SENCKENBERG

Patterns of zooplankton diversity through the depths of the Arctic's central basins

Ksenia N. Kosobokova · Russell R. Hopcroft ·
Hans-Jürgen Hirche

Abstract Metazoan zooplankton diversity is characterized for the oceanic environments of the Arctic Ocean, specifically the deep Nansen, Amundsen, Makarov and Canada Basins. Our species inventory is based on original records from 134 locations where stratified sampling of the entire water column was conducted from the surface to the bottom (or a maximum of 3,000 m) during seven icebreaker expeditions (RV *Polarstern*, 1993-2007, USCGC *Healy*, 2005) and two older expeditions of the Russian drifting ice stations North Pole 22 and 23 (1975-77). Representatives of eight large metazoan taxa, including Cnidaria, Ctenophora, Mollusca, Annelida, Nemertea, Crustacea, Chaetognatha, and Larvacea, all predominately oceanic species, are registered, with a total of 174 species. Crustaceans strongly dominate in terms of the species number (70%), and copepods are the most diverse group amongst them. Comparison with the historical data suggests that the composition of epi- and mesopelagic zooplankton is relatively well characterized to date, while a considerable number of species we encountered in the bathypelagic layers were either unrecorded before, or undescribed. There appears to be no zoogeographical barrier between the Eurasian and Canadian basins throughout the entire depth range. All deep-water and endemic species are found on both sides of the Lomonosov Ridge, suggesting effective exchange of the deep fauna across the ridge. Notable differences in the species composition in the upper and midwater layers are related to the occurrence of Atlantic and Pacific expatriates advected with their respective waters either into the Eastern or Western Arctic. A pronounced increase in Pielou's evenness (J'), Shannon's diversity (H'), and Margalef's species richness (d) indices with depth, with a maximum occurring within the Atlantic layer, followed by a decrease in the deeper layers, was typical for all deep basins. Species-specific depth preferences and ranges result in statistically distinct communities at different depths with high within-depth similarity (60-80%). Differences were detectable between cruises in the epi- and mesopelagic layers (driven by the expatriates), but less so in the bathypelagic zone.

K. N. Kosobokova (✉)
P.P. Shirshov Institute of Oceanology,
Russian Academy of Sciences,
Moscow, Russia
e-mail: xkosobokova@ocean.ru

R. R. Hopcroft
Institute of Marine Science, University of Alaska Fairbanks,
Fairbanks, AK, USA

H.-J. Hirche
Alfred Wegener Institute for Polar and Marine Research,
Bremerhaven, Germany

Introduction

Zooplankton, as the major consumers of primary production in the Arctic, have been a central component of numerous oceanographic studies for more than a century. Initial studies over the Arctic's central deep basins were, however, sporadic and often geographically restricted due to the logistical challenges associated with sampling far offshore. In the past three decades, biological observations in the Arctic Ocean have increased markedly. Expeditions

of modern research ice-breakers can nowadays reach regions previously inaccessible by drifting ice platforms, and allow much more comprehensive and efficient sampling than previously possible. Our zooplankton collections now extend from the Canadian to the Eurasian parts of the Arctic Ocean, in regions virtually unrepresented prior to the RV *Oden* expedition of 1981 (Groendahl and Hernroth 1986).

Based on these data, a synthesis of zooplankton diversity over the entire depth range and in all basins of the Arctic Ocean is now possible and timely given the general increase in public and scientific interest on the topic of marine biodiversity. Approximately 20 publications have included lists of zooplankton species (Table 1) since the first account of Crustacea of the Arctic Ocean, published as a result of Nansen's Fram expedition (Sars 1900). The number of species in each of them seldom exceeded 70, due to limited collections and a variety of taxonomic biases (Kosobokova and Hopcroft 2010). The most recent inventory by Sirenko (2001), based on a compilation of the literature and original data from taxonomic experts, almost doubled this count. Despite its value, several common plankton taxa (Ctenophora, Larvacea, Pteropoda) typically present in the Arctic were omitted. Sirenko's list also failed to discriminate between species occurring in the pelagic and benthic realms, leaving one to guess how many species in several groups occur within the water column, and thereby precluding a simple tabulate of pelagic diversity.

In the past, copepods—as the most diverse and numerically important group—have received the most attention during studies of the faunistic composition of zooplankton in the Arctic Ocean (see Kosobokova and Hopcroft 2010). Other zooplankton taxa, both the robust body forms (Amphipoda, Euphausiacea, Decapoda, Ostracoda) and the more fragile groups (Hydromedusae, Scyphomedusae, Siphonophora, Ctenophora, Larvacea), have received less attention due to their limited occurrence in samples typically obtained by relatively small plankton nets. The common approach has been to identify the most prominent and well-known species, and to disregard poorly known rarer ones, assuming that low abundance equaled to low importance. Moreover, the absence of appropriate identification keys for the non-copepod Arctic fauna made identification challenging compared with detailed accounts available for the copepods from the Norwegian Polar expeditions (Sars 1900) and much improved later keys (Brodsky 1950, 1967). Only much later did poorly distributed identification keys (Tencati 1970; Leung 1970a,b, 1971, 1972; Shirley and Leung 1970; Dawson 1971; Leung et al. 1971; Yingst 1972) and species accounts for one or more (Scott 1969; Pautzke 1979; Kosobokova 1981; Mumm 1993; Sirenko et al. 1996; Kosobokova et al. 1998; Auel and Hagen 2002; Kosobokova and Hirche 2000; Hopcroft et al. 2005; Raskoff et al. 2005, 2010;

Kosobokova and Hopcroft 2010) of the neglected groups appear.

