



Diversity and vertical distribution of mesozooplankton in the Arctic's Canada Basin

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ABSTRACT

The composition and biomass of the zooplankton community within the Canada Basin down to 3000 m was studied during July 2005 at 12 stations. A total of 111 species including 74 species of crustaceans (55 species of copepods, 2 euphausiids, 11 amphipods, 1 decapod, 5 ostracods), 17 cnidarians (12 hydromedusae, 1 scyphomedusae, 4 siphonophora), 1 foraminifera, 4 ctenophores, 2 pteropods, 4 larvaceans, 4 chaetognaths, and 5 polychaetes were identified. Most of the species observed are typical of the Arctic waters, with the notable exception of several Pacific expatriate copepod species, suggesting no zoogeographical barrier between the Canadian and Eurasian basins. Overall species inventories appear unchanged over the past 50 years, and were similar to the Eurasian Basins. Zooplankton biomass averaged $3.6 \pm 0.23 \text{ g DW m}^{-2}$, with $\sim 50\%$ of the biomass concentrated within the upper 100 m; nonetheless significant biomass and the majority of species diversity occurred below 100 m. Copepods represented 91% of the community numerically, followed by pteropods (2.6%), larvacean (1.8%) and shelled protists (1.5%), with other groups each contributing 1% or less. While copepods represented 85% of the total biomass, chaetognaths represented 13% on average (ca. 50% of non-copepod biomass), followed by cnidarians plus ctenophores (4.6%), ostracods (3.6%), and other groups ($\sim 2\%$ or less). Species-specific depth preferences and ranges resulted in statistically distinct communities in different depth strata and showed an orderly departure in similarity with increasing distance between strata. In Arctic waters, because temperature varies relatively little over the water column, so should respiratory rates; hence deep-water species are likely to play a greater role in the transfer or recycling of surface production than is typical of other deep ocean communities.

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1. Introduction

Despite its remoteness, studies of zooplankton communities in the Arctic's Canadian Basin stretch back more than half a century. The earliest collections for the entire water column focused largely on composition and vertical zooplankton distribution obtained by the Russian drifting ice stations North Pole (NP)—2–5 in 1950–1957 (e.g. Brodsky and Nikitin, 1955; Virketis, 1957, 1959), NP—16–23 in 1968–1978 (e.g. Pavshits, 1971, 1977; Kosobokova, 1978, 1980, 1982; Melnikov and Pavlov, 1978; Geynrikh et al., 1983), the American ice islands T-3 (Grainger, 1965; Harding, 1966; Hughes, 1968; Dunbar and Harding, 1968, Pautzke, 1979), Alpha (Johnson, 1963), ARLIS II (Hopkins, 1969a, b) and AIDJEX (Pautzke, 1979). More recent studies have been conducted from ice breakers (Wheeler et al., 1996; Thibault et al., 1999; Kosobokova and Hirche, 2000; Hopcroft et al., 2005; Raskoff et al., 2005; Lane et al., 2008; Ota et al., 2008), and drifting ice

stations are now rare (e.g., SHEBA—Melnikov and Kolosova, 2001; Ashjian et al. 2003). These recent efforts have also focused primarily on processes rather than composition.

In the past, copepods, as the most diverse and numerically important group, have consistently received the majority of attention. Other zooplankton taxa, both the robust body forms (Amphipoda, Euphausiacea, Decapoda, Chaetognatha) and more fragile groups (hydro- and scyphomedusae, Siphonophora, Ctenophora, Larvacea), have received less attention due to their limited occurrence in samples obtained by common vertically deployed plankton nets. Unfortunately, the common approach was to identify well known, widely distributed species and to disregard poorly known rare ones (Polychaeta, Siphonophora, Ctenophora, Ostracoda), with the assumption that low abundance equaled low importance. Additionally, the absence of specialized identification guides for the non-copepod Arctic fauna made identification challenging, compared to the availability of detailed accounts on the copepods from Norwegian Polar expeditions by Sars (1900) and identification keys for polar copepods by Brodsky (1950, 1967). Only later did publications begin to contain species accounts for one (Damkaer, 1975; Raskoff et al., 2005) or more

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(Scott, 1969; Pautzke, 1979; Kosobokova, 1981; Hopcroft et al., 2005) of these neglected groups.

Although our knowledge of the Arctic zooplankton remains fragmentary, our understanding of the pelagic fauna has now progressed to the stage that species list and regional occurrences have been compiled for the Arctic Ocean (Sirenko, 2001). Similarly, the depth distribution of many copepods, and the more common non-copepods, has been summarized in a semi-quantitative manner for the Canadian (Dunbar and Harding, 1968; Kosobokova, 1989) and Eurasian Basins (Kosobokova and Hirche, 2000), but the vertical distribution of many less common species remains poorly characterized. A more quantitative analysis of the vertical structure of Arctic zooplankton, especially the historically understudied groups, thus seems overdue.

Motivated by renewed interest in the topic of biodiversity by programs such as the Census of Marine Life, and a renewed interest in basic exploration of poorly known marine habitats by NOAA's Ocean Exploration program, the time was right for a detailed survey of the zooplankton communities in a deep Arctic Basin. The Hidden Ocean Expedition within the Canada Basin during 2005 was a multi-disciplinary effort designed to document the diversity of life in all of the Arctic Ocean's major habitat realms from the surface to the seafloor (see Bluhm et al., 2010). The zooplankton component of the expedition sought to use traditional techniques such as plankton nets (this study), combined with modern in situ imaging and collection capabilities afforded by a modern ROV (Raskoff et al., 2010), and molecular techniques (Bucklin et al., 2010), to create a more complete and quantitative inventory of the zooplankton in this region. Ultimately, the expedition aimed to provide both a baseline and a comparison with historical data to determine whether zooplankton community structure in the Canada Basin has changed over the past decades.

2. Methods and material

Zooplankton were collected 29 June–25 July 2005, from the US Coastguard Cutter *Healy*. Samples were collected at 12 stations across the cruise track that encompassed stations north of Point Barrow in the Canada Basin, as well as on the shallower Northwind Ridge, and the bathymetrically complex Chukchi Plateau (Fig. 1). All stations were situated in small leads of open water within the otherwise complete ice cover. Samples were collected by a Hydrobios Multinet Type Midi (mouth area 0.25 m², 150 µm mesh) hauled vertically at ~0.5 m/s. The system was equipped with internal and external flow meters and a depth transducer, all monitored and logged in real time. Sampling was conducted to divide the water column into fixed-range strata, using two sequential casts: 3000–2000, 2000–1000, 1000–500, 500–300, 300–0 m and 300–200, 200–100, 100–50, 50–25, 25–0 m. Samples were preserved in 10% formalin (4% formaldehyde) upon retrieval.

All mesozooplankton organisms (>1 mm), and all copepodite stages of *Calanus* and *Metridia*, in the samples were counted from the entire sample and measured under a stereo microscope. For the smaller zooplankton (<0.8 mm), an aliquot (1:8, 1:10) of the sample was counted after fractionation with a stempel-pipette. Most taxonomic groups including Copepoda Calanoida, Ostracoda, Amphipoda, Decapoda, Euphausiacea, Pteropoda, Chaetognatha, Larvacea (= Appendicularia), Siphonophora and hydromedusae were identified to species level. Copepodite stages of most calanoid copepods were counted separately and identified to species level. Exceptions are Discoidae, *Microcalanus*, *Xanthocalanus*, and young (CI–III) stages of *Spinocalanus* (Table 1). Prosome length was used to distinguish early copepodite stages CI–CIII of

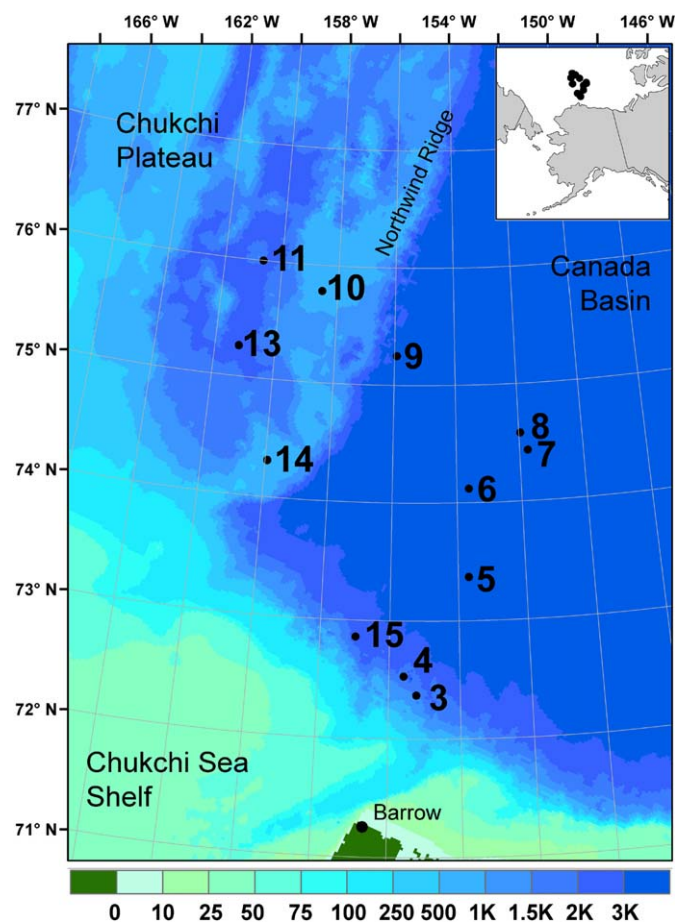


Fig. 1. Map of plankton stations for the USCGC *Healy* Hidden Ocean 2005 cruise.

Calanus belonging exclusively to *C. glacialis* and *C. hyperboreus*. Prosome length was measured from the tip of the cephalosome to the distal lateral end of the last thoracic segment using size criteria of Hirche et al. (1994). Few Copepoda Harpacticoida and the majority of Oncaeidae were not identified to species.

