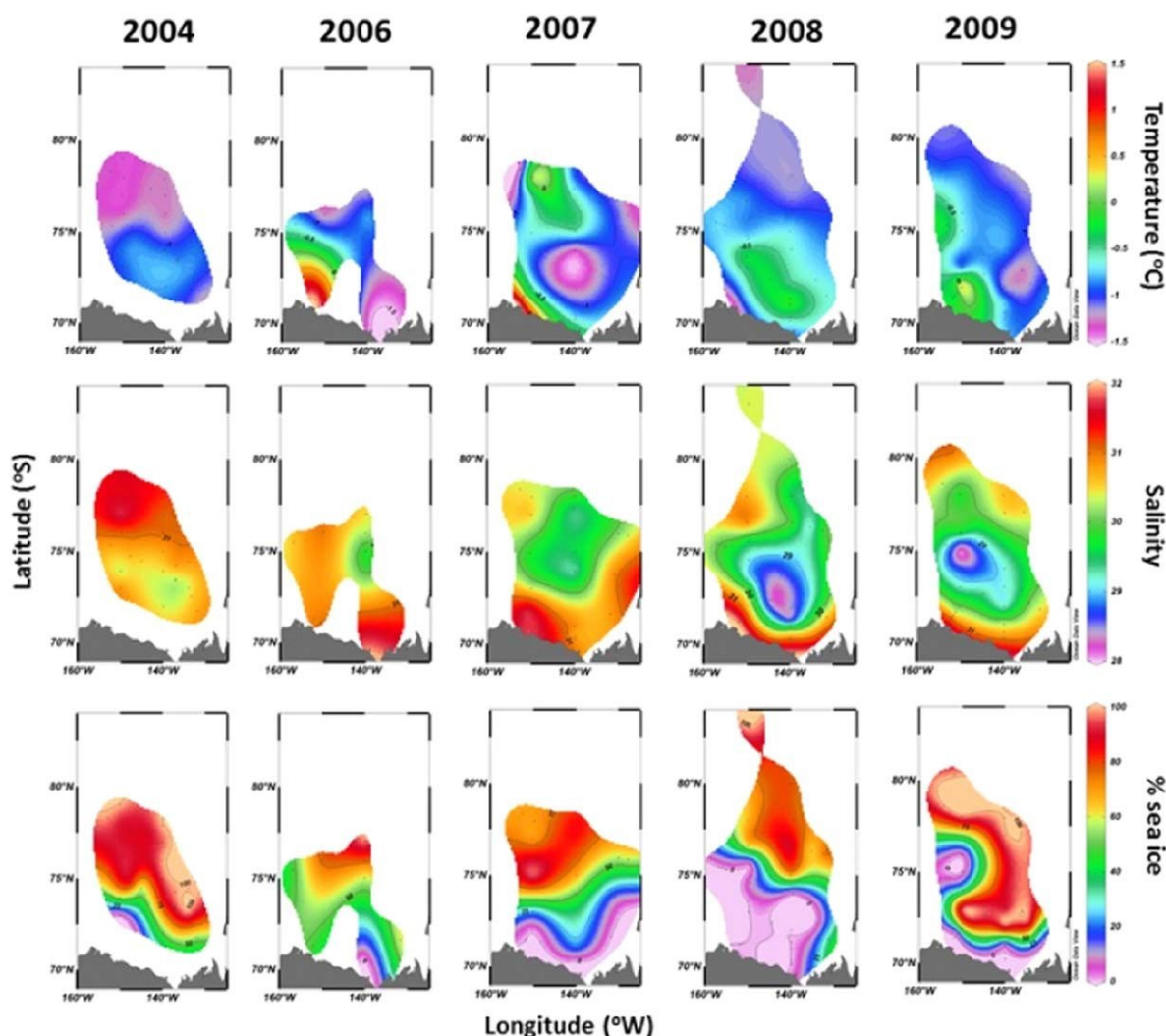


Figure 2. Contour plots of temperature ($^{\circ}\text{C}$), salinity, sea-ice cover (%), value of the chlorophyll *a* maximum (mg m^{-23}), depth of the chlorophyll *a* maximum (m), zooplankton abundance (individuals m^{-23}), and zooplankton biomass ($\text{mg dry weight m}^{-23}$) for each of the survey years 2004, 2006, 2007, 2008, and 2009.

the ARTIST Sea Ice algorithm [Spreen et al., 2008]. The reported sea-ice concentration at each station was determined by a nearest neighbor bilinear interpolation between the four grid cells closest to the actual station location.

2.2. Analysis

Mean values of temperature and salinity were determined for the upper 100 m of the water column, matching the depth stratum sampled for zooplankton composition. Hereafter, any mention of these variables refers to 100 m mean values. Contour plots of spatial distributions of key physical and biological variables were produced using Ocean Data View V4.5.

The similarity of the zooplankton community among stations across all years was estimated using the Bray-Curtis similarity metric, applied after $\log_{10}(x + 1)$ transformation of the data to reduce the influence of the few high abundance/biomass taxa. Similarity matrices were produced for both the abundance and biomass data. Each similarity matrix was clustered using unweighted pair group average sorting to identify zooplankton assemblages. Nonmetric multidimensional scaling (NMDS) was performed on the same similarity matrices to provide a visual representation of station similarities, and to provide additional validation of the station groupings identified by cluster analysis. NMDS has the advantage of summarizing between station community relationships into a low number of dimensions. These data can be regressed or correlated with

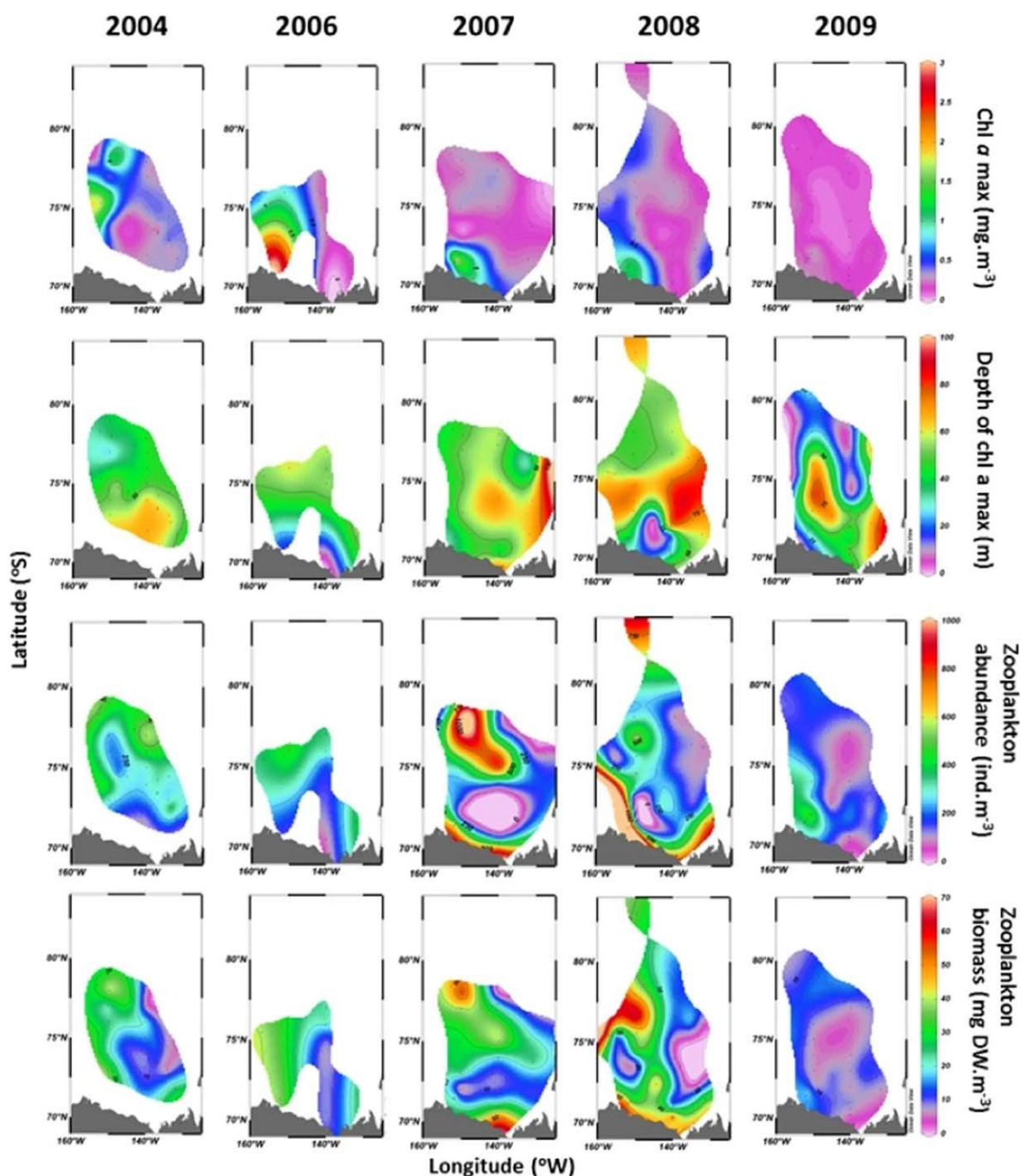


Figure 2. (continued)

station environmental data to provide insight into the factors controlling community composition. The cluster and NMDS analyses were performed using Primer 6.0.