The Arctic Ocean is unique in numerous ways. Its productivity and the zooplankton communities it can support vary widely on glacial/inter-glacial time scales, as does its connectivity to other oceans. Its deep central region is separated into two major basins, the Eurasian and Canadian Basins, by the Lomonosov Ridge which may act as a dispersal barrier to deep-water zooplankton (Brodsky and Pavshtiks 1977), as well as much deeper ridges that demarcate the Nansen and Amundsen Basins within the Eurasian, and the Makarov and Canada Basins within the Canadian Basin. Circulation within and between the basins reflects this bathymetry (Rudels et al. 1994, 2000). At present, the Chukchi Sea and adjoining areas receive a large seasonal influx of Pacific zooplankton species through the shallow Bering Strait (Hopcroft et al. 2010) which can probably not establish self-sustaining populations in the Arctic Ocean (i.e., expatriate species). Similarly, sub-arctic and boreal North Atlantic fauna is transported through the Norwegian and Greenland Seas towards the deep Fram Strait and onto the continental shelf of the northern Barents Sea, and then into the Arctic Ocean (Kosobokova and Hirche 2009). Numerous studies have commented on the definition and distribution of these expatriates (Brodsky and Nikitin 1955; Johnson 1963; Harding 1966; Dunbar and Harding 1968; Pavshtiks 1971; Timofeev 1998; Kosobokova and Hirche 2000; Hirche and Kosobokova 2007; Hopcroft and Kosobokova 2010). Nonetheless, the magnitude and extent of penetration of these species is a subject of some debate and no doubt varies on seasonal, inter-annual and decadal scales.

The major aim of this study was to document the zooplankton species diversity with a detailed inventory of all metazoan planktonic taxa presently recorded from the deep Arctic Ocean. During the last 20 years we have collected zooplankton in all four deep basins of the Arctic Ocean and adjacent waters (Kosobokova and Hirche 2000, 2009; Kosobokova and Hopcroft 2010), using standard models of opening-closing plankton nets with a standard mesh size, sampling relatively standardized depth strata over the entire water column, and with samples analyzed by the same people. This allows for the first time to draw a pan-arctic comparison of fauna, vertical distribution of species richness and diversity and vertical structure of the zooplankton communities.

Material and methods

The material employed for this inventory was collected between 1975 and 2007 during: two expeditions of the Russian drift stations North Pole (NP-22, 1975-76 and

Table 1 Number of zooplankton species in the published species lists for the Arctic Ocean basins (+ present, but not identified to species level; – absent)

Author	Copepoda	Amphipoda	Ostracoda	Euphausiacea	Decapoda	Mysidacea	Hydromedusae	Scyphomedusae	Siphonophora	Ctenophora	Pteropoda	Polychaeta	Nemertini	Chaetognatha	Larvacea	Total	% of Copepoda
Shirshov, 1938	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11	100
Grice, 1962	18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	18	100
Minoda, 1967	32	–	–	–	–	–	–	–	–	–	–	–	–	–	–	32	100
Hughes, 1968	26	–	–	–	–	–	–	–	–	–	–	–	–	–	–	26	100
Sars, 1900	28	8	1	2	1	–	2	–	1	–	–	–	–	–	–	40	70
Bogorov, 1946	27	4	1	–	–	–	2	1	1	1	1	+	–	2	3	42+	<64
Brodsky and Nikitin, 1955	48	5	–	–	–	–	2	1	1	–	–	–	–	–	–	56	86
Virketis, 1957	48	5	3	+	–	–	2	–	–	2	2	+	1	3	5	74+	<65
Johnson, 1963	34	+	+	–	+	–	2	–	–	–	1	–	–	4	–	35+	<97
Grainger, 1965	12	–	1	–	1	–	–	–	2	–	2	+	–	+	+	20+	<60
Harding, 1966 (+ Dunbar and Harding, 1968)	45	9	–	1	–	–	5	–	1	–	2	–	–	+	–	60	75
Kosobokova, 1981	49	8	>1	3	1	–	5	–	1	1	2	2	–	3	–	76+	<64
Mumm, 1993	26	4	2	2	–	–	4	–	1	2	2	+	–	4	2	51+	<51
Sirenko et al., 1996	32	4	+	3	1	2	3	1	1	–	–	2	–	+	–	47+	<68
Kosobokova et al., 1998	49	6	1	1	1	1	8	1	1	4	2	+	–	3	2	83+	<59
Kosobokova and Hirche, 2000	52	6	1	1	1	–	11	1	1	+	2	+	–	2	2	78+	<67
Auel and Hagen, 2002	41	2	1	3	1	–	2+	–	+	–	1	+	–	+	+	48+	<85
Sirenko, 2001	95	18	6	–	1	2	6	1	5	–	–	3	–	4	–	144	66
Hopcroft et al., 2005	24	2	1	2	1	–	1	–	1	–	2	–	–	2	2	36	67
Kosobokova and Hopcroft, 2010	55	11	5	2	1	+	12	1	4	4	2	5	–	4	4	111	50
Present study	91	16	5	4	1	4	17	4	7	9	2	5	1	4	4	174	52

NP-23, 1977-78), six expeditions of the research ice-breaker *Polarstern* (1993, 1995, 1996, 1997, 1998, 2007), and one expedition of the U.S. Coastguard Cutter *Healy* (2005) (Fig. 1). The study area encompasses a zone with depths >200 m, including the continental slope area and all four major deep basins of the Arctic Ocean with 54 stations in the Nansen, 31 in Amundsen, 25 in Makarov, and 24 stations in the Canada Basin (Fig. 1). Data from most cruises is available through ArcOD at http://www.arcodiv.org/Database/Plankton_datasets.html.

Zooplankton from the Russian drifting stations NP-22 and 23 in 1975-76 and 1977-78 were collected with a vertically hauled opening-closing Juday net (mouth opening 0.1 m², mesh size 176 μm). From eight to ten separate successive depth strata from the bottom to the surface were sampled. During the 1993, 1995, 1996, 1997 *Polarstern* and 2005 *Healy* expeditions, zooplankton were collected vertically with a Multinet Type Midi (Hydrobios, Kiel, 0.25 m² mouth opening, 150 μm mesh size). During the 1998 and 2007 *Polarstern* expeditions, a Multinet Type Maxi (0.5 m² mouth opening, 150 μm mesh size) was

deployed. During 1993, five depth strata were sampled from the bottom or 1,500 m to the surface. During all other expeditions up to nine strata within the entire water column or the upper 3,000 m were sampled.