Biomass, estimated as dry-mass but abbreviated as dry-weight (DW) by tradition, was calculated from published (Richter, 1994) and our unpublished taxon-specific length–DW relationships, and individual DW (Kosobokova et al., 1998; Laakmann et al., 2009). For rare crustacean species, wet masses (WW) were calculated according to length–weight regressions established by Chislenko (1968), then converted to DW using a factor of 0.16 established for Arctic zooplankton by Kosobokova (unpubl.), which is similar to values determined by Wiebe et al. (1975). The DW of all hydromedusae was predicted from an equation derived for *Aglantha* (Matthews and Hestad, 1977) and which appeared to be consistent with the few other *L–W* relationships available (Daan, 1986; Richter, 1994; Persad et al., 2003; Møller and Riisgård, 2007). The Scyphozoa DWs were predicted from a relationship for *Aurelia aurita* (Uye and Shimauchi, 2005) using their estimate of $DW = 3.6\% WW$. It is widely acknowledged that the DW to carbon conversion of cnidarians is on the order of 10% (Larson, 1986) while that of crustaceans is more typically 40% (Båmstedt, 1986). Although converting all DW to carbon would be more appropriate, most of the Arctic literature employs DW. Cnidarian DW was normalized (through division by four) so that the carbon to DW content was directly comparable to that of the crustaceans. Protists (foraminiferans, radiolarians and tintinnids) were not included in biomass calculations.

Table 1
List of zooplankton taxa collected in the Canada Basin in 2005, with their mean absolute abundance and biomass (mean \pm SE) and relative contribution of each taxon to abundance and biomass.

No.	New records	Taxa	Abundance, no. m ⁻² , mean \pm SE	% abundance	Biomass, mg DW m ⁻² , mean \pm SE	% biomass
Calanoida						
1		<i>Aetideopsis minor</i>	123 \pm 25	0.08	5.82 \pm 0.89	0.2
2		<i>A. rostrata</i>	200 \pm 68	0.1	20.5 \pm 6.1	0.6
3		<i>Augaptilus glacialis</i>	18.3 \pm 4.4	0.01	6.74 \pm 1.58	0.2
4		<i>Calanus glacialis</i>	1070 \pm 157	0.7	333 \pm 65	9.2
5		<i>C. hyperboreus</i>	1080 \pm 133	0.7	1010 \pm 87	27.7
6		<i>Chiridius obtusifrons</i>	64.2 \pm 11.1	0.04	5.49 \pm 0.90	0.2
7		<i>Chiridiella abyssalis</i>	23.6 \pm 6.2	0.02	5.39 \pm 1.44	0.2
8	+	<i>Disco triangularis</i>	3.23 \pm 1.77	*	0.02 \pm 0.01	*
	+	<i>Discoidae</i> gen spp. ^a	282 \pm 62	0.2	1.98 \pm 0.44	0.05
9		<i>Euaugaptilus hyperboreus</i>	9.14 \pm 3.06	0.01	18.6 \pm 6.7	0.5
10		<i>Eucalanus bungii</i> ^b	0.38 \pm 0.40	*	0.15 \pm 0.16	*
11		<i>Gaetanus brevispinus</i>	74.7 \pm 12.9	0.05	9.55 \pm 2.69	0.3
12		<i>G. tenuispinus</i>	204 \pm 14	0.1	14.5 \pm 1.4	0.4
13		<i>Haloptilus acutifrons</i>	19.1 \pm 3.2	0.01	1.91 \pm 0.39	0.05
14		<i>Heterorhabdus norvegicus</i>	507 \pm 56	0.4	16.7 \pm 1.6	0.5
15		<i>Lucicutia anomala</i>	2.81 \pm 1.20	*	0.47 \pm 0.21	0.01
16		<i>L. pseudopolaris</i>	16.3 \pm 4.4	0.01	2.66 \pm 0.77	0.07
17		<i>L. polaris</i>	18.6 \pm 6.4	0.01	4.46 \pm 1.37	0.1
18		<i>Metridia longa</i>	4204 \pm 341	2.9	255 \pm 29	7.0
19		<i>M. pacifica</i> ^b	0.64 \pm 0.45	*	0.04 \pm 0.03	*
20		<i>Microcalanus</i> spp.	31200 \pm 3290	21.5	218 \pm 23	6.0
21	+	<i>Mimocalanus crassus</i>	30.5 \pm 7.6	0.02	1.93 \pm 0.47	0.05
22		<i>M. damkaeri</i>	5.35 \pm 1.91	*	0.30 \pm 0.12	0.01
23		<i>Neocalanus cristatus</i> ^b	0.65 \pm 0.46	*	1.15 \pm 0.84	0.03
24		<i>Onchocalanus cristogerens</i> ^c	0.60 \pm 0.42	*	0.00 \pm 0.00	*
25		<i>Pareuchaeta barbata</i>	39.9 \pm 12.6	0.03	35.2 \pm 11.8	1.0
26		<i>P. glacialis</i>	444 \pm 34	0.3	283 \pm 17	7.8
27		<i>P. polaris</i>	7.56 \pm 3.20	0.01	7.43 \pm 3.32	0.2
		<i>Pareuchaeta nauplii</i>	99.3 \pm 27.3	0.07	2.84 \pm 0.64	0.08
28		<i>Paraheterorhabdus</i> (= <i>Heterorhabdus</i>) <i>compactus</i>	57.9 \pm 10.5	0.04	4.79 \pm 0.78	0.1
29		<i>Pseudaugaptilus polaris</i>	6.81 \pm 1.83	*	3.71 \pm 1.61	0.1
30		<i>Pseudocalanus minutus</i>	93 \pm 14	0.06	0.82 \pm 0.12	0.02
31	+	<i>P. newmani</i> ^b	Observed	*	Observed	*
32		<i>Pseudhaloptilus</i> (= <i>Pachyptilus</i>) <i>pacificus</i> ^b	45.4 \pm 14.6	0.03	2.17 \pm 1.13	0.06
33		<i>Pseudochirella spectabilis</i>	28.7 \pm 8.5	0.02	8.33 \pm 3.79	0.2
34		<i>Scaphocalanus acrocephalus</i> (= <i>S. magnus</i>)	200 \pm 22	0.1	48.5 \pm 3.5	1.3
35		<i>S. brevicornis</i>	1026 \pm 154	0.7	35.7 \pm 4.8	1.0
36		<i>S. polaris</i>	17.1 \pm 4.2	0.01	3.40 \pm 1.08	0.09
37		<i>Scolecithricella minor</i>	278 \pm 79	0.2	3.69 \pm 0.87	0.1
38		<i>Spinocalanus antarcticus</i>	1470 \pm 201	1.0	54.8 \pm 8.1	1.5
39		<i>S. elongatus</i>	460 \pm 97	0.3	15.0 \pm 3.1	0.4
40		<i>S. longicornis</i>	884 \pm 158	0.6	10.41 \pm 1.69	0.3
41		<i>S. horridus</i>	188 \pm 36	0.1	7.22 \pm 1.34	0.2
42		<i>S. polaris</i>	160 \pm 49	0.1	3.10 \pm 0.96	0.09
		<i>Spinocalanus</i> cop. spp.	5440 \pm 705	3.8	70.7 \pm 9.2	1.9
43	+	<i>Tharybis groenlandicus</i>	13.2 \pm 5.7	0.01	0.19 \pm 0.07	0.01
44		<i>Temorites brevis</i>	52.0 \pm 5.8	0.04	2.33 \pm 0.30	0.06
45		<i>Undinella oblonga</i>	4.21 \pm 2.76	*	0.17 \pm 0.08	*
46		<i>Xanthocalanus</i> sp.	3.17 \pm 1.74	*	0.10 \pm 0.05	*
Cyclopoida and Harpacticoida						
47		Harpacticoida gen. sp. 1	19.3 \pm 11.3	0.01	0.06 \pm 0.03	*
48		<i>Microsetella norvegica</i>	39.4 \pm 16.9	0.03	0.12 \pm 0.05	*
49	+	<i>Lubbockia brevis</i>	8.41 \pm 2.87	0.01	0.10 \pm 0.03	*
50		<i>L. glacialis</i>	70.7 \pm 22.1	0.05	0.27 \pm 0.08	0.01
51		<i>Hyalopontius typicus</i>	9.82 \pm 3.27	0.01	2.95 \pm 0.96	0.08
52		<i>Mormonilla minor</i>	3880 \pm 400	2.7	6.91 \pm 0.65	0.2
53		<i>Oithona similis</i>	28900 \pm 2220	19.9	86.8 \pm 6.7	2.4
54		<i>Triconia borealis</i> CV-VI	4960 \pm 245	3.4	9.92 \pm 0.49	0.3
55		<i>Oncaea parila</i> CV-VI	4130 \pm 386	2.9	8.27 \pm 0.77	0.2
		<i>Oncaeidae</i> spp. ^a	754 \pm 204	0.5	0.45 \pm 0.12	0.01
		<i>Oncaeidae</i> cop.	20300 \pm 1700	14.0	12.20 \pm 1.03	0.3
		Nauplii Calanoida	11900 \pm 1900	8.2	28.6 \pm 4.7	0.8
		Nauplii Cyclopoida	2620 \pm 684	1.8	0.84 \pm 0.22	0.02
		Copepoda eggs	4820 \pm 807	3.3	5.50 \pm 0.92	0.1
Amphipoda						
56	+	<i>Andaniexis abyssii</i>	Observed	*	Observed	*
57		<i>Cyclocaris guilelmi</i>	15.4 \pm 4.5	0.01	8.99 \pm 3.59	0.3
58	+	<i>Eusirogenes arctica</i>	Observed	*	Observed	*
59		<i>Eusirus holmi</i>	0.97 \pm 0.53	*	11.1 \pm 8.1	0.3
60		<i>Lanceola clausi</i>	20.9 \pm 21.9	0.01	2.27 \pm 2.37	0.06

Table 1 (continued)