The species associated with each of the identified station groupings were investigated as follows. The SIMPER (SIMilarity of PERcentages) routine in Primer 6.0 was used to identify the species that contributed most to the Bray-Curtis similarities of stations within the identified station groupings. As outlined above, these similarity levels were based upon comparison of abundance/biomass levels of species within stations across all years. In this study, we present only the species contributing to the first 70% similarity within groups. In addition to SIMPER, indicator species were identified for each station cluster using Indicator Value (IndVal)

analysis [Dufrene and Legendre, 1997]. The IndVal method combines measures of group specificity (A_{ij}) and group fidelity (B_{ij}):

$$A_{ij} = \frac{\text{Nindividuals}_{ij}}{\sum_j \text{Nindividuals}_{ij}}$$

and

$$B_{ij} = \frac{\text{Nsamples}_{ij}}{\sum_j \text{Nsamples}_{ij}}$$

where Nindividuals_{ij} is the mean number of individuals of species i in the samples of group j and $\sum_j \text{Nindividuals}_{ij}$ is the sum of the mean numbers of individuals of species i over all groups. Nsamples_{ij} is the number of samples in group j where species i is present, and $\sum_j \text{Nsamples}_{ij}$ is the number of samples in group j . Subsequently, the IndVal value was calculated as

$$\text{IndVal} = A_{ij} \times B_{ij} \times 100$$

The values of A and B were multiplied as they represent independent information about species distribution, and then multiplied by 100 to produce percentages. An IndVal of $\geq 25\%$ was selected as the cutoff point for indicator species using this method, which meant that a species was present in $\geq 50\%$ of samples in a group and that its relative abundance (or biomass) in that group was $\geq 50\%$. The same method was applied to the biomass data. IndVal analysis was performed using the Labdsv package in R (<http://www.rproject.org>).

To identify the environmental conditions that underpinned the zooplankton assemblage distributions, the first two dimensions of the NMDS analysis were regressed against temperature, salinity, % sea-ice cover, station depth, year, Julian day, latitude, longitude, and the value and depth of the chlorophyll a maximum. The NMDS scores were used as the independent variables and each environmental variable as a dependant variable [Kruskal and Wish, 1978]. The direction cosine (regression weight) c_r of that angle is determined from the formula of Kruskal and Wish [1978]:

$$c_r = \frac{b_1 r_1 + b_2 r_2 + \dots + b_k r_k}{\sqrt{b_1^2 + b_2^2 + \dots + b_k^2}}$$

where $b_1, b_2, \dots, b_k$ are the regression coefficients from the multiple regression $a = b_1 x_1 + b_2 x_2 + \dots + b_k x_k$, and k is the number of independent variables (in this case the two NMDS dimensions). Using c_r , lines representing the contribution (regression weight) of environmental variables to the grouping of station specific assemblage types were plotted on the NMDS ordination. All calculations were made using the Vegan package in R (<http://www.rproject.org>).

3. Results

3.1. Distribution of Physical and Biological Properties

Mean temperature in the upper 100 m of the water column ranged between 1.5 and 21.5°C (Figure 2). Although relatively high temperatures ($>0.5^\circ\text{C}$) were observed in the southwest basin and shelf in 2006 and 2007 (Figure 2), mean values overall increased from 2004 to 2008 (Figure 3). Temperature tended to decrease with increasing latitude (Figure 2 and Table 2), but showed considerable horizontal variability.

Salinity was always lowest in the central basin, associated with the Beaufort Gyre (Figure 2). The mean salinity of the stations sampled decreased from 2004 to 2008 and remained low in 2009 (Figure 3). This interannual decrease was largely due to the freshening of the Beaufort Gyre, clearly evident in the salinity contours (Figure 2).

In all years, sea-ice cover increased from south to north, into the deep Canada Basin, and the shelf waters of the Beaufort Sea were largely ice free in summer/fall (Figure 2). In 2007 and 2008, the Canada Basin was ice free south of 74°N and 75°N , respectively (Figure 2), despite these surveys being 1–2 weeks earlier than

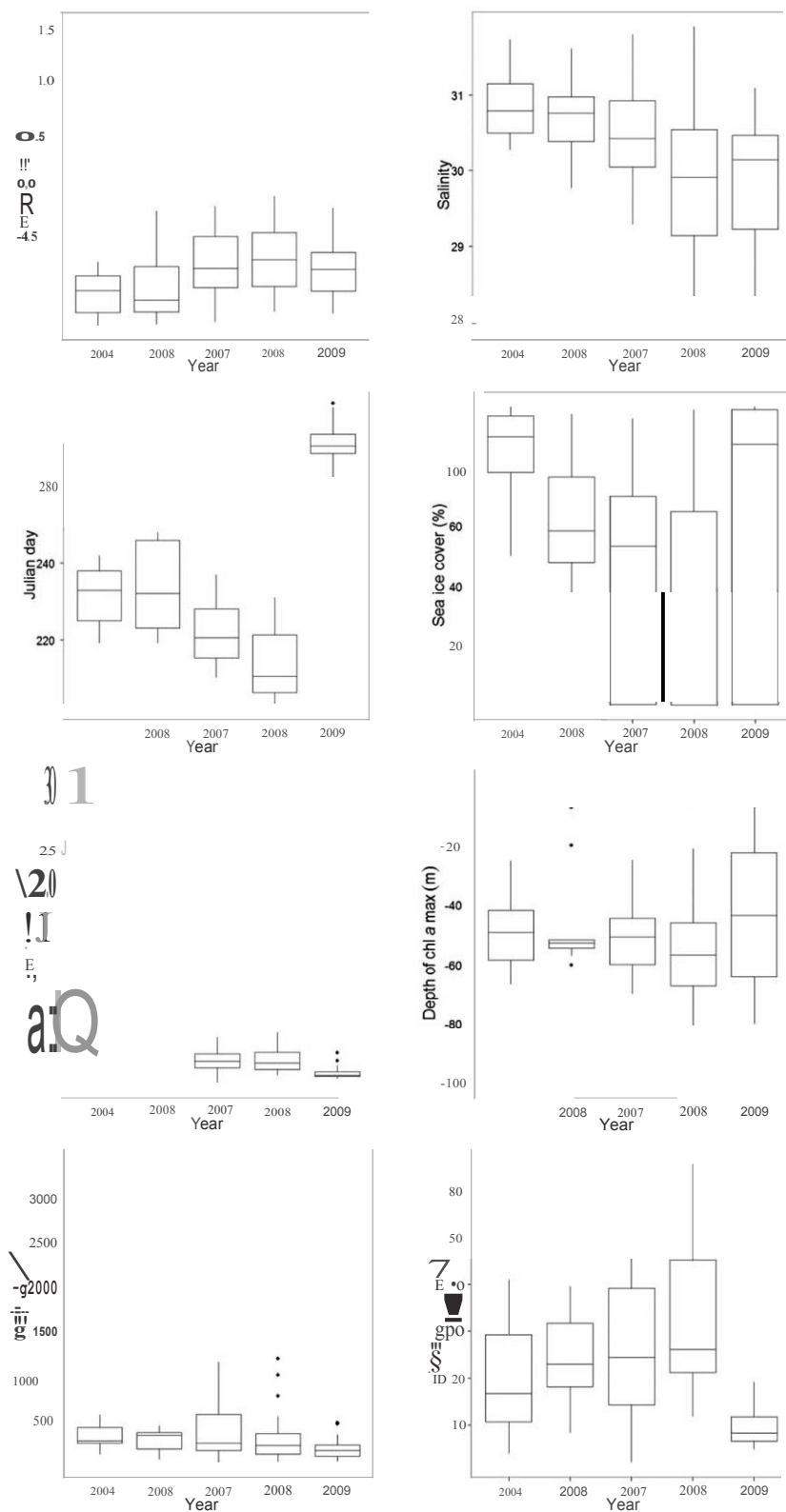


Figure 3. Box-and-whisker plots of temperature (°C), salinity, Julian day, sea ice cover (%), value of the chlorophyll *a* maximum (mg m⁻³), depth of the chlorophyll *a* maximum (m), zooplankton abundance (individuals m⁻³) and zooplankton biomass (mg dry weight m⁻³) for each of the survey years: 2004, 2006, 2007, 2008, and 2009. The dark line inside the box for each variable represents the median. The bottom and top edges of the box represent the first and third quartiles, respectively. The vertical error bars extend to the lowest and highest data value inside a range of 1.5 times the interquartile range, respectively, while dots represent data points outside this range.

Table 2. Pearson Correlation Coefficients Between Environmental Parameters

	Latitude	Longitude	Julian Day	Depth	Temperature	Salinity	Sea Ice	Cmax	DCM
Latitude	1								
Longitude	0.23	1							
Julian Day	0.04	20.08	1						
Bottom depth	0.59 ^a	0.05	0.1	1					
Temperature	20.39 ^a	0.26 ^b	20.06	20.28 ^b	1				
Salinity	0.01	0.11	20.20 ^c	20.36 ^a	20.14	1			
Sea ice	0.60 ^a	20.19	0.29 ^b	0.47 ^a	20.44 ^a	0.08	1		
Cmax	20.10	20.33 ^a	20.29 ^b	20.21 ^b	0.28 ^b	0.41 ^a	20.06	1	
DCM	0.01	0.26 ^b	20.11	0.20	20.16	20.28 ^b	0.01	20.16	1

^ap < 0.001.

^bp < 0.01.

^cp < 0.05.

those in 2004 and 2006 (Table 1). The 2009 survey occurred in late fall, a minimum of 2 weeks later than the preceding four survey years, and high ice cover was observed (>60%) except over the shelf/shelf-break and the east central Canada Basin adjacent to the Northwind Ridge (Figure 2), reflecting annual sea-ice regrowth.

The mean value of chlorophyll a maximum depth was <0.5 mg m⁻³ in all years (Figure 3). In 2004, when the southwest Beaufort Shelf was not sampled, the highest chlorophyll a maximum concentrations were recorded in the western basin in the vicinity of the Northwind Ridge (Figure 2). In all subsequent years, the highest values were always observed in the region of the southwest basin and on the Beaufort Shelf. The highest chlorophyll a maximum values occurred in 2006 and values were uniformly low in 2009 because of seasonality. The mean depth of the chlorophyll a maximum ranged between 42 m in 2009 and 53 m in 2008 (Figure 3). The deepest chlorophyll a maximum depths were recorded in 2007, 2008, and 2009, all of these years having values >75 m. The negative correlation between salinity and the depth of the chlorophyll a maximum indicated that the chlorophyll a maximum depth was strongly associated with freshwater input. The shallowest chlorophyll a maximum depths were observed outside the low salinity core of the Beaufort Gyre and on the shelf (Figure 2).