With the Midi Multinet two successive vertical hauls were performed at all stations. Sampling intervals were typically bottom (or 3,000 m)-2,000-1,000-500(750)-300-0 m for the deep casts, and 300-200-100-50-25-0 m for the shallow casts. With the Maxi Multinet one vertical cast was typically performed with the following sampling layers: bottom (3,000 m)-2,000-1,000-750(500)-300-200-100-50-25-0 m. All samples were preserved in 10% borax-buffered formalin (4% formaldehyde) upon retrieval.

All mesozooplankton, including all copepodite stages of calanoid copepods, as well as larval and adult macro-zooplankton were identified according to most recent taxonomy (Sirenko 2001; Razouls et al. 2005–2009) from the entire sample and measured where relevant under a stereo microscope. Most taxonomic groups, including Scypho- and Hydromedusae, Siphonophora, Ctenophora, Polychaeta, Mollusca (Gymnosomata, Thecosomata), Crus-

Fig. 1 Location of 134 zooplankton stations employed in this study. *PS ARK - Polarstern* cruises, *NP* - Russian drifting stations North Pole, *HLY 05/2-Healy* Ocean Exploration-2 cruise
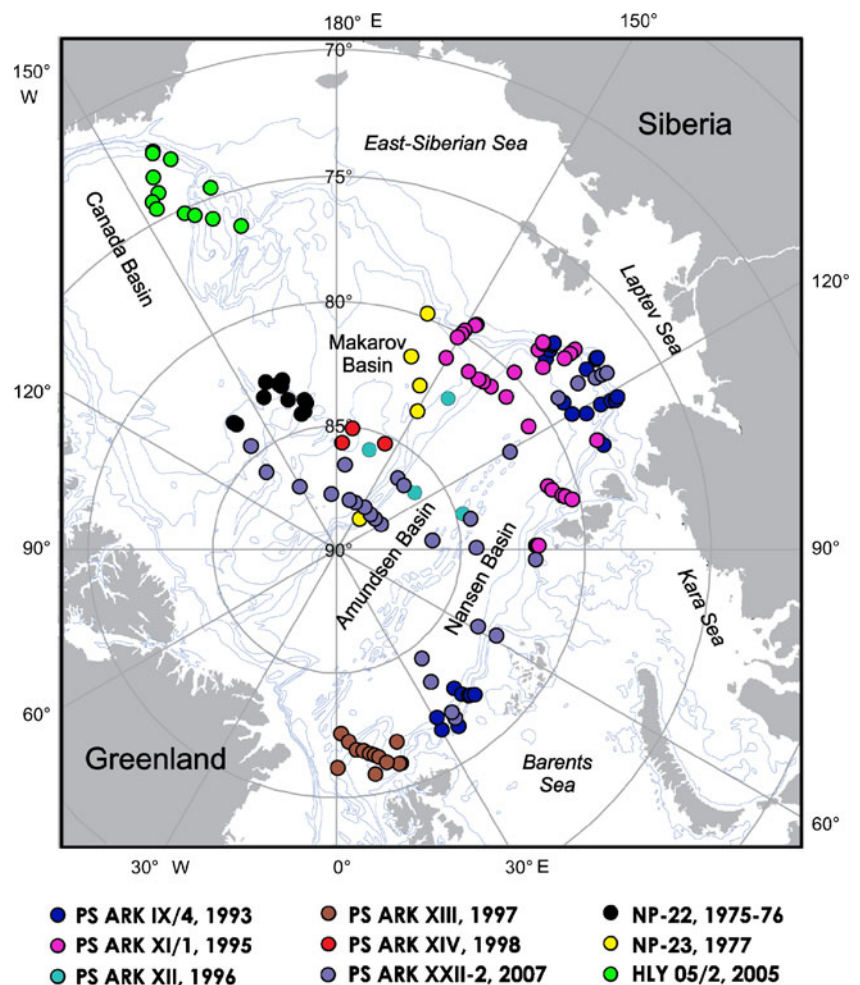
tacea (Copepoda Calanoida, Ostracoda, Hyperiidea, Gammaridea, Mysidacea, Decapoda, Euphausiacea), Chaetognatha, and Larvacea (= Appendicularia) were identified to species level. Copepodite stages of most calanoid copepods were counted separately and identified to species level. Exceptions are Discoidae, *Microcalanus*, *Xanthocalanus*, and young (CI-III) stages of *Spinocalanus*. Prosome length was used to distinguish early copepodite stages CI-CIII of *Calanus* spp. according to size criteria of Hirche et al. (1994). The majority of Ostracoda (4-5 species), Harpacticoida (2-3 species) and Oncaeidae (5-6 species) were not routinely identified to species level, except for most common species (Table 2, ESM Table A). All organisms >1 mm were counted from the entire sample. For the smaller zooplankton (<1 mm), an aliquot (1:8, 1:10) of the sample was counted after fractionation with a Stempel-pipette.

To analyze geographical ranges, we assigned all recorded species into seven categories, according to their geographical distribution based on data summarized by Razouls et al. (2005–2009) and a wide variety of sources for other taxa (e.g., World Register of Marine Species, http://www.marinespecies.org, WoRMS). These categories include: species found in the Arctic Ocean only (Arctic endemics, cryopelagic and new species), species found in the Arctic and North Atlantic, in the Arctic and North Pacific, in the Arctic and sub-arctic (both North Atlantic and North Pacific), widely distributed/cosmopolitans (whose range includes several geographical zones), bipolar species, and species of unknown biogeographic status (predominantly rare hyperbenthic species).