No.	New records	Taxa	Abundance, no. m ⁻² , mean ± SE	% abundance	Biomass, mg DW m ⁻² , mean ± SE	% biomass
61	+	<i>Mimoneustes sphaericus</i>	Observed	*	Observed	*
62		<i>Onisimus glacialis</i>	0.29 ± 0.31	*	1.05 ± 1.09	0.03
63		<i>Scina pusilla</i>	Observed	*	Observed	*
64		<i>Themisto libellula</i>	14.7 ± 5.4	0.01	26.6 ± 6.7	0.7
65		<i>T. abyssorum</i>	168 ± 46	0.1	30.6 ± 6.7	0.8
66	+	<i>Rachotropis (inflata?)</i>	Observed	*	Observed	*
Decapoda						
67		<i>Hymenodora glacialis</i>	7.64 ± 2.35	0.01	39.1 ± 12.4	1.1
Euphausiacea						
68		<i>Thysanoessa inermis</i>	1.32 ± 0.77	*	3.85 ± 2.25	0.1
69		<i>T. raschii</i>	1.36 ± 0.83	*	4.77 ± 3.05	0.1
Mysidacea						
			0.31 ± 0.32	*	1.01 ± 1.05	0.03
Ostracoda						
70		<i>Boroecia maxima</i>	1350 ± 56	0.9	125 ± 22	3.4
71		<i>B. borealis</i>	observed	*	*	*
72	+	<i>Boroecia</i> sp. nov.	44.6 ± 1.86	0.03	3.99 ± 2.23	0.1
73		<i>Procerocia vitjazi</i>	44.0 ± 1.83	0.03	3.98 ± 2.86	0.1
74		<i>Discoconchoecia elegans</i>	Observed	*	*	*
Polychaeta						
75	+	<i>Phalascophorus pictus borealis</i>	54.9 ± 7.88	0.04	0.99 ± 0.18	0.03
76	+	<i>Pelagobia longicirrata</i>	Observed	*	Observed	*
77	+	<i>Tomopteris septentrionalis</i>	Observed	*	Observed	*
78	+	<i>Typhloscolex muelleri</i>	191 ± 21.3	0.1	7.30 ± 1.17	0.2
79	+	<i>Minuspio</i> sp. nov.	Observed	*	Observed	*
Pteropoda						
80		<i>Limacina helicina</i>	3770 ± 723	2.6	5.04 ± 0.87	0.1
81		<i>Clione limacina</i>	5.50 ± 2.08	*	0.33 ± 0.17	0.01
Chaetognatha						
82		<i>Parasagitta</i> (= <i>Sagitta</i>) <i>elegans</i>	2.59 ± 1.09	*	9.35 ± 3.79	0.3
83		<i>Sagitta maxima</i>	23.1 ± 6.6	0.02	12.5 ± 5.2	0.3
84		<i>Eukrohnia hamata</i>	1090 ± 83	0.8	445 ± 42	12.1
		<i>E. hamata</i> eggs	198 ± 156	0.1	0.10 ± 0.08	*
85	+	<i>Heterokrohnia involucrium</i>	Observed	*	Observed	*
Appendicularia						
86		<i>Fritillaria borealis</i>	1180 ± 234	0.8	1.91 ± 0.38	0.05
87		<i>F. polaris</i>	Observed	*	Observed	*
88		<i>Oikopleura vanhoeffeni</i>	1350 ± 229	0.9	22.5 ± 8.1	0.6
89	+	<i>Oikopleura gorskyi</i>	4.96 ± 3.10	*	0.01 ± 0.00	*
Foraminifera						
90		<i>Neogloboquadrina pachyderma</i>	2020 ± 260	1.4	0.00 ± 0.00	nd
Hydromedusae						
91		<i>Aglantha digitale</i>	140 ± 19	0.1	12.0 ± 2.0	0.3
92		<i>Aeginopsis laurentii</i>	0.94 ± 0.52	*	0.19 ± 0.20	0.01
93		<i>Narcomedusae</i> sp. nov.	5.95 ± 2.01	*	1.35 ± 0.57	0.04
94	+	<i>Botrynema brucei</i>	1.84 ± 1.37	*	5.54 ± 3.97	0.2
95		<i>B. ellinorae</i>	24.9 ± 6.3	0.02	12.1 ± 6.0	0.3
96	+	<i>Crossota norvegica</i>	0.30 ± 0.32	*	0.69 ± 0.72	0.02
97		<i>Homoeonema platygonon</i>	30.6 ± 6.4	0.02	0.03 ± 0.01	*
98	+	<i>Margelopsis hartlaubi</i>	3.54 ± 1.99	*	0.00 ± 0.00	*
99		<i>Paragotaea bathybia</i>	6.08 ± 2.04	*	0.01 ± 0.00	*
100		<i>Sminthea arctica</i>	78.0 ± 14.4	0.05	10.5 ± 1.9	0.3
101	+	<i>Solmundella bitentaculata</i>	0.61 ± 0.63	*	0.00 ± 0.00	*
102		<i>Rhabdoon reesi</i> ^d	11.4 ± 2.6	0.01	0.02 ± 0.02	*
Scyphomedusae						
103		<i>Atolla tenella</i>	4.44 ± 1.81	*	19.4 ± 13.8	0.5
Siphonophora						
104		<i>Dimophyes arctica</i>	540 ± 57	0.4	108 ± 11	3.0
105		<i>Marrus orthocanna</i>		nd		nd
106		<i>Muggiaea bargmannae</i>		nd		nd
107		<i>Rudjakovia plicata</i>		nd		nd
Ctenophora						
108		<i>Beroe cucumis</i>	1.74 ± 1.13	*	0.45 ± 0.44	0.01
109		<i>Mertensia ovum</i>	0.42 ± 0.44	*	0.05 ± 0.06	*
110		<i>Ctenophora</i> sp. 1	4.54 ± 1.60	*	0.40 ± 0.33	0.01
111		<i>Ctenophora</i> sp. 2	2.84 ± 1.11	*	0.14 ± 0.06	*

*—biomass and abundance <0.01%; nd—biomass not calculated.

^a Composite groups of unidentified species.^b Pacific expatriates.^c Presumably *Onchocalanus cristatus* in Harding (1966).^d *Yakovia polynae* in Margulis (1989) and *Pararhysomedusae reesi* in Shirley and Leung (1970).

For copepods, vertical distribution ranges and mean abundances of each species within sampled depth intervals were first explored in a tabular fashion according to Mumm (1993). More quantitative approaches to community abundance patterns were explored using the Primer (V6) software package to reveal patterns in zooplankton communities (e.g., Clarke and Warwick, 2001; Wishner et al., 2008; Schnack-Schiel et al., 2008). The data were power transformed (either square root or 4th root), and the Bray–Curtis similarity index between stations was calculated employing all taxonomic categories as well as only those that contributed at least 3% to any sample (to remove very rare species occurring somewhat randomly in collections). The Bray–Curtis similarity was calculated between each sample. Significant groups within the hierarchical clustering ($\alpha = 5\%$) were established with the SIMPROF routine. The Bray–Curtis similarity matrix was subjected to multi-dimensional scaling (MDS) to establish the “distance” between samples, and then projected onto 2-D plots, to which cluster groupings were then superimposed. Insight into the species combinations responsible for each cluster was explored by the SIMPER routine, as well as by performing cluster analysis as above between the species (Hopcroft et al., 2009).

Temperature and salinity data from CTD casts were binned into 1 m depth intervals, and an average value calculated for each multinet sampling interval. Relationships between zooplankton community composition and averaged variables were explored with Primer's BEST routine using physical data normalized as recommended within Primer, which accounts for the different measuring scales of environmental factors (Clarke and Warwick, 2001).

3. Results

3.1. Physical oceanography of the region

The Arctic water column is characterized by a complex layering of water masses and transition zones at all stations (Fig. 2), which are best highlighted on a log scale (see McLaughlin et al., 2002, 2005). During summer, from the surface to 20–40 m, the Polar Surface Water temperature remained relatively constant ($\sim 1.2^\circ\text{C}$) with slowly increasing salinity. Below this zone, temperature typically increased rapidly at 40–60 m in the Bering Sea Summer Water by nearly 1.0°C , and then declined in the Bering Sea Winter Water to a temperature minimum at 140–170 m. The temperature minimum signaled the transition into Atlantic waters from the Fram Strait Branch, with a steady increase in temperature and salinity to a depth of 400 m. Below 400 m, salinity remained high while temperature decreased, due in part to influences of the Barents Sea Branch, to a depth of ~ 2000 m, where water transitioned to the deep-basin Arctic Bottom Waters that have little mixing with other water layers and consequently have long ventilation times. Particularly in waters above 200 m, slight differences in the depth range of the different water masses at different stations might be expected to blur distinctions between the associated fauna that were sampled at fixed depth intervals.

3.2. Zooplankton composition

A total of 111 species including 74 species of crustaceans (55 species of copepods, 2 euphausiids, 11 amphipods, 1 decapod, 5 ostracods), 17 cnidarians (12 hydromedusae, 1 scyphomedusae, 4 Siphonophora), 1 foraminifera, 4 ctenophores, 2 pteropods, 4 larvaceans, 4 chaetognaths, and 5 polychaetes were identified in the present collections (Table 1). Most of the species observed are

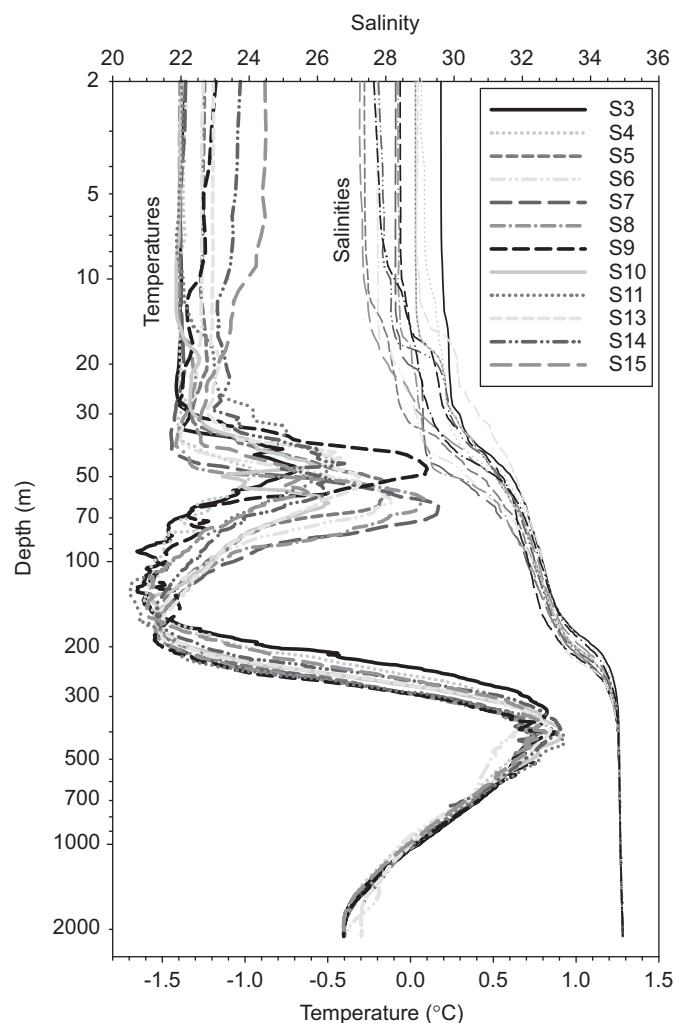


Fig. 2. Temperature and salinity profiles of stations 3–15 plotted on a log depth scale. Temperature in heavy lines, salinity in lighter lines.