Correlation analysis summarized the relationships between environmental variables between years. Bottom depth and sea-ice concentration increased with latitude, while temperature decreased (Table 2). The chlorophyll a maximum was highest on the warmer more saline shelf, and these chlorophyll a maxima occurred at shallower depths. There was a significant temporal component to both sea-ice extent and the value at the chlorophyll a maxima, the former increasing later in the season and the latter decreasing.

In all years, zooplankton abundance was generally elevated in the vicinity of the Northwind Ridge and along the Beaufort Shelf, and was lowest in the eastern part of the basin (Figure 2). Abundance levels did not exceed 600 ind m⁻³ in 2004 and 2006 but reached >1000 ind m⁻³ at some stations in 2007 and 2008, in both shelf and basin regions. In 2009, zooplankton abundance only exceeded 200 ind m⁻³ in the south western basin and on the shelf. Zooplankton biomass distribution generally reflected that of abundance. However, in 2008, the highest biomass levels, in the vicinity of the Northwind Ridge, did not correspond with the highest abundance levels, indicating a significant contribution of low abundance, large “heavy” taxa. The highest average station biomass was recorded in 2008 (Figure 3). Biomass patches exceeding 50 mg DW m⁻³ were observed in 2007 and 2008, at both shelf and basin stations, whereas 2009 biomass was always <20 mg DW m⁻³. Overall, biomass appeared to increase between 2004 and 2008.

3.2. Zooplankton Community Composition—Abundance

Eight station groups were identified from the cluster analysis of zooplankton abundance data, with three outliers, two on the shelf in 2006 and one on the shelf in 2007 (Figure 4). The largest station groupings were Cluster D (40), F (19), A (17), and G (12) (number of stations shown in parenthesis). Clusters B, C, E, and H, all comprised <6 stations. Overall, the station groupings identified by cluster analysis were well replicated by the NMDS ordination (Figure 5). Zooplankton assemblage similarity was high within all stations clusters (>62%), and in all cases >70% of the within group similarity came from a pool of 12 taxa (Table 3). Clusters A, B, and H occurred predominantly on the shelf/shelf-break, while Clusters C-G occurred in the deep basin.

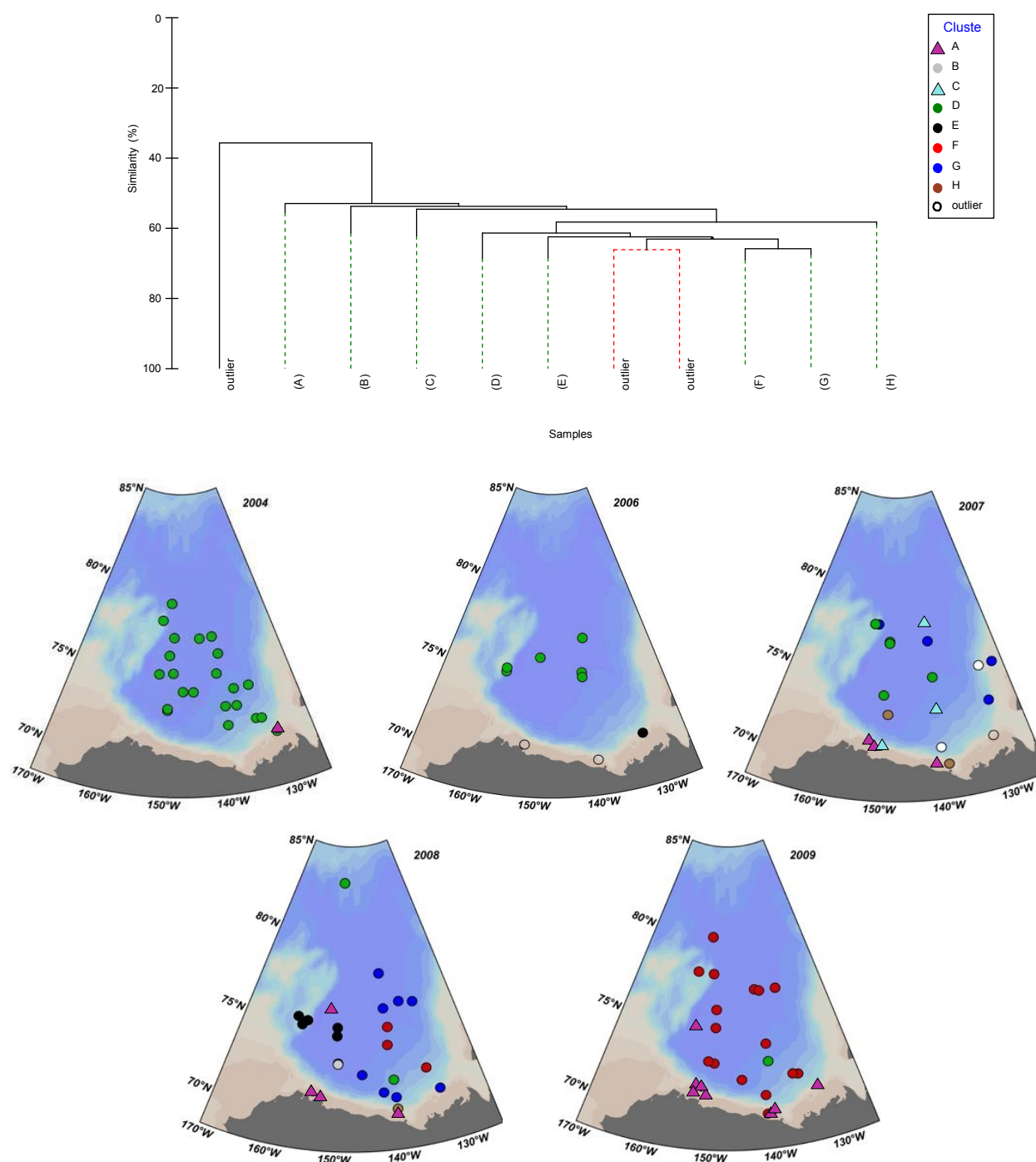


Figure 4. (upper panel) Dendrogram of station clusters identified from the Bray-Curtis similarity matrix of $\log_{10}(x + 1)$ transformed zooplankton abundance data, using unweighted pair group average sorting. (lower panel) The distribution of station clusters across the Canada Basin for each survey year. The symbols on the map follow the dendrogram cluster key. Empty cells indicate outliers.

The species that contributed most to similarity within clusters were the cyclopoid copepod *Oithona similis*, followed by the calanoid copepod *Microcalanus pygmaeus* (Table 3). The former species contributed >19% to similarity within all station groups, and the latter 5–21%. Cluster A was characterized by relatively high abundances for most taxa (Table 3) and the IndVal analysis identified a large number of indicator taxa (Figure 6). The latter included taxa that were primarily shelf associated (e.g., *Pseudocalanus* spp., barnacle larvae, benthic polychaete larvae, *Calanus* copepodites, and calanoid nauplii), as well as taxa that were common in the basin proper (e.g., *O. similis*, *Calanus glacialis*, *Calanus hyperboreus*) (Table 3 and Figure 6). Clusters B–H

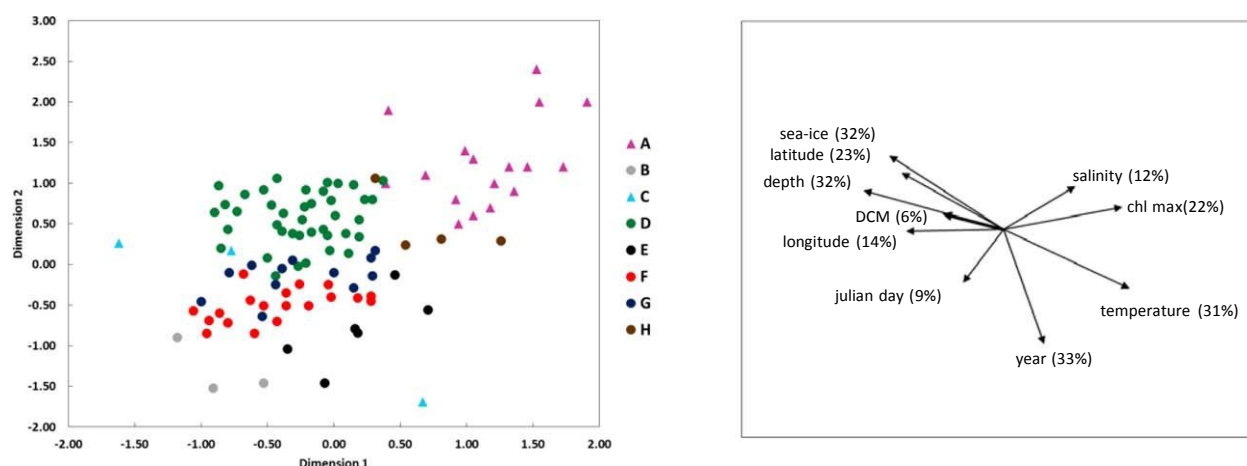


Figure 5. (left panel) Distribution of stations according to the scores of the first two dimensions of the NMDS analysis of the Bray-Curtis similarity matrix of $\log_{10}(x + 1)$ transformed zooplankton abundance data (stress value 5 0.21). The stations are color coded according to the groupings identified by cluster analysis (Figure 4). (right panel) Significant multiple regression vectors for environmental variables versus the first two NMDS scores, with the percent (%) contribution to variance in zooplankton assemblage structure indicated. Line length represents correlation strength, and the angle of the line represents the direction of forcing relative to the station distribution in the left panel.

shared high IndVals for *Microcalanus pygmaeus*, *Eukrohnia hamata*, *O. similis*, *Paraeuchaeta* spp., and ostracods. *Calanus glacialis* (45), *C. hyperboreus* (43), *Metridia longa* (34) also had high IndVals in Clusters B–H (values in parenthesis), indicating the importance of these species in the basin. *Limacina helicina*, foraminifera, *Aegina citrea*, and *Typhloscolecidae* were indicators of Clusters D–H, and *Themisto* spp. of Cluster H.