To study the vertical structure of the zooplankton communities, collections of five expeditions (1993, 1995, 1996, 1998, 2005) were used where there was relative consistency in the depth strata sampled. Community abundance patterns were explored using the Primer (V6) software package (e.g., Clarke and Warwick 2001a, 2006; Hopcroft et al. 2010; Kosobokova and Hopcroft 2010). In a few cases (i.e., ostracods) we lacked full taxonomic resolution across the entire dataset and identification was reduced to a coarser level. The abundance data were power transformed (4th root), and reduced to taxonomic categories that contributed at least 3% to any sample after transformation (to remove very rare species occurring somewhat randomly in collections). The Bray-Curtis similarity was calculated between each sample, with significant groups within the group-averaged hierarchical clustering ($\alpha = 5\%$) established using the SIMPROF routine. The Bray-Curtis similarity matrix was also subjected to multi-dimensional scaling (MDS) to establish the "distance" between samples, and then projected onto two-dimensional (2D) 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 (e.g., Hopcroft et al. 2010).

Several metrics were used to quantify biodiversity using the species-accumulation and DIVERSE routines in PRIMER. For this purpose, the dataset from all cruises was reduced to the most consistent set of non-overlapping strata, which required the aggregation of data for those cases where the 200-500 strata had been sampled as two layers (i.e., 200-300, 300-500). Nauplii and copepod eggs were removed, although a few genus-level categories of earlier copepodites were retained along with their adults separated to species. Some species were aggregated to account for differences in taxonomic resolution between cruises. Ultimately the dataset employed for diversity metrics had 125 taxa. Three taxon accumulation curves were considered for each layer: the number of taxa observed (S_{obs}), a Michaelis-Menton based fit to the taxa curve yielding S_{Max}, and the non-parametric Chao2 estimator which predicts the expected number of taxa that would be observed for an infinite number of samples. The Chao2 estimator is particularly sensitive to the presence of rare species (i.e., observed only once or twice), and therefore typically predicts a higher number of species than the other approaches (Magurran 2004).

Several alpha-diversity indices were calculated: number of taxa in each sample S, Pielou's evenness J', Shannon's diversity H' (as log-e), Margalef's species richness d, and the $ES(n)$ rarefaction. Both Margalef's richness and rarefaction estimators standardize effort for the number of individuals present in samples, so are less sensitive to sampling effort than S or H' (Clarke and Warwick 1999, 2001b, Magurran 2004), but required the use of raw counts rather then values standardized for sampling volume. Rarefaction attempts to standardize for same sample size, so we calculated the expected near-minimum observed count of 1,000 randomly chosen individuals: ES(1000). Each of these indices was calculated on a per sample basis, thereby allowing calculation of confidence intervals for each stratum.

Results

Zooplankton composition. Residents and expatriates

A total of 169 metazoan plankton species were identified in our net collections (Table 2). Five more species of pelagic Cnidaria collected by other sampling gears during the same expeditions (Raskoff et al. 2010) were added to the inventory to make the present list as complete as possible, raising the total species number up to 174 (Tables 1, 2, and ESM). Representatives of the following eight metazoan higher taxa were recorded: Cnidaria, Ctenophora, Mollusca, Nemertea, Annelida, Crustacea, Chaetognatha and Larvacea (Tables 1, 2, and ESM). Two taxonomic groups,

Table 2 Original list of metazoan plankton species and depth preferences of particular species. *E* epipelagic (0-200 m), *M* mesopelagic (200-1,000 m), *B* bathypelagic (1,000-3,000 m), *A* abyssopelagic (>3,000 m), *H* hyperbentic (benthopelagic, bottom-associated, *C* cryopelagic (sea ice-associated). Preferred depth range (depth range where the bulk of population is concentrated) is determined according to the original data. *(*)* Species collected by other sampling gears than plankton nets during the same expeditions (see Raskoff et al. 2010)