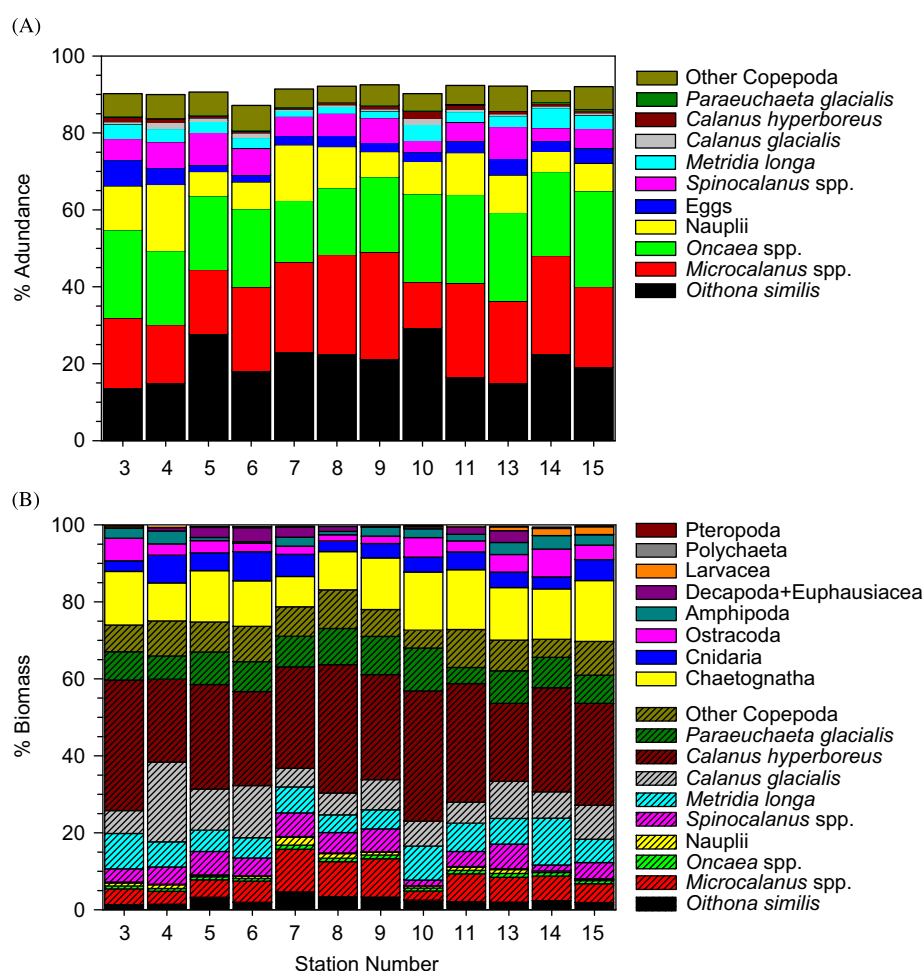
typical of Arctic waters, with the notable exception of the copepods *Eucalanus bungii*, *Neocalanus cristatus*, *Metridia pacifica*, *Pseudocalanus newmani* and *Pseudhaloptilus* (= *Pachyptilus*) *pacificus*. Specimens of all five species were found very rarely, and as late developmental stages (CVs and adults) only. One species of larvacean, *Fritillaria polaris*, has only been reported infrequently (Virketis, 1957; Melnikov and Kolosova, 2001), while another larvacean, *Oikopleura gorskyi*, has only been reported from its type locality in Norwegian fjords (Flood, 2000) and is a new record for the Arctic. Three species, a narcomedusae sp. nov., a polychaete *Minuspio* sp. nov., an ostracod *Boroecia* sp. nov. are new to science and are currently under description (Raskoff, Gagaev, Angel, unpublished). Several small-sized deep-water copepod species occurring below 500 m were not identified to species level, including ca. six deep-living oncaeids, and ca. 12 small calanoids with definitive size of 0.5–0.7 mm predominantly belonging to the Discoidae family. Some of the latter are new, undescribed species, and some require taxonomic revision (V.N. Andronov, personal communication).

Of the 11 large taxonomic groups present, copepods were the most important in terms of abundance ($91.0 \pm 0.45\%$: mean \pm standard error), while other groups had limited numerical contribution (Table 2). Of these, pteropods, larvaceans, foraminiferans and ostracods (predominantly *Boroecia maxima*) contributed from 1% to 2.6% on average, although pteropods (predominantly larvae and juveniles of *Limacina helicina*) and

Table 2

Relative contribution (%) of the different taxonomic groups to the total zooplankton abundance in the Canada Basin, July 2005.

Station No.	3	4	5	6	7	8	9	10	11	13	14	15	Mean \pm SE
Depth, m	1935	2149	3847	3848	3845	3847	3200	1407	1498	845	1349	2380	
Copepoda	90.3	90.1	90.7	87.2	91.4	92.1	92.5	90.2	92.3	92.2	90.9	92.1	91.0 \pm 0.45
Amphipoda	0.5	0.3	0.1	0.06	0.04	0.03	0.05	0.3	0.06	0.3	0.3	0.1	0.2 \pm 0.04
Euphausiacea+Decapoda	0.02	0.02	0.02	0.02	0.01	0.02	0	0.01	0.01	0.02	0	0.01	0.01 \pm 0.002
Ostracoda	1.6	1.1	1.2	1.1	0.6	0.6	0.6	1.0	0.6	1.0	1.6	1.5	1.0 \pm 0.12
Cnidaria+Ctenophora	0.5	0.8	0.6	0.7	0.5	0.4	0.6	0.8	0.6	0.5	0.6	1.0	0.6 \pm 0.05
Polychaeta	1.7	0.2	0.2	0.2	0.2	0.1	0.1	0.2	0.2	0.3	0.4	0.2	0.3 \pm 0.13
Pteropoda	0.9	2.4	3.5	6.3	3.9	3.1	1.9	2.2	1.1	2.4	2.5	1.1	2.6 \pm 0.45
Chaetognatha	1.1	0.7	0.7	0.7	0.5	0.6	0.7	1.0	2.2	0.7	1.2	0.9	0.9 \pm 0.13
Larvacea	1.9	2.4	1.2	3.0	0.9	1.8	1.3	3.1	2.0	1.9	1.4	0.9	1.8 \pm 0.22
Foraminifera+Radiolaria+Tintinnina	1.5	2.1	1.7	0.8	2.0	1.5	2.2	1.2	0.9	0.7	1.0	2.2	1.0 \pm 0.16

**Fig. 3.** (A) Relative contribution (%) of the copepod species, eggs and nauplii to the total zooplankton abundance (non-copepods groups not shown); (B) Relative contribution (%) of different taxa to the total zooplankton biomass.

larvaceans contributed up to 3.0–6.3% at some locations. The average proportion of chaetognaths was even lower ($0.9 \pm 0.1\%$); other groups occurred regularly but were rare (amphipods, polychaetes, cnidarians), or were both rare and irregular in occurrence (euphausiids, decapods, ctenophores).

Among the copepods, the contribution of calanoids and cyclopoids was very similar, 46% and 45%, respectively (Table 1). Harpacticoid copepods were of minor importance (Table 1). The small copepods *Oncaea* spp. ($20.8 \pm 0.8\%$), *Microcalanus* spp. ($21.5 \pm 1.4\%$) and *Oithona similis* ($19.9 \pm 1.5\%$) were major contributors to total zooplankton abundance (Fig. 3A). Altogether, these smaller species contributed from 50% to 70% of the total.

Other important copepod groups were nauplii, eggs, and several species of the calanoid *Spinocalanus* (Fig. 3A).

In terms of biomass, copepods remained the most important group ($74.2 \pm 1.2\%$, Table 1, Fig. 3B). The chaetognaths ranked second ($12.8 \pm 0.7\%$), followed by cnidarians and ctenophores ($4.7 \pm 0.5\%$) and ostracods ($3.6 \pm 0.5\%$), while amphipods and decapods plus euphausiids alternated between stations in ranking of importance (Fig. 3B). Chaetognaths represented ca. 50% of the total non-copepod biomass. Among the copepods, cyclopoids contributed $<4\%$ of the total biomass, while calanoids contributed 70% on average (Table 1). Four large Arctic calanoid copepods *Calanus hyperboreus*, *C. glacialis*, *Paraeuchaeta glacialis* and *Metridia*

longa dominated biomass at all stations; however, the average contribution of *C. hyperboreus* ($27.7 \pm 1.4\%$) was 3–4 times higher than *C. glacialis*, *P. glacialis* and *M. longa* (9.2 ± 1.4 , 7.8 ± 0.5 and $7.0 \pm 0.6\%$, respectively). Interestingly, the small calanoid copepod *Microcalanus* spp., one of the three most important contributors to the total zooplankton abundance (Fig. 3A), was almost as important in terms of biomass ($6.0 \pm 0.8\%$) as *M. longa* (Fig. 3B).

3.3. Vertical abundance and biomass distribution

Estimates of abundance, biomass and composition of the zooplankton community were surprisingly consistent over the sampling area, particularly after excluding cnidarians and ctenophores, which showed large variation between locations due to their generally low numbers compared to other groups.

The vertical profiles of total zooplankton abundance (Fig. 4A) and biomass (Fig. 4B) showed overall similarity among stations, with much of the variability in the top 100 m (Table 3). The maxima for both measurements occurred within the Polar Surface Water, either in the upper 0–25 (mean 1170 ind m^{-3} , 21 mg DW m^{-3}), or subsurface 25–50 m (mean 1310 ind m^{-3} , 38 mg DW m^{-3}) layer. Below 50 m, a progressive decrease in zooplankton abundance and biomass was observed, followed by a slight increase in the 200–300 m layer (mean 151 ind m^{-3} , $3.75 \text{ mg DW m}^{-3}$), the transition between the Pacific halocline and Atlantic Water (Fig. 4A,B). Below 300 m, there was a slow decrease of both parameters to the bottom or lower sampling limit (3000 m, mean 5.7 ind m^{-3} , $0.13 \text{ mg DW m}^{-3}$).