Considering the interannual pattern of cluster distribution, 2004 was dominated by Cluster D. Cluster D had no IndVal indicators, but SIMPER analysis identified *O. similis*, *L. helicina*, *F. borealis*, and *M. pygmaeus* as key species to within cluster similarity and they occurred at highest average densities within this cluster (Table 3). One Cluster A station was observed on the south-east shelf. Similarly, 2006 was dominated by Cluster D, with one station that differed, this time on the south-east shelf (Cluster G). Comparison among survey years showed that the representation of Cluster D began to decrease in the Canada Basin after 2006: 2007 (5), 2008 (2), and 2009 (1).

Both 2007 and 2008 were characterized by a highly heterogeneous zooplankton assemblage composition. In addition to five Cluster D stations located in the west-central deep basin, 2007 was represented by Clusters A (3), B (2), C (3), G (4), and H (2) (Figure 4). In 2008, Cluster G (8) was the most represented station cluster, the others including Cluster A (3), Cluster D (2), Cluster E (5), and Cluster H (2). Three Cluster F stations were present in the east central basin in 2008, the first of the survey years in which this zooplankton assemblage was observed. With the exception of Cluster A, which includes species only found on the shelf, differences between the cluster types were primarily driven by variation in the abundances of the same pool of

Table 3. Station Groupings Identified by Cluster Analysis of Abundance Data Across All Survey Years (Within Group Percentage Similarity in Parenthesis) and Abundance Levels (individuals m^{-2}) of the Taxa Contributing to the First 70% of Within Group Similarity^a

Cluster	A (62.38%)	B (66.65%)	C (64.53%)	D (71.56%)	E (72.34%)	F (72.35%)	G (72.31%)	H (63.85%)
<i>Oithona similis</i>	146.15 (19.42%)	17.08 (27.58)	95.58 (37.63%)	196.91 (25.13%)	107.50 (21.73%)	100.69 (28.74%)	94.69 (22.95%)	150.77 (21.63%)
<i>Pseudocalanus</i> spp.	210.06 (16.61%)	0.41	5.75 (14.65%)	0.93	4.05	6.67	0.82	10.83
<i>Calanoid nauplii</i>	67.44 (9.32%)	0.23	5.40	9.50	6.46	3.23 (5.04%)	4.78 (6.23%)	1.23
<i>Limacina helicina</i>	26.42 (7.29%)	2.94	0.06	64.37 (14.07%)	2.88	4.36	10.91 (7.82%)	24.8 (12.78%)
<i>Calanus copepodites</i>	68.52 (7.22%)	1.00	0.53	2.77	26.83 (17.66%)	1.63	2.76	12.90 (7.59%)
<i>Fritillaria borealis</i>	18.59	0.06	4.34	22.05 (7.80%)	0.00	1.34	0.26	0.00
<i>Microcalanus pygmaeus</i>	14.01 (5.03%)	3.99 (13.69%)	14.09 (13.07%)	82.23 (20.46%)	9.63 (7.08%)	22.37 (20.55%)	24.45 (16.38%)	33.82 (10.90%)
<i>Calanus glacialis</i>	5.89	5.23 (16.55%)	0.95	3.51	12.27 (13.71%)	4.96 (10.31%)	7.19 (11.20%)	5.06 (7.13%)
<i>Calanus hyperboreus</i>	6.64	5.64 (16.88%)	1.78	6.44 (5.91%)	9.22 (11.80%)	0.64	6.77 (9.37%)	7.35 (8.91%)
<i>Metridia longa</i>	3.85	1.76	0.59	2.43	1.94	3.00 (5.78%)	2.55	8.63
<i>Oikopleura vanhoefeni</i>	13.71 (6.97%)	2.35	0.00	1.48	0.53	1.67	3.08	2.03
Foraminifera	4.73	0.00	2.70	7.80	1.29	0.11	1.35	18.67 (6.21%)

^aThe value in parentheses adjacent to group specific abundance levels is the percent contribution to similarity of that taxon to that station grouping. Taxon similarity contributions are only indicated for those taxa contributing to the first 70% similarity within each cluster.

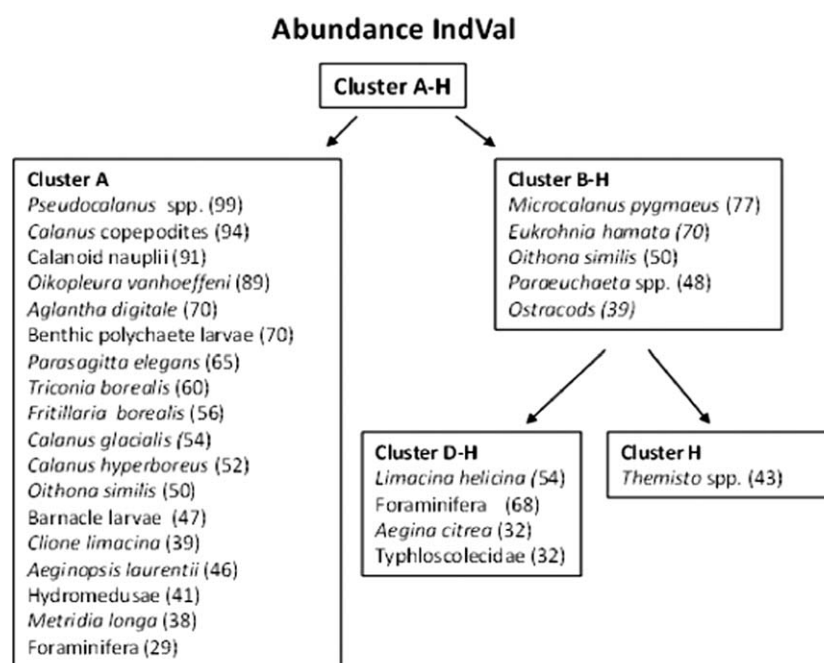


Figure 6. Indicator species identified by Indicator Value (IndVal) analysis [Dufrene and Legendre, 1997] at each level of separation in the cluster analysis of zooplankton abundance data. IndVals selected were all ≥ 25 , which meant that a species was present in $\geq 50\%$ of samples in a group and that its relative abundance within that group was $\geq 50\%$. Only the maximum IndVals were indicated for any one taxon.

species. Clusters B, C, and G were characterized by substantially lower densities of *O. similis*, *M. pygmaeus*, and *L. helicina* than Cluster D, while Cluster H stations was characterized by high densities of foraminifera (Figure 6 and Table 3). *Calanus glacialis* and *C. hyperboreus* were important contributors to the separation of Cluster E with both of these species having their highest densities in this cluster (Table 3). Cluster F had mid-range densities for the typical basin species *O. similis*, *M. pygmaeus*, and *C. glacialis*, but it had the lowest average densities for *C. hyperboreus* (Table 3).

Table 4. Results of the Multiple Regression of the First Two NMDS Dimensions and Environmental Variables, for the Abundance and Biomass Analyses^a

		Direction Cosines				Significance
		x ₁	x ₂	r ²	p	
Abundance	Year	0.271	20.963	0.328	0.001	b
	Bottom depth	20.943	0.333	0.322	0.001	b
	Sea ice	20.775	0.632	0.318	0.001	b
	Temperature	0.862	20.508	0.312	0.001	b
	Latitude	20.819	0.573	0.228	0.001	b
	Chl a max	0.972	0.234	0.218	0.001	b
	Longitude	20.999	20.024	0.139	0.001	b
	Salinity	0.799	0.602	0.119	0.006	c
	Julian Day	20.519	20.854	0.089	0.013	d
	DCM	20.949	0.314	0.062	0.038	d
Biomass	Julian Day	20.968	0.249	0.671	0.001	b
	Year	20.827	20.562	0.402	0.001	b
	Temperature	20.149	20.989	0.239	0.001	b
	Sea ice	20.050	0.999	0.182	0.001	b
	Bottom depth	20.228	0.974	0.155	0.001	b
	Longitude	0.261	0.965	0.152	0.001	b
	Chl a max	0.576	20.817	0.136	0.001	b
	Salinity	0.996	20.092	0.112	0.005	c
	Latitude	0.095	0.996	0.083	0.015	d
	DCM	0.169	0.986	0.050	0.087	d

^aVariables are arranged in order of strongest to lowest correlation. DCM 5 depth (m) of the deep chlorophyll maximum.

^bp < 0.001.

^cp < 0.01.

^dp < 0.05.