No. species	Taxon	Nansen Basin (ARK IX/1, XI/1, XII, XXII/2)	Amundsen Basin (ARK IX/1, XI/1, XII, XXII/2)	Makarov Basin (ARK XI/1, XIV, XXII/2, NP-23)	Canada Basin (NP-22, OE-05)	Preferred depth range
	Copepoda					
1	*Acartia longiremis* (Lilljeborg, 1853)	+	+			E
2	*Aetideopsis minor* (Wolfenden, 1904)	+	+	+	+	M-B
3	*A. rostrata* G.O.Sars, 1903	+	+	+	+	B
4	*Arctokonstantinus hardingi* Markhaseva & Kosobokova, 2001	+				B
5	*Augaptilus glacialis* G.O.Sars, 1900	+	+	+	+	M-B
6	*Bradyidius similis* (Sars 1900)	+				M-H
7	*Brodskius* sp.n.				+	B
8	*Byrathis* (= *Xanthocalanus*) *laptevorum* Markhaseva, 1998		+			B-H
9	*Calanus glacialis* Jaschnov, 1955	+	+	+	+	E-M
10	*C. hyperboreus* Kroyer, 1838	+	+	+	+	E-B
11	*Calanus finmarchicus* (Gunnerus, 1765)	+	+	+		E-M
12	*Chiridiella abyssalis* Brodsky, 1950	+	+	+	+	A
13	*C. reductella* Markhaseva 1996	+	+	+	+	M-B
14	*C. sarsi* Markhaseva, 1983	+	+		+	B-A
15	*Chiridius obtusifrons* G.O.Sars, 1903	+	+	+	+	M
16	*Disco hartmanni* Schulz, 1993		+		+	B
17	*D. minutus* Grice & Hulsemann, 1965				+	B
18	*D. triangularis* Markhaseva & Kosobokova, 1998		+	+	+	B
19	*Drepanopus bungei* G.O.Sars, 1898		+			E
20	*Euaugaptilus hyperboreus* Brodsky, 1950	+	+	+	+	B-A
21	*Eucalanus bungii* Geisbrecht, 1892				+	E-B
22	*Eurytemora richingsi* Heron & Damkaer, 1976	+	+		+	C
23	*Gaetanus brevispinus* (G.O.Sars, 1900)	+	+	+	+	M-B
24	*G. tenuispinus* (G.O.Sars, 1900)	+	+	+	+	M
25	*Haloptilus acutifrons* (Giesbrecht, 1892)	+	+	+	+	M-B
26	*Heterorhabdus norvegicus* (Boeck, 1872)	+	+	+	+	E-M
27	*Jaschnovia brevis* (Farran, 1936)	+			+	C
28	*J. tolli* (Linko, 1913)	+	+	+	+	C
29	*Lucicutia anomala* Brodsky, 1950	+	+	+	+	B-A
30	*L. polaris* Brodsky, 1950	+	+	+	+	B-A
31	*L. pseudopolaris* Heptner, 1969	+	+	+	+	B-A
32	*Mimocalanus crassus* Park, 1970	+	+	+	+	A
33	*M. damkaeri* Vyshkvartzeva, 1983	+	+	+	+	M-A
34	*Metridia longa* (Lubbock, 1854)	+	+	+	+	E-M
35	*M. lucens* Boeck, 1864	+				E-M
36	*M. pacifica* Brodsky, 1950				+	E-M
37	*Microcalanus pusillus* G.O.Sars, 1903	+	+	+	+	E-M
38	*M. pygmaeus* (G.O.Sars, 1900)	+	+	+	+	M-B
39	*Neocalanus cristatus* Kroyer, 1848				+	E-B
40	*Onchocalanus cristogerens* Markhaseva & Kosobokova, 1998	+	+	+	+	B
41	*Paraeuchaeta barbata* (Brady, 1883)	+	+	+	+	M-B
42	*P. glacialis* (Hansen, 1886)	+	+	+	+	E-M
43	*P. norvegica* (Boeck, 1872)	+	+	+		E-M
44	*P. polaris* Brodsky, 1950	+	+	+	+	B-A
45	*Paraheterorhabdus compactus* (G.O.Sars, 1900)	+	+	+	+	B
46	Discoidae sp.n. 1				+	B
47	Discoidae sp.n. 2				+	B
48	Discoidae sp.n. 3			+		B

Table 2 (continued)

No. species	Taxon	Nansen Basin (ARK IX/1, XI/1, XII, XXII/2)	Amundsen Basin (ARK IX/1, XI/1, XII, XXII/2)	Makarov Basin (ARK XI/1, XIV, XXII/2, NP-23)	Canada Basin (NP-22, OE-05)	Preferred depth range
49	*Phaennocalanus unispinosus* Markhaseva, 2002		+			B
50	*Pleuromamma robusta* (F. Dahl, 1893)	+				M-B
51	*Pseudaugaptilus polaris* Brodsky, 1950	+	+	+	+	M-B
52	*Pseudeuchaeta arctica* Markhaseva, 1986		+			B-H
53	*Pseudhaloptilus pacificus* (Johnson, 1936)			+	+	M
54	*Pseudoammalothrix laminata* (Farran, 1926)			+		B-H
55	*Pseudocalanus acuspes* (Giesbrecht, 1881)	+	+		+	E
56	*P. major* G.O.Sars, 1900	+	+	+		E
57	*P. minutus* (Kroyer, 1848)	+	+	+	+	E
58	*P. newmani* Frost, 1989				+	E
59	*Pseudochirella batillipa* Park, 1978		+	+		B-A
60	*P. spectabilis* (G.O.Sars, 1900)	+	+	+	+	M-B
61	*Rhincalanus nasutus* Giesbrecht, 1888	+				M-B
62	*Ryocalanus admirabilis* Andronov, 1974			+		B-H
63	*Scaphocalanus acrocephalus* (Th. Scott, 1893)	+	+	+	+	M
64	*S. brevicornis* (G.O.Sars, 1900)	+	+	+	+	M
65	*S. polaris* Brodsky, 1950	+	+	+	+	B-A
66	*Scolecitrichopsis alvinae* (Grice & Hulsemann, 1970)	+				B-H
67	*S. (=Xanthocalanus) polaris* Brodsky, 1950	+	+	+		B-H
68	*Scolecithricella minor var.occidentalis* Brodsky, 1950	+	+	+	+	E-B
69	*Spinocalanus antarcticus* Wolfenden, 1906	+	+	+	+	M
70	*S. elongatus* Brodsky, 1950	+	+	+	+	A
71	*S. horridus* (=*longispinus*) Wolfenden, 1911	+	+	+	+	B-A
72	*S. longicornis* G.O.Sars, 1900	+	+	+	+	M
73	*S. polaris* Brodsky, 1950	+	+	+	+	B-A
74	*Temorites brevis* G.O.Sars, 1900	+	+	+	+	M-B
75	*Tharybis groenlandicus* (Tupitzky, 1982)	+	+	+	+	B
76	*Undinella oblonga* G.O.Sars, 1900	+	+	+	+	B
77	*Xanthocalanus borealis* G.O.Sars, 1900		+			M-B
78	*X. polarsternae* Markhaseva, 1998		+			B-H
79	*X. profundus* G.O.Sars, 1907		+			B-H
80	*X. spinodenticulatus* Markhaseva, 1998		+			B-H
81	*Lubbockia brevis* Farran, 1908	+	+	+	+	B
82	*L. glacialis* G.O.Sars, 1900	+	+	+	+	B
83	*Oithona atlantica* Farran, 1908	+	+	+		E
84	*O. similis* Claus, 1866	+	+	+	+	E
85	*Oncaea parila* (= *O. notopus*) Heron, 1977	+	+	+	+	M
86	*Triconia borealis* (G.O.Sars, 1918)	+	+	+	+	E-M
87	*Hyalopontius typicus* G.O.Sars, 1909	+	+	+	+	B
88	*Mormonilla minor* Giesbrecht, 1891	+	+	+	+	M-B
89	*Monstrilla* sp.	+				E
90	*Microsetella norvegica* (Boeck, 1864)	+	+	+	+	E
91	*Tisbe furcata* (Baird, 1850)	+	+	+	+	E
	Ostracoda					
1	*Boroecia maxima* (Brady & Norman, 1896)	+	+	+	+	M-B
2	*B. borealis* (Sars, 1866)	+	+	+	+	M-B
3	*Boroecia* sp.				+	B
4	*Discoconchoecia elegans* (Sars, 1866)	+	+	+	+	B
5	*Proceroecia vityazi* (Rudjakov, 1962)	+	+	+	+	B
	Amphipoda Hyperiidea					
1	*Lanceola clausi* Bovallius, 1885	+	+	+	+	M-B
2	*Mimonectes sphericus* Bovallius, 1885	+	+	+	+	M-B
3	*Scina borealis* G.O.Sars, 1882	+	+	+	+	M-B
4	*S. pusilla* (?) Chevreux, 1919				+	M