The averaged vertical distribution of integrated abundance (ind m^{-2}) indicated that ca. 45% of zooplankton organisms were concentrated in the upper 0–50 m layer, which represented <2% of the entire water column. Below 50 m, integrated abundance was at least two times lower in each sampled layer. However, nearly 50% of all organisms occurred below 100 m (Fig. 5A). The general distribution pattern of copepod and non-copepod taxa was similar, but the latter did not exceed 10% of copepod integrated abundance in any layer (Fig. 5A).

The averaged vertical distribution of integrated biomass (mg DW m^{-2}) indicated that a large portion of the zooplankton stock, ca. 40%, was concentrated in the top 50 m, with 1/3 in the uppermost 0–25 m layer (Fig. 5B). Half of the total stock was present in the upper 100 m (Fig. 5B). Copepods comprised 70–90% of total biomass in each sampled layer above 200 m. Between 200 m and the bottom (or lower sampling limit), the contribution of other groups increased, varying between 35% and 40% (Fig. 5B). Total zooplankton biomass integrated over the entire water column, varied from 2.97 to 5.26 g DW m^{-2} (mean $3.64 \pm 0.23 \text{ g m}^{-2}$). At all locations over the continental slope (stns. 3, 4 and 15) and on the Chukchi Plateau (stns. 11 and 13) biomass values were 25–40% higher in comparison to the deep Canada Basin.

3.4. Vertical distribution of copepod species

The dominant copepod species demonstrated different vertical patterns (Fig. 6). Abundance and biomass of the dominant suspension-feeders, *Calanus glacialis* and *C. hyperboreus*, was

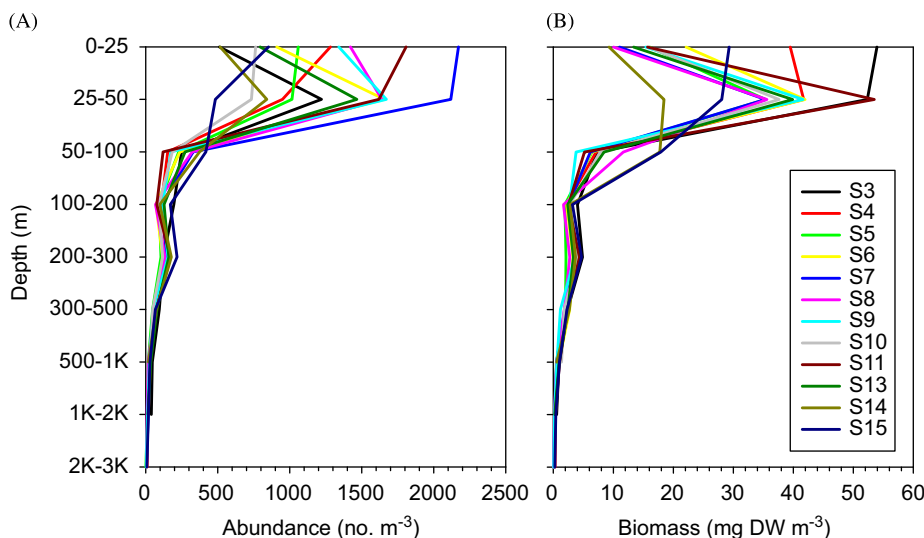


Fig. 4. Vertical distribution of zooplankton abundance, ind m^{-3} (A) and biomass, mg m^{-3} (B) at stations 3–15 in the Canada Basin.

Table 3

Abundance and biomass range and mean \pm SE in different water masses in the study area.

Water mass	Depth (m)	Abundance (ind m^{-3})		Biomass (mg DW m^{-3})	
		Mean \pm SE	Range	Mean \pm SE	Range
Polar Surface Water	0–25	1170 ± 163	522–2290	21.0 ± 4.1	9.3–53.9
	25–50	1310 ± 146	492–2140	38.4 ± 2.9	18.4–53.5
Bering Sea Summer Water	50–100	286 ± 28	137–445	8.8 ± 1.4	3.8–17.9
Bering Sea Winter Waters	100–200	119 ± 13	72–212	2.6 ± 0.2	1.7–4.0
Atlantic layer	200–300	151 ± 9	108–217	3.8 ± 0.2	2.1–4.9
	300–500	67.7 ± 4.1	50.6–95.4	2.2 ± 0.1	1.2–2.7
	500–1000	29.2 ± 3.1	18.4–52.4	0.82 ± 0.08	0.5–1.4
	1000–2000	18.1 ± 3.2	9.4–43.4	0.31 ± 0.04	0.2–0.5
Arctic Bottom Water	>2000	5.7 ± 0.2	1.0–9.9	0.13 ± 0.04	0.05–0.31

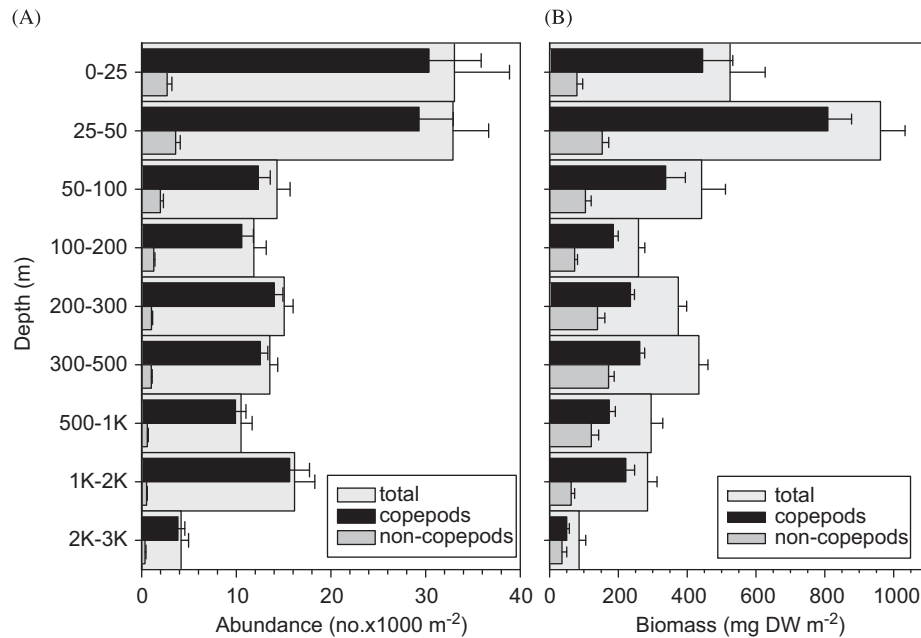


Fig. 5. Average vertical distribution of integrated zooplankton abundance, ind $\times 1000 \text{ m}^{-2}$ (A) and biomass, mg DW m^{-2} (B). Black bars show contribution of copepods, dark grey bars—contribution of other taxa, whiskers are standard error.

concentrated predominantly in the upper layers, with single specimens of both species found down to the maximum sampled depths (Fig. 6A,C). Maximum *C. glacialis* abundance and biomass were present in the surface layer (0–25 m), with a 5–10-fold decrease in the 25–50 m layer followed by a sharp decrease below this. Whereas *C. hyperboreus* peaked in the subsurface layer at 25–50 m (Fig. 6A,C), a pronounced decrease in abundance and biomass below 50 m was similar to that of *C. glacialis*.

The omnivorous *M. longa* and carnivorous *P. glacialis* were concentrated in deeper waters, with significantly lower abundance and biomass than the *Calanus* species (Fig. 6B,D). The majority of *M. longa* occurred between the surface and 500 m, with highest abundance between 200 and 500 m (Fig. 6B), peaking between 200 and 300 m. Highest *M. longa* biomass occurred in the upper layer (25–100 m) due to the predominance of late-stage copepodites. High abundance and low biomass between 200 and 500 m was related to the prevalence of numerous early stage copepodites of lower weight. *P. glacialis* occupied a similar depth range (0–500 m), but with highest abundance between 25 and 100 m. While its abundance maximum was shifted upward relative to *M. longa*, the layers of highest biomass (25–100 m) were similar (Fig. 6D).

The remaining copepod species had wide but characteristic depth-distribution ranges (Fig. 7), and inhabited at least two (Polar surface and Atlantic Water or Atlantic and Arctic bottom water) or three water masses. The deeper depth preferences of most species resulted in extremely low diversity in the surface waters, and a pronounced increase in diversity with depth, followed by a modest decline below 2000 m (Fig. 8).

3.5. Vertical patterns of the zooplankton community

The relative contribution of the major taxonomic groups was not uniform with depth (Fig. 9). In Polar waters above 50 m, copepods and chaetognaths dominated (~80% and ~15% of total biomass, respectively). Below 50 m, copepods decreased gradually comprising ~60% in the core of the Atlantic layer (300–1000 m).

Between 1000 and 2000 m, copepods (predominantly cyclopoids) again increased in importance (~80%), while below 2000 m they decreased to <60%. Other groups increased with depth, with each group exhibiting a specific pattern. Chaetognaths contributed ~13% above 1000 m, and then declined abruptly. Cnidarians and ctenophores gradually increased from ~6% at 100 m to ~12–15% between 500 m and the bottom. Ostracods increased in the upper layers, to a maximum of 16–17% between 200 and 300 m (the upper border of Atlantic layer), followed by declines to <2%, between 500 and 2000 m with a slight increase between 2000 and 3000 m. Amphipods demonstrated maximum contribution in the deepest stratum, between 2000 and 3000 m (Fig. 9).

Multivariate analyses of community structure revealed almost identical patterns regardless of the degree of transformation used, if the entire species set was used or only those contributing at least 3% were employed. The only notable difference in these analyses was the level of similarity at which significant minor and major clusters emerged. Similar to our more subjective interpretation of copepod patterns, the cluster analysis also revealed distinct depth layers (Fig. 10). Only the two shallowest strata failed to separate as statistically distinct in their entirety, suggesting predictable changes in community composition with depth in all other strata.

Applying multi-dimensional scaling (MDS) to the similarity data matrix revealed three major patterns (Fig. 10B). Firstly, clustering appears to be largely related to depth, with the low stress value (0.06) confirming the 2-D representation of multi-dimensional space is excellent. Secondly, there is some overlap within the upper two strata, but otherwise there is a clear trajectory of community difference across depth layers, with several transitory samples that failed to cluster as tightly arising because bottom depth restricted collection to incomplete strata. Thirdly, we believe the higher variability within the deep-bottom strata, reflects variable inclusion of the unique near-bottom epibenthic communities dependent on sampling proximity to abyssal plain.