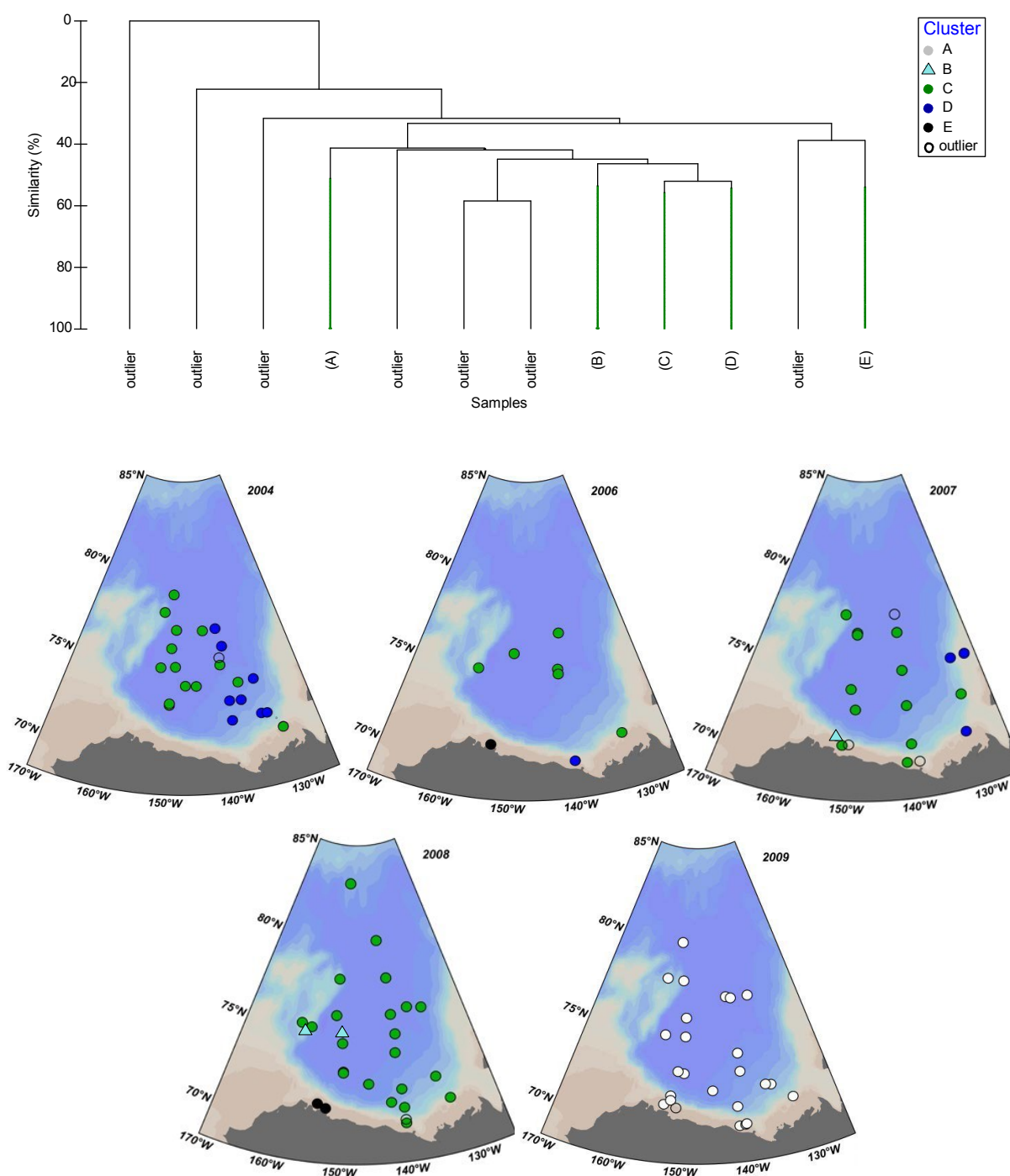


Figure 7. (upper panel) Dendrogram of station clusters identified from the Bray-Curtis similarity matrix of $\log_{10}(x + 1)$ transformed zooplankton biomass data, using unweighted pair group average sorting. (lower panel) The distribution of station clusters across the Canada Basin is presented for each survey year.

The 2009 survey was dominated by Cluster F samples in the basin and Cluster A samples in the shelf/shelf-break region (Figure 4). A single Cluster A station was observed in the vicinity of the Northwind Ridge in both 2008 and 2009.

Year, bottom depth, sea ice and temperature had similar correlation levels with zooplankton community structure ($>31\%$; Figure 5 and Table 4). The direction cosines showed that the year effect operated along an axis separating Clusters D (primarily 2004), G (primarily 2007 and 2008), and F (primarily 2009). Bottom

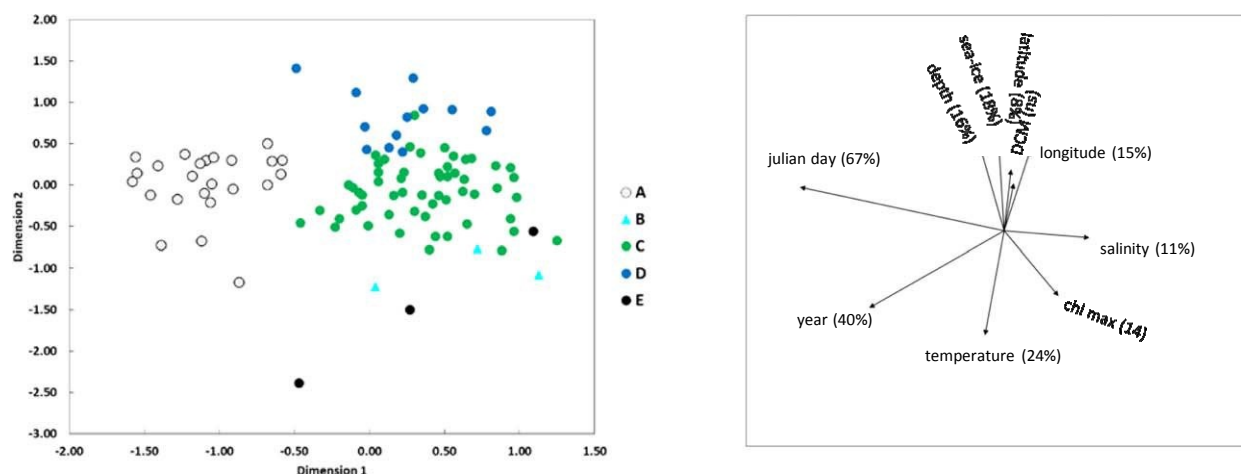


Figure 8. (left panel) Distribution of stations according to the scores of the first two dimensions of the NMDS analysis of the Bray-Curtis similarity matrix of $\log_{10}(x+1)$ transformed zooplankton biomass data (stress value 5 0.19). The stations are color coded according to the groupings identified by cluster analysis (Figure 7). (right panel) Significant multiple regression lines for environmental variables versus the first two NMDS scores, with the percent (%) contribution to variance in zooplankton assemblage structure indicated. Line length represents correlation strength, and the angle of the line represents the direction of forcing relative to the station distribution in the left panel.

depth, sea ice, latitude and temperature all co-varied significantly (Table 2), confirming the occurrence of lower temperatures and greater sea-ice cover in the higher latitudes of the deep basin. These conditions were most strongly correlated with the Cluster D assemblage typical of 2004 and 2006 (Figure 5). The opposite conditions, typifying the shelf, favored Cluster A and also contributed to the separation of B, C, E, and H (clusters occurring predominantly in the 2007–2009 surveys) from Cluster D. Cluster A also had a strong positive correlation with the value of the chlorophyll maximum and salinity, and negative correlation with longitude, which indicated it was found primarily on the productive southwest shelf. Julian day had a weak influence on the assemblage structure as determined by abundance data.

3.3. Zooplankton Community Composition—Biomass

A total of five station groups were identified from the cluster analysis of species biomass data, with six outliers, three of which occurred in 2007 (Figure 7). This station clustering was well supported by the NMDS ordination (Figure 8). Of the clustered stations, 56 fell within Cluster C, 24 in Cluster A, 13 in Cluster D, and three each in Clusters D and E. A total of 10 zooplankton taxa contributed to greater than 70% of the similarity within all clusters (Table 5). The application of biomass data shifted the focus away from the small, highly abundant taxa which dominated community abundance (e.g., *O. similis* and *M. pygmaeus*; Table 3), to a suite of larger taxa (Table 5).

The first cluster to separate in the biomass dendrogram was E (rv35% level of similarity; Figure 7). Cluster E comprised only three stations, all of which occurred on the south-west shelf, one in 2006 and two in 2008. Cluster E had highest IndVals for a number of taxa, including *C. glacialis*, barnacle larvae, benthic polychaete

Table 5. Station Groupings Identified by Cluster Analysis of Biomass Data Across All Survey Years (Within Group Percentage Similarity in Parenthesis) and Biomass Levels (mg DW m^{-2}) of the Taxa Contributing to the First 70% of Within Group Similarity^a

Cluster	A (63.55%)	B (57.95%)	C (61.15%)	D (63.85%)	E (59.11%)
<i>Aglantha digitale</i>	2.244 (23.33%)	2.231	1.160	0.006	3.431 (7.07%)
Barnacle larvae	0.033	0.329	0.053	0.005	14.649 (24.83%)
<i>Calanus glacialis</i>	1.511 (19.1%)	5.961 (28.38)	2.577 (15.47%)	0.652	4.579 (17.04%)
<i>Calanus hyperboreus</i>	0.497	12.464 (27.72%)	12.624 (36.91%)	4.762 (41.16%)	6.210
<i>Hydromedusa</i>	0.041 (14.91%)	2.129 (18.4%)	0.603	0.141	0.164
<i>Limacina helicina</i>	0.479	0.849	5.182 (17.64%)	1.134 (15.27%)	1.575
<i>Metridia longa</i>	1.879 (20.2%)	0.365	1.141	0.193	0.042
<i>Oikopleura vanhoeffeni</i>	0.195	0.105	0.693	0.237	4.597 (20.66%)
<i>Paraeuchaeta</i> sp.	1.162	0.249	0.975	1.147 (16.72%)	1.399
<i>Pseudocalanus</i> spp.	0.065	0.258	0.043	0.001	1.788 (7.35%)

^aThe value in parenthesis adjacent to group specific biomass levels is the percent contribution to similarity of that taxon to that station grouping. Taxon similarity contributions are only indicated for those taxa contributing to the first 70% similarity within each cluster.