Table 2 (continued)

No. species	Taxon	Nansen Basin (ARK IX/1, XI/1, XII, XXII/2)	Amundsen Basin (ARK IX/1, XI/1, XII, XXII/2)	Makarov Basin (ARK XI/1, XIV, XXII/2, NP-23)	Canada Basin (NP-22, OE-05)	Preferred depth range
5	*Themisto abyssorum* Boeck, 1870	+	+	+	+	E-B
6	*T. libellula* Lichteinstein, 1822	+	+	+	+	E-B
	Amphipoda Gammaridea					
1	*Andaniexis abyssi* (Boeck, 1871)	+	+	+	+	M-B
2	*Apherusa glacialis* (Hansen, 1888)	+	+	+	+	M
3	*Cyclocaris guilelmi* Chevreux, 1899	+	+	+	+	M-B
4	*Cyphocaris bouvieri* Chevreux, 1916	+	+	+	+	M
5	*Eusirogenes arctica* Tencati, 1968	+			+	B
6	*Eusirus holmi* Hansen, 1887	+	+	+	+	B
7	*Gammarus wilkitzkii* Birula, 1897	+	+	+	+	C
8	*Onisimus glacialis* (G.O.Sars, 1900)	+	+	+	+	C
9	*O. nanseni* Sars, 1900	+	+	+	+	C
10	*Rhachotropis inflata* (G.O.Sars, 1883)	+	+	+	+	B
	Mysidacea					
1	*Birsteiniamysis inermis* (Willemoes-Suhm, 1874)	+	+	+		B
2	*Boreomysis arctica* (Krøyer, 1861)	+	+	+		M
3	*B. nobilis* G.O. Sars, 1885	+	+	+		B
4	*Pseudomysis abyssi* G.O.Sars, 1885	+				B
	Euphausiacea					
1	*Meganyctiphanes norvegica* (M. Sars, 1857)	+				M
2	*Thysanoessa longicaudata* (Krøyer, 1846)	+	+			M
3	*T. inermis* (Krøyer, 1846)	+	+	+	+	M
4	*T. raschii* (M. Sars, 1864)	+	+	+	+	E-M
	Decapoda					
1	*Hymenodora glacialis* (Buchholz, 1874)	+	+	+	+	B-A
	Hydrozoa					
1	*Aeginopsis laurentii* Brandt, 1838	+	+	+	+	E
2	*Aglantha digitale* (O.F. Muller, 1776)	+	+	+	+	E
3	*Bathykorus bouilloni* Raskoff, 2010	+	+	+	+	B-A
4	*Benthocodon hyalinus* Larson, 1990				+(*)	H?
5	*Botrynema brucei* Browne, 1908	+	+	+	+	B-A
6	*B. ellinorae* (Hartlaub, 1909)	+	+	+	+	M-B
7	*Crossota millsae* Thuesen, 2003				+(*)	H?
8	*C. norvegica* Vanhöffen, 1902	+	+	+	+	M-B
9	*Homoeonema platygonon* Browne,1903	+	+	+	+	M
10	*Margelopsis hartlaubi* Browne, 1903			+	+	M
11	*Paragotoea bathybia* Kramp, 1942	+	+	+	+	M-B
12	*Plotocnide borealis* Wagner, 1885		+		+	E
13	*Ptychogastria polaris* Allman, 1878		+		+	H
14	*Ptychogena hyperborea* Kramp, 1942		+		+	B
15	*Rhabdoon reesi* (Shirley & Leung, 1970)	+	+	+	+	M
16	*Sminthea arctica* Hartlaub, 1909	+	+	+	+	M-B
17	*Solmundella bitentaculata* (Quoy & Gaimard, 1833)	+	+	+	+	M-B
	Scyphozoa					
1	*Atolla tenella* Hartlaub, 1909	+	+	+	+	M-B
2	*Chrysaora melanaster* Brandt, 1838				+(*)	E
3	*Cyanea capillata* (L., 1758)				+(*)	E
4	*Nausithoe limpida* Hartlaub, 1909				+(*)	M
	Siphonophora					
1	*Crystallophyes amygdalina* (Moser, 1925)	+	+	+	+	M
2	*Dimophyes arctica* (Chun, 1897)	+	+	+	+	M
3	*Gilia reticulata* (Totton, 1954)	+	+	+		M
4	*Marrus orthocanna* (Kramp, 1942)	+	+		+	M
5	*Muggiaea bargmannae* Totton, 1954	+	+	+	+	M

Table 2 (continued)