In any given depth stratum, the community is distinct, while the species themselves failed to cluster (not shown), suggesting a

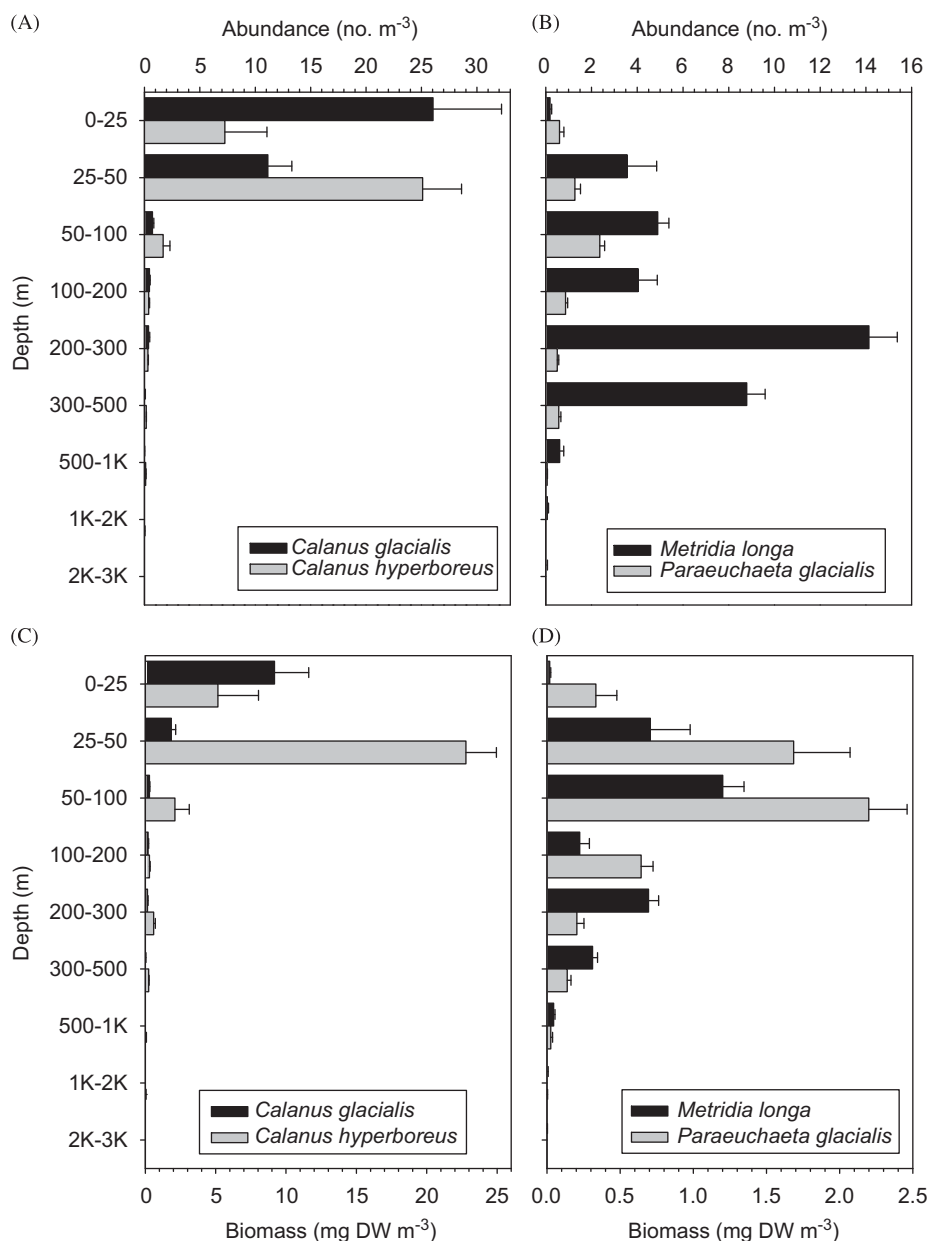


Fig. 6. Averaged patterns of vertical distribution of the dominant copepod species. *Calanus glacialis* and *C. hyperboreus*: (A) abundance, ind m⁻³; (C) biomass, mg m⁻³. *Metridia longa* and *Paraeuchaeta glacialis*: (B) abundance, ind m⁻³; (D) biomass, mg m⁻³. Whiskers are standard error (note: x-axis scales are different).

gradual, but predictable, change in species composition between layers, as some species decline in abundance or disappear, and others increase or appear. Attempts to relate community clusters to environmental variables showed depth to be highly correlated (Spearman correlation = 0.83), while the inclusion of additional variables (e.g., temperature, salinity) lowered the correlation, suggesting neither of these variables per se were driving community structure, or were simply highly confounded with depth. In contrast, when grouped at 60–70% similarity, the clusters more or less represent a Polar mixed layer between 0 and 50 m, Bering Sea Summer Water between 50 and 100 m, a Bering Shelf Winter Water/Fram Strait Branch water group between 100 and 500 m, a Fram Strait Branch/Barents Sea Branch water group between 500 and 1000 and 1000 and 2000 m, and deep Arctic waters below 2000 m.

4. Discussion

4.1. Species inventory

Despite the relatively limited number of stations occupied during this study, a total of 111 different species were recorded (Table 1), representing the majority of the species typifying the central Arctic basins (Sirenko, 2001). Comparison of our data with other published lists shows that among 111 species found in this study, 88 species have been previously recorded in the Canadian Basin (Brodsky and Nikitin, 1955; Virketis, 1957, 1959; Harding, 1966; Shirley and Leung, 1970; Damkaer, 1975) and the Canada Basin in particular (Kosobokova, 1981; Hopcroft et al., 2005; Raskoff et al., 2005). Three species found (one Narcomedusae, one Ostracoda and one Polychaeta, Table 1) are new to science. Four

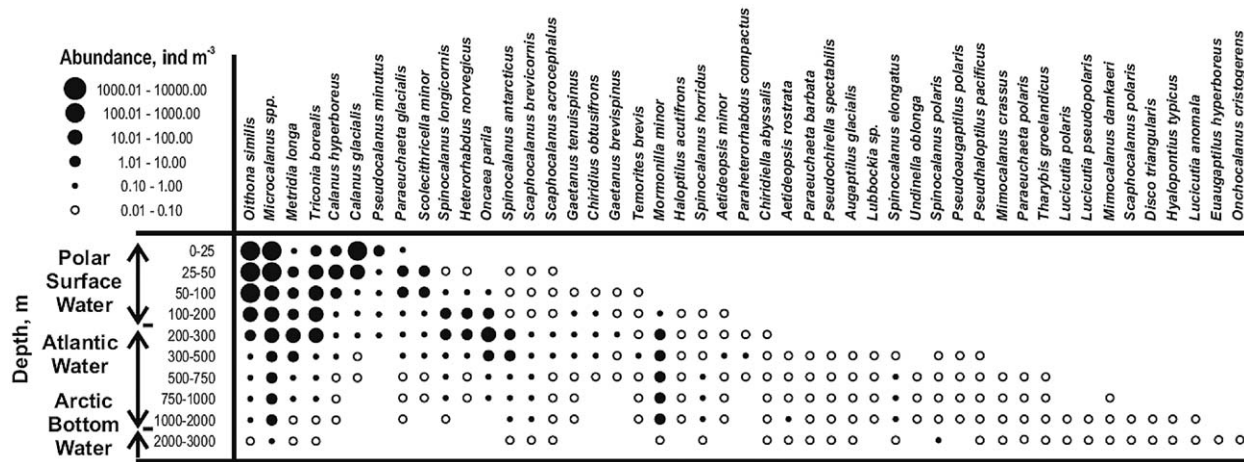


Fig. 7. Generalized vertical distribution patterns of 47 copepod species in the study area (mean of 12 stations).

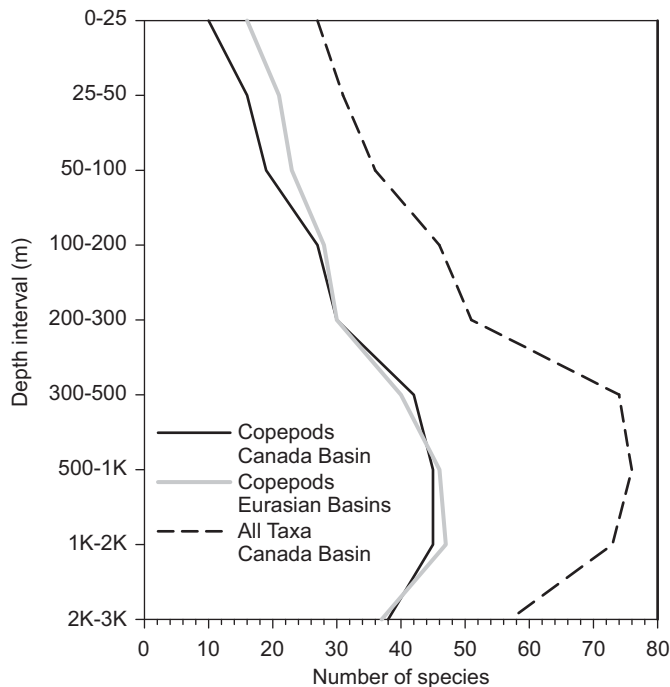


Fig. 8. Vertical distribution of zooplankton species diversity in the Canada Basin (present study) and Eurasian Basins (Eurasian Basins data modified from Kosobokova and Hirche, 2000).

copepod species, four hydromedusae, five Polychaeta, one Larvacea, and four Amphipoda species are listed for the Canada Basin for the first time (Table 1). Two species, the copepod *Onchocalanus cristogerens* and the hydromedusa *Rhabdoon reesi*, have not been previously recorded, but appear to have been described in the Canadian Basin previously under other names. *O. cristogerens* was described as a new species from the Arctic Ocean (Markhaseva and Kosobokova, 1998), with the suggestion that Harding (1966) identified it as *O. cristatus*, and *Pararhysomedusa reesi* (Shirley and Leung, 1970) and *Yakovia polynae* (Margulis, 1989) have been redescribed and synonymized with *R. reesi* (Stepanjants and Kosobokova, 2006).