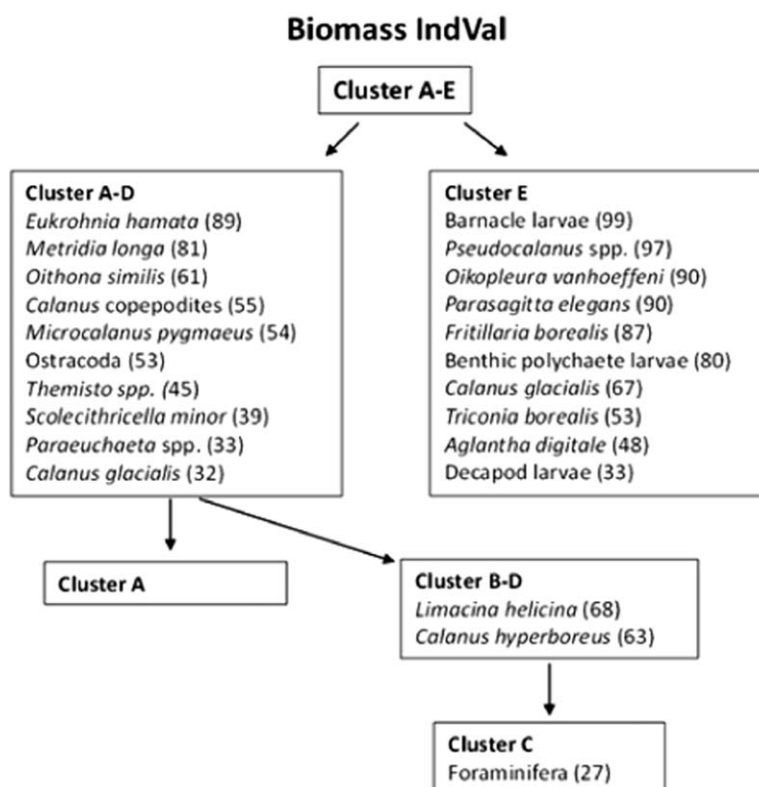


Figure 9. Indicator species identified by Indicator Value (IndVal) analysis [Dufrene and Legendre, 1997] at each level of separation in the cluster analysis of zooplankton biomass data. IndVals selected were all ≥ 25 , which meant that a species was present in $\geq 50\%$ of samples in a group and that its relative biomass in that group was $\geq 50\%$. Only the maximum IndVals were indicated for any one taxon.

larvae, *Pseudocalanus* spp., *A. digitale*, decapod larvae, *Fritillaria borealis*, *O. vanhoeffeni*, *Triconia borealis*, and *Parasagitta elegans* (Figure 9). Clusters A–D, comprising the majority of the sampled stations had the highest IndVals for *E. hamata*, *M. longa*, *O. similis*, *Calanus copepodites*, *M. pygmaeus*, Ostracoda, *Themisto* spp., *Scolecithricella minor*, and *Paraeuchaeta* spp. These therefore represented the dominant taxa in terms of frequency of occurrence and biomass in the Canada Basin during our study. In addition to having highest IndVals in Cluster E, *C. glacialis* had an IndVal of 32% in the combined Clusters A–D. Clusters B–D were made distinct by the highest IndVals for *C. hyperboreus* and *L. helicina* (Figure 9).

In the 2004 survey year only two assemblage types were evident amongst the stations sampled, Clusters C and D, with Cluster C dominating the western side of the basin and Cluster D the eastern side (Figure 7). These two clusters were made distinct by the lower biomass of most taxa in Cluster D, including *C. hyperboreus*, *C. glacialis*, and *L. helicina* (Table 5). By contrast, Cluster C had the highest biomass of *C. hyperboreus* and *L. helicina* and together these two species contributed 54% to similarity within that group. Overall, the Cluster C community dominated stations in 2006, 2007, and 2008 (Figure 7).

In 2006, one Cluster D station was located on the south eastern shelf, while in 2007 three Cluster D stations were located on the eastern shelf. No Cluster D stations were present in 2008. An additional Cluster, B, had one representative station in 2007 and two in 2008. These stations had a high biomass of *C. hyperboreus* and *C. glacialis*, the highest biomass of hydromedusae, and low biomass of *L. helicina* (Table 5). The 2009 survey year differed from the previous years in being solely represented by Cluster A (Figure 7). This cluster did not appear in any other year and was typified by the lowest biomass of *C. hyperboreus* and *L. helicina*, and high biomass of *A. digitale* and *M. longa* (Table 5).

Contrary to the abundance analysis, the strongest single correlate with zooplankton assemblage structure based on biomass was Julian Day (67%) (Figure 8 and Table 4). The direction cosines indicated that Julian Day was primarily responsible for the separation of Cluster A (2009) samples from those collected in 2004–

Table 6. Pearson Correlation Coefficients Between Zooplankton Taxon Abundance Levels (Individuals m^{-23}) and Environmental Parameters

	Latitude	Bottom Depth	Sea Ice	Temperature	Longitude	Julian Day	Salinity	Cmax	DCM
Basin taxa									
Microcalanus pygmaeus	0.48 ^a	0.37 ^a	0.50 ^a	20.38 ^a	20.01	20.03	0.07		
Oithona similis	0.31 ^a	0.21 ^b	0.21 ^b	20.11	20.22 ^b	20.04	20.03		
Eukrohnia hamata	0.34 ^a	0.41 ^a	0.18	20.17	20.14	20.14	0.01		
Paraeuchaeta spp.	0.22 ^b	0.30 ^c	0.13	20.23 ^b	20.09	0.27 ^c	20.18		
Fritillaria borealis	0.04	0.02	0.29 ^c	20.11	20.13	0.02	0.37 ^a	0.36 ^c	
Shelf taxa									
Aeginopsis laurentii	20.26 ^a	20.29 ^c	20.13	0.20 ^b	20.01	0.28 ^c	0.06		
Oikopleura vanhoeffeni	20.28 ^c	20.31 ^c	20.26 ^c	0.24 ^c	20.06	0.16	0.05		20.21 ^b
Pseudocalanus spp.	20.45 ^a	20.43 ^a	20.40 ^a	0.21	20.04	0.06	0.15		
Hydromedusae	20.26 ^a	20.25 ^b	20.20 ^b	0.39 ^a	0.01	0.26 ^c	20.03		
Calanus copepodites	20.28 ^a	20.51 ^a	20.45 ^a	0.3 ^c	20.43 ^a	20.34 ^a	0.31 ^c	0.37 ^a	
Benthic polychaete larvae	20.34 ^c	20.35 ^a	20.25 ^b	0.18	0.03	0.15	0.06		
Barnacle larvae	20.24 ^b	20.37 ^a	20.20 ^b	0.32 ^a	20.25 ^a	20.19	0.25 ^b		
Calanoid nauplii	20.07	20.31 ^c	20.21 ^b	0.13	20.20 ^b	20.14	0.26 ^c	0.22 ^b	
Triconia borealis	20.09	20.20 ^b	20.19	0.02	20.10	20.20 ^b	0.13		
Seasonal migrants									
Themisto spp.	0.03	0.09	20.18	20.02	20.20 ^b	20.35 ^a	0.07		
Calanus glacialis	0.11	20.07	20.12	0.03	20.23 ^b	20.23 ^b	20.15		
Calanus hyperboreus	0.19	0.05	20.10	20.23 ^b	20.20 ^b	20.74 ^a	0.26 ^c		
Limacina helicina	0.14	0.01	0.19	20.15	0.04	20.27 ^b	0.21 ^b		
Foraminifera	0.04	0.07	0.04	20.08	20.03	20.37 ^a	0.25 ^c		
Metridia longa	0.17	0.15	20.03	0.01	20.33 ^a	0.25 ^c	20.13		
Thysanoessa raschii	20.15	20.14	20.19	0.09	20.16	0.24 ^b	20.03		
Isopod	20.12	0.01	0.04	20.02	0.08	0.41 ^a	20.27 ^c		
Aglantha digitale	20.17	20.13	20.29 ^c	0.28 ^c	20.30 ^c	0.38 ^a	20.22 ^c		

^ap < 0.001.

^bp < 0.05.

^cp < 0.01.

2008. The 2009 samples were collected a minimum of 2 weeks later in the year than the previous surveys. It is therefore not surprising that the separation of Cluster A was also significantly influenced by Year. Year was also correlated with the separation of Cluster D (primarily 2004) from Cluster C (2006–2008). This “Year effect” appeared to be most strongly driven by the interannual increase in temperature, but was also influenced by latitude, bottom depth, and sea-ice cover. Longitude had a relatively strong correlation coefficient and operated in the direction separating Cluster D, located in the eastern Canada Basin, from Clusters C and E, located primarily in the west. The chlorophyll a maximum had a 14% correlation with assemblage structure, contributing to the separation of Clusters B and E on the southwest shelf. As with the abundance analysis, the depth of the chlorophyll maximum was weakly correlated with zooplankton assemblage structure.