No. species	Taxon	Nansen Basin (ARK IX/1, XI/1, XII, XXII/2)	Amundsen Basin (ARK IX/1, XI/1, XII, XXII/2)	Makarov Basin (ARK XI/1, XIV, XXII/2, NP-23)	Canada Basin (NP-22, OE-05)	Preferred depth range
6	*Nectadamas* (= *Nectopyramis*) *diomedeae* (Bigelow, 1911)	+	+	+	+	M
7	*Rudjakovia plicata* Margulis, 1982	+	+	+	+	B
	Ctenophora					
1	*Aulacoctena* sp. n.	+			+(*)	B
2	*Beroe cucumis* Fabricius, 1780	+	+	+	+	E
3	*Bolinopsis infundibulum* (Müller, 1776)	+	+	+	+	E
4	*Bathyctena* sp.				+(*)	B
5	*Dryodora glandiformis* (Mertens, 1833)				+	E
6	*Mertensia ovum* (Fabricius, 1780)	+	+	+	+(*)	E
7	*Pleurobrachia pileus* (Müller, 1776)	+	+	+	+(*)	E
8	Cydippid sp. 1				+(*)	M
9	Cydippid sp. 2				+	H?
	Mollusca Gymnosomata and Thecosomata (Pteropods)					
1	*Clione limacina* (Phipps, 1774)	+	+	+	+	E-M
2	*Limacina helicina* (Phipps, 1774)	+	+	+	+	E-M
	Nemertea					
1	*Dinonemertes arctica* Korotkevich, 1977	+		+	+(*)	B-A
	Polychaeta					
1	*Phalacrophorus pictus borealis* Reibish, 1895	+	+	+	+	M-B
2	*Minuspio* sp. n.	+				B
3	*Pelagobia longicirrata* Gravier, 1911	+	+	+	+	M-B
4	*Tomopteris septentrionalis* Steenstrup, 1849	+				E-M
5	*Typhloscolex muelleri* Busch, 1851	+	+	+	+	E-M
	Chaetognatha					
1	*Parasagitta elegans* (Verill, 1873)	+	+	+	+	E-M
2	*Pseudosagitta* (=*Sagitta*) *maxima* (Conant, 1896)	+	+	+	+	M-B
3	*Eukrohnia hamata* (Möbius, 1875)	+	+	+	+	E-B
4	*Heterokrohnia mirabilis*[a] Ritter-Zahony, 1911	+	+	+	+	B-H
	Appendicularia (= Larvacea)					
1	*Fritillaria borealis* Lohmann, 1896	+	+	+	+	E
2	*F. polaris* Berntstein, 1934	+	+	+	+	E
3	*Oikopleura* (= *Vexillaria*) *vanhöffeni* Lohmann, 1896	+	+	+	+	E
4	*O.* (= *Vexillaria*) *gorskyi* Flood, 2000				+	E
174	Total	136	134	124	141	

[a] There remains uncertainty if this should actually be considered *Heterokrohnia involucrum* Dawson 1968: recent molecular evidence suggests the species in the Arctic is distinct from *H. mirablis* (Jennings et al. 2010)

Crustacea and Cnidaria, accounted for >86% of the total number of species. Crustacea included 91 species of Copepoda (80 Calanoida, 6 Cyclopoida, 1 Siphonostomatoida, 1 Mormonilloida, 1 Monstrilloida, 2 Harpacticoida), 5 Ostracoda, 16 Amphipoda (6 Hyperiidea, 10 Gammaridea), 4 Mysidacea, 4 Euphausiacea, 1 Decapoda, contributing 70% to the total. The pelagic cnidarians included 17 species of Hydromedusae, 4 Scyphomedusae, and 7 Siphonophora, making up another 16%. The rest consisted of 9 Ctenophora, 2 Mollusca, 1 Nemertea, 5 Polychaeta, 4 Chaetognatha, and 4 Larvacea.

The presence of reproductively active females, eggs, larvae, different size classes and life stages in the majority of species provide evidence that these species breed successfully within the Arctic Ocean. In contrast, 26 species from various taxa were represented by only late developmental stages and non-reproducing adults (summary in Table 3, stage data not shown), indicating the absence of local reproduction. We consider these species to be expatriates, advected into the Arctic basins from the North Atlantic, North Pacific and Arctic shelf seas.

All expatriates had restricted distribution within the study area. Several entrants from the North Atlantic (*Metridia lucens*, *Pleuromamma robusta*, *Rhincalanus nasutus*, *Meganyctiphanes norvegica*) were found in very low numbers only north-east of Spitsbergen in the area where Atlantic water enters the Eurasian Basin (Rudels et al. 1994). Others were more abundant and demonstrated

Table 3 List of expatriate species observed with the Arctic Ocean basins

Atlantic expatriates	Pacific expatriates	Neritic (shelf) expatriates
Calanus finmarchicus	*Neocalanus cristatus*	*Acartia longiremis*
Oithona atlantica	*Eucalanus bungii*	*Drepanopus bungei*
Metridia lucens	*Metridia pacifica*	*Pseudocalanus acuspes*
Rhincalanus nasutus	*Pseudhaloptilus pacificus*	*P. minutus*
Pleuromamma robusta		*P. major*
Paraeuchaeta norvegica		*P. newmani*
Meganyctiphanes norvegica		*Bradyidius similis*
Thysanoessa longicaudata		*Monstrilla* sp.
Tomopteris septentrionalis		*Aglantha digitale*
		Plotocnide borealis
		Cyanea capillata
		Chrysaora melanaster
		Parasagitta elegans

wider distribution, occurring along the perimeter of the Nansen and Amundsen Basins (*Thysanoessa longicaudata*, *Tomopteris septentrionalis*), or over the entire eastern Nansen and Amundsen Basins (*Calanus finmarchicus*, *Paraeuchaeta norvegica*, *Oithona atlantica*). The abundance of the latter three species, the most numerous Atlantic expatriates, decreased from the west to the east along the Eurasian continental slope and in direction to the central deep basins (see also Kosobokova and Hirche 2009). Their easternmost records were observed in the western part of the Makarov Basin close to the sill of the Lomonosov Ridge. In the Canada Basin, none of them were recorded. The distribution of entrants from the Pacific (Table 3) was restricted to the Canadian Basin, where they were advected through the Bering Strait with Pacific water. Shelf expatriates were usually present north of the shelf margin of the Arctic seas which are widely open to the Arctic basin proper (Laptev, East-Siberian and Chukchi Seas), but were seldom occurring north of the continental slope.