Comparison of our species list for the Canada Basin with inventories for the Eurasian Basin (Mumm, 1993; Sirenko et al., 1996; Kosobokova et al., 1998; Kosobokova and Hirche, 2000)

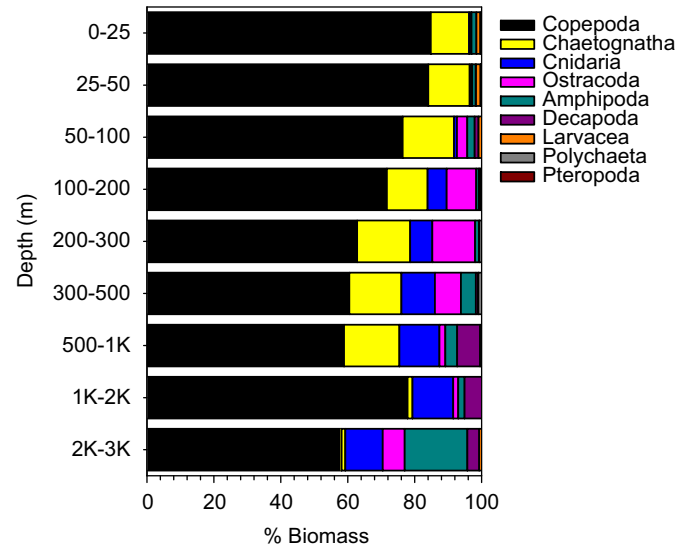


Fig. 9. Relative contribution of the major taxonomic groups to the zooplankton community across the sampling strata.

indicates a close similarity in species composition in the two basins. In total, 104 of the 111 species found in the present study are also present in the Eurasian Basin. Exceptions are the copepods *E. bungii*, *N. cristatus*, *M. pacifica*, and *P. newmani*, which are restricted to the Canadian Basin. These species are common inhabitants of the North Pacific, and are often expatriated with Pacific water into the Chukchi Sea (Stepanova, 1937a, b; Jaschnov, 1940; Hopcroft et al., 2010), and further north into the Arctic Ocean (Brodsky and Nikitin, 1955; Johnson, 1963; Harding 1966; Dunbar and Harding, 1968; Pavshitskiy, 1971). While the first three have been repeatedly found in the Canadian Basin, *P. newmani* is described north of 74°N for the first time. All four species are found in the Arctic Ocean, but only as later developmental stages, with the absence of young stages regarded as an indication of their reproductive failure in the Arctic (Brodsky and Nikitin, 1955). A further species, the North Pacific midwater copepod *P. (= Pachyptilus) pacificus*, was found at four stations in this survey, and several times previously in the Canadian Basin as late copepodites and adults (Kosobokova, 1981). It is likely to belong to the same group of the Pacific expatriates. However, a

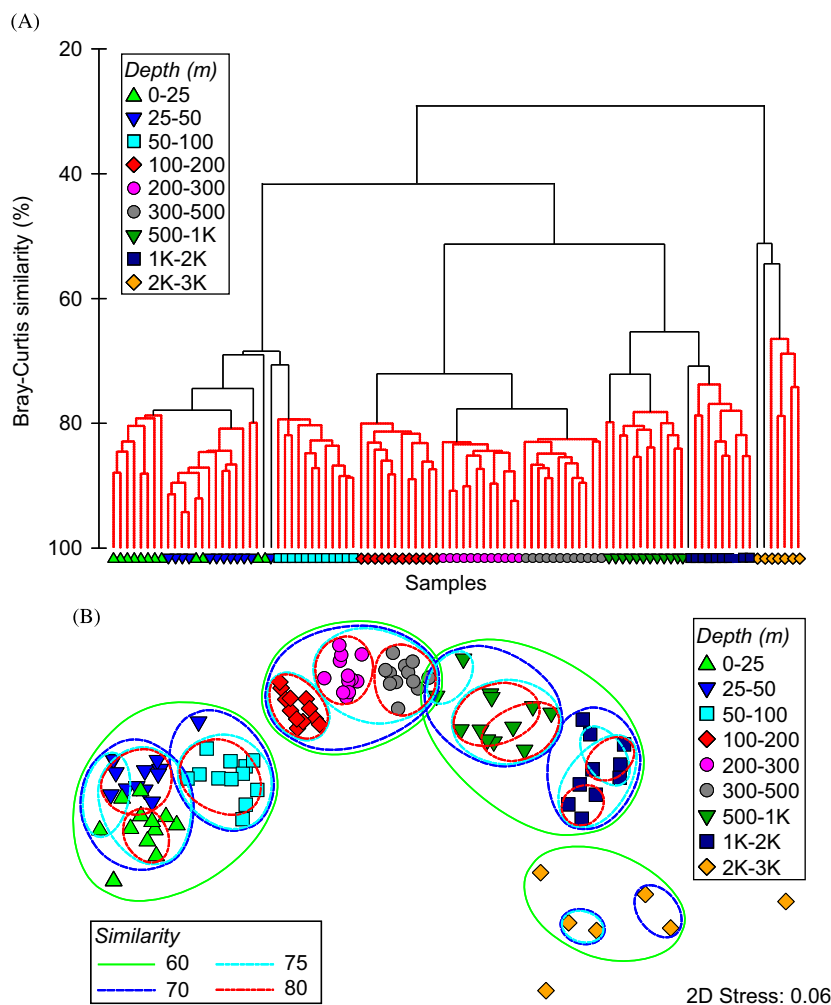


Fig. 10. Multivariate analysis of community similarity, presented as example for 4th-root transformed abundances and species contributing at least 3% to the transformed data. (A) Weighted-pair clustering, black lines connect statistically distinct groups at $p = 0.05$. (B) Two-dimensional representation of multi-dimensional community structure, where distance between samples is proportional to their similarity. Percentage similarity is represented by surrounding circles.

mechanism that would consistently transport low abundances of a mesopelagic species across the shallow Bering Shelf is not readily apparent. *P. pacificus* has not yet been observed in the Eurasian Basin (Mumm, 1993; Kosobokova et al., 1998; Kosobokova and Hirche, 2000); thus we are inclined to believe it also fails to reproduce in the Arctic.

Another striking difference to the Eurasian Basins is the complete absence of Atlantic expatriates in the Canada Basin. The most notable absence is the copepod *C. finmarchicus*, a common and abundant member of plankton communities in the Eastern Arctic (Mumm, 1993; Kosobokova and Hirche, 2000; Hirche and Kosobokova, 2007). Although enormously high numbers of this Atlantic species are continuously advected into the Arctic via Fram Strait and the Barents Sea shelf with Atlantic water (Hirche and Mumm, 1992; Kosobokova and Hirche, 2009), it almost completely disappears from the pelagic community east of the Lomonosov Ridge. Only a few specimens of *C. finmarchicus* have been found as far as the Makarov Basin, and then still close to the Lomonosov Ridge (Johnson, 1963; Kosobokova, 1981; Thibault et al., 1999; Kosobokova and Hirche, 2000). Similar to Pacific expatriates, *C. finmarchicus* fails to reproduce or maintain a local population in the Arctic Ocean. Other Atlantic expatriates (*Oithona atlantica*, *Paraeuchaeta norvegica*, *Metridia lucens*, *Pleuromamma robusta*, *Rhincalanus nasutus*) present in the Eurasian Basin (Kosobokova, 2009) have not yet been found in the Canadian

Basin (Brodsky and Nikitin, 1955; Johnson, 1963; Harding, 1966; Kosobokova, 1981).

In general, we conclude that apart from differences in the distribution of Pacific and Atlantic expatriates, species composition in the Western and Eastern Arctic is similar, suggesting successful between-basin fauna exchange across the underwater ridges (Kosobokova and Hirche, 2000). This is true for all Arctic meso- and bathypelagic species, and contrary to the suggestion of Brodsky and Pavshchikov (1976) that the Canadian Basin hosts a unique deep-water community of Arctic endemics, with the Lomonosov Ridge acting as a zoogeographical barrier for penetration of this deep-water fauna into the Eurasian Basin.

We suggest that the new species found in the Canadian Basin during this expedition are simply a consequence of more detailed faunistic analyses. Thus, the species composition in the Canada Basin remains essentially the same as it was 50–60 (Brodsky and Nikitin, 1955; Virketis, 1957, 1959; Harding, 1966) and 30 (Kosobokova, 1981) years ago. The zooplankton communities consist of predominately oceanic species (e.g., Ashjian et al., 2003; Hopcroft et al., 2005; Lane et al., 2008) typical of an area with water masses of a strictly Arctic Ocean origin. The advection of Pacific fauna remains very low (Table 1), despite expectation that the contribution of Pacific and Arctic shelf species will increase due to climate change and/or changing circulation regimes (Lane et al., 2008; Hopcroft et al., 2008).

In terms of diversity, the Canada Basin displays a pattern found for many oceanic communities (Vinogradov, 1970), with a pronounced increase in species diversity with depth (Fig. 8). Extremely low species diversity in the upper layers occurs in the Canada (Kosobokova, 1989) and Eurasian basins (Kosobokova and Hirche, 2000), the Antarctic (Schnack-Schiel et al., 2008), and to some extent even in subarctic waters (Mackas and Tsuda, 1999). In the Arctic, it could be explained by less favorable conditions in the uppermost layers due to striking temperature and salinity gradients and higher predation risk. Species diversity reaches a maximum in the Atlantic layer, between 300 and 2000 m, followed by a decrease in the deeper layers in the Canada (Fig. 10) and Eurasian basins (Kosobokova, 2009). The decrease in the deepest layers could be an artifact of the limited number of samples collected at depths below 2000 m, resulting in an underestimation of diversity. In this study, at least a dozen small calanoid species and several deep-water oncaeids were not identified, so their inclusion in the species inventory would reverse the decline in diversity observed at the deepest sampling interval.

4.2. Abundance and biomass

4.2.1. Integral taxonomic contribution

As typical for most Arctic zooplankton studies, copepods were the most important group of zooplankton in terms of species number, abundance and biomass (Hopkins, 1969a; Mumm et al., 1998; Kosobokova and Hirche, 2000; Auel and Hagen, 2002; Ashjian et al., 2003; Hopcroft et al., 2005). Small copepods (both calanoids and cyclopoids) dominated numerically, while a few large calanoids dominated the biomass (Hopcroft et al., 2005).