3.4. Species-Environment Correlations

Species-environment correlations provided additional insights into the factors driving zooplankton assemblage structure and their distributions (Table 6). Abundances of *M. pygmaeus*, *O. similis*, *E. hamata*, and *Paraeuchaeta* spp. were all positively correlated with latitude, bottom depth and sea-ice extent, and negatively correlated with temperature. *Fritillaria borealis* abundance was positively correlated with sea ice and salinity. These species were all indicators of the deep basin (Tables 3 and 5). Conversely, abundances of *Aeginopsis laurentii*, *Oikopleura vanhoeffeni*, *Pseudocalanus* spp., hydromedusae, *Calanus* copepodites and nauplii, benthic polychaete larvae, barnacle larvae, and *T. borealis* were all negatively correlated with latitude, bottom depth, and sea-ice extent reflecting a distribution that was centered in the southern basin and shelf/shelf-break waters. These groups typified Clusters A and H of the abundance analysis (Figure 6 and Table 3), and Cluster E of the biomass analysis (Figure 9 and Table 5). Abundances of *Themisto* spp., *C. glacialis*, *C. hyperboreus*, *Calanus* copepodites, *T. borealis*, *L. helicina*, and foraminifera all had significant negative correlations with Julian Day, while *Paraeuchaeta* spp., *Metridia longa*, *Thysanoessa raschii*, isopods and *Aglantha digitale*, *A. laurentii* and hydromedusae were all positively correlated with Julian Day. Such correlations indicated a seasonal component to the occurrence of these taxa. The abundances of several species were negatively correlated with longitude reflecting higher abundance levels on the western side of the basin, as indicated by Figure 2. Only three taxa were significantly correlated with the chlorophyll a maximum

concentration, *Fritillaria borealis*, *Calanus copepodites*, and calanoid nauplii. *Oikopleura vanhoeffeni* and *Calanus copepodites* were both negatively correlated with the depth of the chlorophyll *a* maximum.

4. Discussion

This study represents the first multiyear analysis of zooplankton community composition in the Canada Basin. As outlined in the introduction, the survey years of 2004–2009 spanned a period of intense change both in the physical and biological dynamics of the region. Here we first characterize the zooplankton composition in the Canada Basin, assess its spatial and seasonal variability, and subsequently consider interannual variability in the context of observed physical and biological change.

4.1. Zooplankton Assemblage Structure

Consistent with past observations [Auel and Hagen, 2002; Hopcroft et al., 2005; Hopkins, 1969; Thibault et al., 1999], our study found the Canada Basin epipelagic zooplankton community to be characterized by low diversity and high dominance of a small number of species. Six taxa alone (*Calanus glacialis*, *Calanus hyperboreus*, *Limacina helicina*, *Microcalanus pygmaeus*, *Oithona similis*, and *Pseudocalanus* spp.) accounted for 77–91% of the zooplankton abundance in all survey years, and 70–80% of zooplankton biomass in 2004–2008. Copepods were the dominant group, with the major contributors to abundance being cyclopoids, small calanoids, and calanoid nauplii, and to biomass being the large calanoid *C. hyperboreus* in particular, as well as *C. glacialis*. Previous studies have shown the latter two species to contribute up to 70% to total biomass in the Beaufort Sea [Darnis et al., 2008; Hopcroft et al., 2005]. The pteropod *L. helicina* was an important contributor to both abundance and biomass measures. During the 1994 Arctic Ocean section this species was found to be particularly important in the Canada Basin, contributing ~8% to total zooplankton in this region [Thibault et al., 1999]. Between 2004 and 2008 *L. helicina* averaged 8–18% of total zooplankton abundance, and 16–32% of zooplankton biomass. It should be noted that the 236 μ m mesh net used in this study focussed on the mesozooplankton size fraction, and would have substantially undersampled copepod nauplii, and the early copepodite stages of the highly abundant small copepod species *O. similis*, *T. borealis*, *M. pygmaeus*, and *Pseudocalanus* spp. [Hopcroft et al., 2005]. Our sampling therefore underestimated total zooplankton abundance and biomass, although, given the relatively small contribution of the aforementioned species to biomass, our biomass data approximate that of the total zooplankton population in the upper 100 m of the water column [Hopcroft et al., 2005]. Annual mean dry weight biomass ranged from 9.5 mg m^{-23} in 2004 to 32.5 mg m^{-23} in 2008. The low end of this range is similar to levels reported by Hopcroft et al. [2005], while the high end is similar to levels reported by Thibault et al. [1999].

4.2. Spatial Variability

The most prominent spatial pattern observed in these data was the separation between the shelf/shelf-break and deep basin stations. The division between these two regions was evident in their physical properties, phytoplankton biomass, and zooplankton composition. The shelf waters were characterized by a distinct set of fauna which included the typically neritic taxa *Pseudocalanus* spp. and *Parasagitta elegans* [Darnis et al., 2008; Hopcroft et al., 2005; Walkusz et al., 2010], larval forms of benthic groups, e.g., barnacles, polychaetes, and decapods, and other taxa that were more abundant on the shelf than in basin waters, including *Calanus* copepodites and calanoid nauplii. The deep basin fauna was dominated by the later stages of *C. hyperboreus* and *C. glacialis*, *O. similis*, *L. helicina*, and *M. pygmaeus*. However, these characteristic basin taxa were typically also present in shelf waters, and the distinction between shelf and basin was most strongly seen in the absence of shelf taxa from the latter region. The spatial separation of the shelf and basin communities was largely consistent between years, although the presence of shelf/shelf-break stations in the basin proper in 2008 and 2009 indicates at least some mesoscale shelf-basin connectivity, possibly through periodic offshore eddy transport [Carmack and MacDonald, 2002; Spall et al., 2008]. The majority of the samples (89%) in this study were collected in the basin, in waters deeper than 1000 m. Here the negative correlation between the abundance of a number of species and longitude highlighted greater density levels in the western basin which were associated with a shallower and larger chlorophyll *a* maximum.

4.3. Seasonality

In the highly seasonal polar environment, it is necessary to consider the seasonal timing of sampling in assessing interannual variability. In the case of the zooplankton, seasonality includes vertical migrations for

many species, a prime example in the Canada Basin being *C. hyperboreus* [Ashjian et al., 2003]. The older copepodites (CIII–CV) and adults of this species spend only a few months at the surface, rising to the upper 100 m during July/August, before descending to intermediate depths (400–500 m) during late summer, and to ~500 m in September [Ashjian et al., 2003]. *Calanus glacialis* also undergoes seasonal migration [Kolosova and Melnikov, 2001; Slagstad and Tande, 1990], with observations of adults/CV copepodites centered below 200 m during winter in the Canada Basin [Ashjian et al., 2003], while *Limacina helicina* has been shown to become more dispersed through the water column during winter [Kobayashi, 1974]. Since our sampling in 2009 occurred in the second half of September it is most likely that the extremely low *C. hyperboreus* biomass and reduced biomass of *C. glacialis* and *L. helicina* in that year can be attributed to sampling occurring in the upper 100 m of the water column, above the fall vertical distribution maxima for these species. Conversely, *Metridia longa* biomass was highest in 2009 compared to previous years, consistent with observations of enhanced surface biomass of this species in late summer/fall [Ashjian et al., 2003; Kolosova and Melnikov, 2001].

Another seasonal effect is change in the size of individuals within a taxon. As already noted, the 236 μ m mesh net used in this study would have undersampled the nauplii and the early copepodite stages of small copepod species such as *O. similis*, *T. borealis*, *M. pygmaeus*, and *Pseudocalanus* spp. However, these species are characterized by sustained and/or continuous reproduction, and vertical distributions centered in the upper 100 m of the water column over the summer months if not all of the year [Ashjian et al., 2003; Hopcroft et al., 2005; Lischka and Hagen, 2005; Nishibe and Ikeda, 2007]. It is therefore unlikely that the difference in sampling dates between the 2004 and 2008 survey years, or indeed 2009, could account for the observed differences in the abundance distribution of these taxa. Indeed, high density patches of these taxa were found in all survey years and, as discussed in section 4.4, it was the change in the spatial distribution and frequency of occurrence of these taxa that was the greatest difference in the abundance data between years. Seasonal change in size may also change a species seasonal biomass distribution. The hydrozoan *A. digitale* was the primary indicator species of the 2009 basin assemblage in the biomass analysis, yet this species was not an indicator for the basin stations in the abundance analysis. This points to seasonal growth in size of *A. digitale* as the most likely factor in their large contribution to 2009 biomass.

The seasonal cycles of migration and growth of the large, high biomass taxa discussed above accounts for the importance of seasonal timing in the biomass based community measures in this study. The correlation strength between season and abundance based community measures was half that of the biomass analysis, pointing to both a weaker seasonality amongst the smaller high abundance taxa and low contribution of the larger taxa to abundance based estimates. However, in both cases, the role of seasonality in shaping the observed zooplankton assemblages demonstrates the importance of investigating interannual change using data collected at the same time of year. For this reason, we focus the discussion below on data collected from 2004 to 2008.

4.4. Interannual Variation in the Canada Basin Community Composition

Different insights are gained into interannual change in the zooplankton assemblage structure between 2004 and 2008 when considering the abundance and biomass data. In the abundance analysis, the 2004 survey was remarkable for the dominance of one assemblage type characterized by the highest densities of the typical basin taxa *O. similis*, *L. helicina*, *M. pygmaeus*, and *F. borealis* (Cluster D). This high density assemblage persisted in 2006 but was greatly reduced in 2007 and nearly absent in 2008. Both the 2007 and 2008 surveys were remarkable for the heterogeneity of the zooplankton assemblage structure. In particular, the low salinity center of the Beaufort Gyre was associated with greatly reduced densities of the typical basin taxa listed above (Clusters C and G in 2007 and Clusters F and G in 2008). The freshening of the Beaufort Gyre is associated with increased Ekman convergence and freshwater input of sea-ice melt, causing a deepening of the nutricline and the depth of the chlorophyll a maximum within the gyre [McLaughlin and Carmack, 2010]. Although mean phytoplankton biomass remained relatively constant between 2004 and 2009 [Li et al., 2009], the data presented here show that the chlorophyll a maximum concentrations had substantial spatial variability. In all years, chlorophyll a maximum concentrations were highest in the western basin and on the shelf but low in the central Beaufort Gyre, reflected by the significant negative correlation with salinity. Although the mean basin phytoplankton biomass may have remained relatively constant over the study period, regional phytoplankton biomass levels appeared to change, with indications of reductions in the freshening Beaufort Gyre. The zooplankton abundance data suggest that this may have impacted

secondary production in the basin since the freshening central gyre in 2007 and 2008 was associated with the lowest zooplankton densities in this study. The highly significant correlations between Cluster D and temperature (negative) and sea-ice concentration (positive) further support the suggestion that the freshening of the Beaufort Gyre has significantly impacted zooplankton densities.

The biomass data present a different picture to that of abundance. The Canada Basin became more consistently dominated by a high biomass assemblage between 2004 and 2008, largely due to the high biomass of *C. hyperboreus*. This trend was evident in the consistently increasing values of mean annual biomass over this time period. The high biomass assemblage occurred both inside and outside the Beaufort Gyre, in contrast to observations for *O. similis*, *L. helicina*, *M. pygmaeus*, and *F. borealis*. We suggest that this difference may be attributed to the life histories of these taxa.

Microcalanus pygmaeus and *O. similis* are copepod species with a broad global distributional range and large physiological tolerance limits [Choe and Deibel, 2008; Darnis et al., 2008; Gallienne and Robins, 2001]. In addition, both have been demonstrated to be omnivorous, feeding on phytoplankton and microzooplankton [Atkinson, 1996; Hopkins et al., 1993; Michels and Schnack-Schiel, 2005]. They are therefore expected to be highly adaptable to changing conditions and are able to remain active year round. Accordingly, both species have sustained reproductive periods, in some cases continuous throughout the year [Ashjian et al., 2003; Atkinson, 1998; Lischka and Hagen, 2005; Schnack-Schiel, 2001]. They are expected to produce multiple generations per year, and survive for >1 year. Due to their relatively short generation time, they are also expected to complete their life cycle within the Canada Basin which would make them dependent on autochthonous basin production. Thus, a decline in phytoplankton biomass in the Beaufort Gyre associated with the deepening of the nutricline is expected to directly impact their production and abundance levels.

Unlike the aforementioned species, *C. hyperboreus* and *C. glacialis* both have multiyear life cycles with diapause, ontogenetic migration, and pulsed reproduction in spring/early summer [Ashjian et al., 2003]. Both species produce and utilize substantial lipid stores to overwinter [Kattner and Hagen, 1995]. Low condition factor has been recorded for *C. hyperboreus* in the Canada Basin relative to the Chukchi Shelf and Northwind Ridge, as well as low egg production rates [Ashjian et al., 2003], and low densities of early copepodite stages [Lane et al., 2008], which indicates that the Canada Basin presents unfavorable conditions for recruitment.

The persistence and biomass increase of *C. hyperboreus* and *C. glacialis* between 2004 and 2008, despite continued low phytoplankton biomass in the Canada Basin supports the contention of Lane et al. [2008] that they are sustained by the more productive shelf and shelf/break regions of the Beaufort and Chukchi seas [Lane et al., 2008; Llinas et al., 2009]. These authors propose that *C. hyperboreus* and *C. glacialis* are transported from overwintering depths in the deep basin to the shelf/shelf-break by upwelling along the Chukchi and Beaufort shelves. Since this upwelling is wind driven it occurs during sea ice break up [Carmack and Chapman, 2003], and thus transports plankton to the shelf at the onset of the spring/early summer productive period. In our study highest densities of *C. hyperboreus* and *C. glacialis* copepodites were recorded on the south west shelf and western basin, associated with higher phytoplankton biomass, whereas they were scarce in the deep basin. Enhanced shelf/shelf-break primary production would be expected to support rapid growth of early copepodite stages and lipid storage prior to off shelf advection through Ekman drift/eddy shedding. The lipid stores of *C. hyperboreus* and *C. glacialis* enable them to survive the winter period and low summer productivity in the basin. In this way, *C. hyperboreus* and *C. glacialis* in the Canada Basin may be largely sustained by allochthonous shelf production. Enhanced coastal upwelling under reduced sea-ice conditions in a warming Arctic could support an increase in biomass of *C. hyperboreus* and *C. glacialis* in the Canada Basin despite continued low or even decreasing phytoplankton biomass in that region.

The final species we consider here is *Limacina helicina*. This thecosome pteropod was a key component of the Canada Basin zooplankton community during our study, both in terms of abundance and biomass. Although average densities of this species did not show a clear interannual trend, density distributions were more uniform across the basin in 2004 and 2006 than in 2007 and 2008. The latter years were generally characterized by low densities in the basin with a few high density stations. A potentially important factor in *L. helicina* distributions is aragonite undersaturation caused by sea-ice melt [Yamamoto-Kawai et al., 2009a]. Significant *Limacina* shell dissolution was recently observed in the Southern Ocean [Bednarsek et al., 2012] at aragonite undersaturation levels similar to those reported by Yamamoto-Kawai et al. [2009a] in the

Canada Basin in 2008. Undersaturated aragonite levels may have contributed to the low *L. helicina* densities recorded in the Canada Basin in 2008 and is expected to be of increasing relevance to Arctic *L. helicina* in the coming decade [Yamamoto-Kawai et al., 2009a]. *Limacina helicina* is considered to have a 1.5–2 year life cycle in the central Arctic [Kobayashi, 1974], and following the mechanism outlined above for *C. hyperboreus* and *C. glacialis*, the basin population may also benefit from allochthonous shelf production. Indeed, densities in 2007 and 2008 appeared to be enhanced at the shelf/shelf-break environment. Enhanced upwelling of aragonite undersaturated deep water (rv125 m depth) onto the Beaufort/Chukchi shelves due to the retreat of the ice edge away from the shelf-break [Yamamoto-Kawai et al., 2009a] may therefore contribute to reduced shelf population viability with significant consequences for both the shelf and basin distributions of this important species.

As a final comment on interannual change, we reiterate what has been suggested in previous studies, that Arctic Ocean ecosystems were already in transition prior to the 2000s. Although the period 2004–2009 was one of intense change in the Canada Basin, declines in sea-ice extent and sea ice thinning have been recorded since the advent of satellite observations in 1979 [Comiso et al., 2008; Stroeve et al., 2012]. During the late 1990s sea-ice melt and freshening of the halocline in the Canada Basin was proposed to be the cause for a decrease in the biomass of ice diatoms and ice associated invertebrates [Melnikov and Kolosova, 2001]. A number of studies have recently pointed to an increased abundance and biomass of zooplankton over the last 50 years in both the Canada Basin and Chukchi Sea [Hopcroft et al., 2005; Kosobokova and Hopcroft, 2010; Lane et al., 2008]. Such increases support predictions of enhanced production following, first, the retreat of the ice edge away from the Beaufort shelf, favoring upwelling [Carmack and Chapman, 2003] and second, greater seasonal sea-ice melt in the deep Canada Basin enhancing light penetration [Lee and Whittedge, 2005]. However, limited comparative sampling in previous decades, differences in sampling gears, seasonal timing and the spatial distribution of sampling effort all introduce bias into between survey comparisons and make it difficult to quantitatively assess changes [Hopcroft et al., 2005; Kosobokova and Hopcroft, 2010]. In this light, there is an urgent need for improved biological monitoring programs in the Canada Basin. Ideally, such programs should include a seasonal component, first to place data in the context of seasonal biological cycles and second to provide observations on interannual changes in phenology associated with changes in the timing of sea-ice melt and phytoplankton bloom development. Changes in phenology are likely to be of particular importance for the biomass dominant *C. glacialis* and *C. hyperboreus*, due to their reproductive and growth cycles being tightly coupled to that of phytoplankton [Ashjian et al., 2003], with significant implications for the higher trophic levels that prey on them [Edwards and Richardson, 2004].

5. Conclusions

Between 2004 and 2008 substantial spatial heterogeneity developed in the zooplankton assemblage structure of the Canada Basin, with the highest heterogeneity observed in 2008. In both 2004 and 2006, the Canada Basin was largely dominated by a single zooplankton assemblage characterized by high densities of *O. similis*, *L. helicina*, *M. pygmaeus*, and *F. borealis*. This zooplankton community composition broke down in 2007 and 2008, a change that was significantly correlated with increased temperature and marked declines in sea-ice extent. The increased heterogeneity in zooplankton assemblage structure was associated with a reduction in the density dominant taxa described above. In particular, we observed reduced densities of these taxa in the freshening Beaufort Gyre in 2007 and 2008, even though their densities remained high on the Beaufort Shelf and in the western Canada Basin. Over the same time period, the biomass of the large calanoid copepods *C. hyperboreus* and *C. glacialis* showed an increasingly consistent spatial distribution of high biomass levels. We propose that the different interannual patterns of these two groups are related to their life history differences. A greater dependence on autochthonous basin production by short lived (<1 year), year around reproducers such as *O. similis* and *M. pygmaeus* makes them more susceptible to changes in primary production in the freshening Beaufort Gyre, already an extremely oligotrophic environment. Conversely, long lived (≥2 year), spring/early summer reproducers such as *C. hyperboreus* and *C. glacialis* are supported by high allochthonous production on the Beaufort and Chukchi shelves which enables them to accumulate lipid stores supporting their multiyear life histories. The order of magnitude higher abundance of *C. hyperboreus* and *C. glacialis* copepodite stages on the south west shelf and in the western basin support this hypothesis. Nutrient delivery to the shelf regions of the Canada Basin by enhanced coastal

upwelling may continue to support high densities of species with a multiyear life history in the Canada Basin, despite ongoing low, or even declining, basin primary production, provided those species are not sensitive to aragonite undersaturation.

Acknowledgments

We acknowledge financial and ship time support from Fisheries and Oceans Canada, the U.S. National Science Foundation Office of Polar Programs (grant OPP-0424864) support for the Beaufort Gyre Exploration Project and its PI Andrey Proshutinsky, and the National Sciences and Engineering Research Council of Canada. We greatly appreciate the assistance and support of the men and women of the Canadian Coast Guard icebreaker Louis S St Laurent for their assistance in sample collection. We thank four anonymous reviewers whose insightful comments greatly improved the final manuscript.

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