Many other zooplankton groups are consistently underappreciated, consequently we made a concerted effort to quantitatively assess the role of the non-copepod groups in this study to address questions concerning their importance in the Canada Basin. Neither of the two most numerical non-copepod 'herbivorous' groups, pteropods (predominantly *L. helicina*) and larvaceans, exceeded 3% total abundance (Table 2), and their biomass was low compared to all other groups. Pteropods and larvaceans undergo rapid population increases with locally favorable feeding conditions. In polar environments, short-term "blooms" of larvaceans usually coincide with increased primary productivity (Hopkins, 1969a; Acuna et al., 2002; Deibel et al., 2005) due to their high fecundity, short generation times, and rapid growth rates (Hopcroft et al., 1998; López-Urrutia et al., 2003). Significant larvacean abundance and notable biomass has been observed recently in Arctic waters (e.g., Hopcroft et al., 2005, 2010; Deibel et al., 2005; Lane et al., 2008), although it is not clear if this represents an increase in their abundance, or simply greater attention has been paid to their presence. In contrast, growth rates of *L. helicina* are low (Fabry, 1989) and generation times long (Conover and Lalli, 1972; Kobayashi, 1974; Dadon and Cidre, 1992; Shkoldina, 1999), but favorable food may result in high reproductive rates, with transient swarms of juveniles, such as encountered in this study.

Other taxonomic groups were generally of lower numerical importance than pteropods and larvaceans, but relatively more important in terms of their biomass. Chaetognaths represented about half the non-copepod biomass, and are widely recognized as one of the most important copepod predators in Arctic waters (Mumm, 1993; Richter, 1994; Kosobokova and Hirche, 2000; Auel and Hagen, 2002), while ostracods are recognized as important scavengers (Chavtur and Bashmanov, 2007). Notably, cnidarians (including ctenophores) ranked as the second most important group of non-copepod predators after chaetognaths when their

biomass is appropriately normalized to allow comparison. A fuller consideration of the importance of cnidarians and ctenophores as predators during this expedition occurs elsewhere in this issue (Raskoff et al., 2010; Purcell et al., 2010).

4.2.2. Vertical abundance and biomass structure

Vertical patterns of zooplankton abundance and biomass indicate relatively uniform distribution over the study area. These patterns with a large portion of the zooplankton concentrated in the uppermost layers at all studied locations (Fig. 4A,B) were consistent with other observations on annual cycles of the zooplankton distribution (Hopkins, 1969a; Pautzke, 1979; Kosobokova, 1982; Ashjian et al., 2003) and typical of the Arctic summer. The much lower abundance and biomass per unit volume below 100 m, has led to the mindset that deeper layers are unimportant. When we consider units of per square meter, thereby allowing for the absolute contribution in each layer, we find that about half of all mesozooplankton occurs below 100 m numerically, and the same holds true in terms of biomass, at least for the copepods. The consequence is that, in the Arctic, the importance of the unique assemblages of mesopelagic and bathypelagic species is extremely under-appreciated. Elsewhere in the world it is argued that zooplankton at these depths can be ignored because they live in much colder waters than the surface species, and therefore contribute proportionately little to community processes such as grazing and carbon recycling (i.e. respiration). Clearly this argument does not hold in the Arctic, where temperatures, and consequently respiration rates will differ little across depth; hence the deep-water zooplankton is a more equal player in the consumption and recycling of carbon.

Within the upper 100 m water layer, a pronounced surface maximum of abundance and biomass results from seasonal aggregation of almost the entire populations of the large-bodied Arctic suspension-feeding copepods *C. hyperboreus* and *C. glacialis* (Fig. 6A,C). Moreover, both these species had their abundance and biomass maxima within the upper layer 0–50 m, although *C. hyperboreus* demonstrated a deeper maximum compared to *C. glacialis*. Several seasonal studies showed that *C. hyperboreus* concentrates in the uppermost waters by early summer, and descends to intermediate depths (~400–500 m) during late summer (Brodsky and Pavshitskiy, 1976; Geynrikh et al., 1983; Ashjian et al., 2003). The shift of the *C. hyperboreus* maximum to the 25–50 m subsurface layers might indicate the onset of autumnal descent during end of July (Fig. 6A,C), but it is equally possible *C. hyperboreus* simply avoids the reduced salinity experienced within the surface layer in comparison to its sibling species.

Other dominant copepod species showed slightly (e.g., *M. longa*) or considerably deeper (e.g., *P. glacialis*) abundance and biomass maxima compared to *Calanus* spp. (Fig. 6B,D), but due to relatively lower input to the total they did not remarkably affect the general patterns. Although *M. longa* also performs seasonal migrations (Kosobokova, 1981; Geynrikh et al., 1983; Pertzova and Kosobokova, 2003; Ashjian et al., 2003), its seasonal ascent in the Arctic takes place later compared to *Calanus* species (Geynrikh et al., 1983). *Paraeuchaeta* spp. seems to perform little seasonal migrations (Skarra and Kaartvedt, 2003). The depths where these omnivores and carnivores concentrate are presumably related to distribution of their food sources. This is no doubt the case for the numerous other species not reported here in detail. As illustrated in this study, most copepod species have relatively characteristic depth distributions (e.g., Kosobokova and Hirche, 2000; Laakmann et al., 2009).

Similar to copepods, depth specificity in many non-copepods results in the relative contribution of each taxonomic group being

non-uniform across depth, and hence some groups became more or less important depending on the depth strata. As the best described community components, copepods and chaetognaths depth-distribution was consistent with other studies (Kosobokova and Hirche, 2000, and references therein). The contribution of cnidarians and ctenophores increased with depth, but the lack of attention to this group in all but a handful of studies that are limited to abundances (Scott, 1969) precludes any comparison to the literature. As is typical, the importance of ostracods, represented almost entirely by *B. maxima*, peaked at mid-depths (in our study at the upper border of Atlantic layer). Notably both abundance and biomass of ostracods were much higher (and our peaks deeper) than a recent data compilation for this species (Chavtur and Bashmanov, 2007), likely due to differences in mesh size and sampling depths. The amphipods demonstrated maximum contribution in the deepest stratum, but like other non-copepod groups, comparable data are limited, and where present often restricted to much shallower waters (e.g., Auel and Werner, 2003; Hopcroft et al., 2005).

These more descriptive patterns are fully supported by the multivariate analysis, which in addition to showing the general distinctness of each sampling stratum, indicated four groupings of slightly wider separation within the water column. A very narrow epipelagic zone of 50 m thickness hosted the copepod–chaetognath-dominated community with a high proportion of filter-feeding copepods. This layer transitioned into one at 50–100 m (the Bering Sea Summer Water) where the community structure began to acquire mesopelagic faunal character with a lower importance of copepods, almost constant contribution of chaetognaths and increasing proportions of cnidarians and ctenophores, ostracods, amphipods and decapods moving deeper. Below 1000 m, the change to the bathypelagic took place with a shift back to a copepod- and jelly-dominated community, with an almost complete absence of pelagic chaetognaths. Below 2000 m, in the Arctic Bottom waters, however, copepods declined again in favor of amphipods, cnidarians, ctenophores, and ostracods. In summary, it is the unique distributions of all species, linked both to depth preferences and water mass affinities that are responsible for the clear transition of zooplankton communities between our sampling strata, much as it occurs with zooplankton elsewhere in the world (Yamaguchi et al., 2002; Robison, 2004; Wishner et al., 2008; Gaard et al., 2008; Schnack-Schiel et al., 2008).

4.3. Regional and Panarctic comparison

The integrated biomass showed very little variation between sampling locations with slightly higher biomass over the continental slope north of Point Barrow and over the Chukchi Plateau, which are assumed to be more productive than the deep Canada Basin (Ashjian et al., 2003). However, consistent with recent biomass assessments from the Canadian Basin (Wheeler et al., 1996; Thibault et al., 1999; Ashjian et al., 2003; Hopcroft et al., 2005), our data indicate that zooplankton biomass in this sub-basin is greater than historically believed. Our average of 3.6 g m^{-2} is at least 2–3 times higher than earlier assessments for the Canadian Basin (Hopkins, 1969a, b; Pautzke, 1979; Kosobokova, 1982). Ashjian et al. (2003) and Hopcroft et al. (2005) suggest that the zooplankton stock may have been underestimated previously due to biased sampling techniques. Furthermore, regional variability in zooplankton distribution may also be superimposed on methodological problems in some surveys. For instance, during drift of NP-22 in 1975 zooplankton was collected in one of the poorest areas of the Arctic Ocean: the Central Beaufort Gyre (Melnikov and Pavlov, 1978; Kosobokova, 1982), and much of the

T3 drift zooplankton data (Pautzke, 1979) also come from a region with perpetually thick ice cover. Thus, in both cases there might be bias towards low estimates.

In a broader geographical context, it has been suggested that the zooplankton stock in the Canadian Basin is on average poorer than in the Eurasian Basin (Kosobokova and Hirche, 2000), a conclusion supported by this and other Canadian Basin studies (Thibault et al., 1999; Ashjian et al., 2003; Hopcroft et al., 2005), and a recent data compilation for the Eurasian Basin (Kosobokova and Hirche, 2009). The most striking differences are for biomass along the Siberian continental slope in the Eurasian Basin, where average values of 6.9 g m^{-2} were reported (Kosobokova and Hirche, 2009), about twice of what we found in the Canada Basin. The most likely reason for the differences is an absence of strong allochthonous zooplankton input in the Canadian Basin compared to the slope regions of the Eurasian Basin (Kosobokova and Hirche, 2000, 2009). Although there is significant inflow of allochthonous zooplankton through Bering Strait (Springer et al., 1989; Hopcroft et al., 2010), and strong cross-shelf and along-shelf transport of zooplankton (Ashjian et al., 2005; Lane et al., 2008; Llinás et al., 2009), the volume of inflow from the Atlantic into the Arctic Ocean is 5–8 times greater than that of the Pacific (Carmack and Wassmann, 2006).

5. Conclusions

In some respects, the composition of the Arctic Ocean zooplankton appears to be relatively well characterized, yet ~25% of the species encountered were either unrecorded from the Canada Basin or undescribed. With a handful of exceptions, such as species expatriated from sub-polar waters, there seems to be no zoogeographical barrier between the Canadian and Eurasian basins throughout the entire depth range, and no apparent change in species membership over the last 50 years of zooplankton sampling in the Canadian Basin.

During summer, much of the zooplankton biomass in the basin is concentrated within the upper 50–100 m, but significant biomass and the majority of species diversity occurs below this layer. Although copepods, particularly a few mostly herbivorous species, dominate the biomass, other groups, notably predators such as chaetognaths and cnidarians contribute significantly, especially below the surface layer. Species-specific depth preferences and ranges result in statistically distinct communities at different depths, all of which participate actively in the recycling of matter and energy with the deep-water column of the Arctic Ocean. The degree to which the seasonally compressed productivity in the Arctic Ocean is recycled within the water column compared to other deep oceans, and how this might change in the future, would seem to be logical directions for future research.

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