Geographical characterization

Species commonly encountered in the study area could be assigned to two major categories: those known from the Arctic Ocean only, and those with wider distribution. Members of the first group are the Arctic endemic pelagic copepods *Mimocalanus damkaeri*, *Spinocalanus elongatus*, *S. horridus* (=*longispinus*), *Chiridiella reductella*, *Paraeuchaeta polaris*, *Scaphocalanus polaris*, *Lucicutia pseudopolaris*, the hydromedusa *Rhabdoon reesi*, the siphonophore *Rudjakovia plicata*, and the larvacean *Fritillaria polaris*. The ice-associated endemic copepods *Jaschnovia tolli*, *J. brevis*, *Eurytemora richingsi*, and the endemic amphipods *Onisimus glacialis*, *O. nanseni*, *Eusirus holmi*, *Eusirogenes arctica*, *Apherusa glacialis*, and *Gammarus wilkitzkii* also belong to this category. Although

these copepod and amphipod species are most abundant in association with the ice, our observations of their occurrence at various depths at stations where ice was absent suggest they can at least be counted as pelagic transients.

The other group of species known so far only from the Arctic Ocean includes 12 more recently described species, for which most of the type specimens were obtained from the cruises reported here. These include: the copepods *Arctokonstantinus hardingi*, *Onchocalanus cristogerens*, *Pseudeuchaeta arctica*, *Phaennocalanus unispinosus*, *Byrathis* (=*Xanthocalanus*) *laptevorum*, *Xanthocalanus polarsternae*, *X. spinodenticulatus*, *Disco triangularis*, *Brodskius* sp. n., Discoidea sp.n. 1, Discoidea sp.n. 2, Discoidea sp.n. 3. (Markhaseva 1998, 2002; Markhaseva and Kosobokova 1998, 2001; Andronov and Kosobokova, personal communication), and the hydromedusae *Bathykorus bouilloni* (Raskoff 2010), as well as (at least) four undescribed species: the ostracod *Boroecia* sp. n. (Angel, personal communication), the polychaete *Minuspio* sp. n. (Gagaev, personal communication), ctenophores *Aulococtena* sp., *Bathyctena* spp. and several other cydippids (Raskoff et al. 2010).

Beyond the endemic and recently found new rare species listed above, the remaining fauna is also known outside of the Arctic Ocean: in non-Arctic waters in the North Atlantic or North Pacific or both, some from the Antarctic and/or deep waters in the tropics. The proportion of different categories assessed both within the total number of species and only the copepods was very similar for most categories, although the species known from the Arctic Ocean only were more numerous among the copepods (31%) than among all taxa (26%) (Fig. 2). After species known from the Arctic Ocean only, the North Atlantic and widely distributed species are the most important elements of the fauna. The former contribute 25% and 19%, while the latter 25% and 28% to all taxa and copepods, respectively
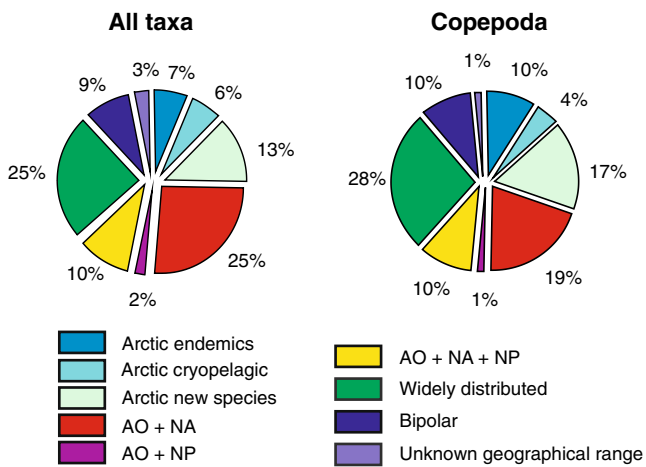
Fig. 2 Contribution of different geographical categories to the total number of zooplankton species (all taxa) and Copepoda. *AO* Arctic Ocean, *NA* North Atlantic, *NP* North Pacific

(Fig. 2). The low shares of North Pacific species (1% and 2% in all taxa and copepods, respectively) are noteworthy. The species regarded to be bipolar at present contribute 9% and 10% to all taxa and copepods, respectively; however bipolar status of many of them is currently under reassessment both in terms of morphology and genetics (Allcock et al. unpublished).

Regional differences within the Arctic Ocean

Among 148 resident species, 103 (69%) were recorded in all four deep basins of the Arctic Ocean, and ten species (7%) were recorded in only three of them (Table 2, and ESM). Of the remainder, nine species (6%) were recorded from two basins, and 27 (18%) from only one basin. Of 36 species recorded in one or two basins only, 18 are new to science, undescribed or recently described new species, 17 are seldom occurring deep-water species, and one is a fragile epipelagic ctenophore, *Dryodora glandiformis* that may have been present in some samples but becomes unrecognizable after preservation. In summary, most of these 36 species are rare, deep-water animals.

Comparison of the Eurasian Basin (Nansen and Amundsen Basins) and Canadian Basin (Makarov and Canada Basins) shows that 129 (87%) of 148 resident species were recorded in the Eurasian Basin and 137 (92%) species in the Canadian Basin. The differences in the faunistic composition of plankton between the Eurasian and Canadian Basins arise from poorly known and therefore seemingly restricted distribution of the deep-water rare species (Table 2, and ESM).

Vertical distribution and community structure

The multivariate analysis of community similarity suggests two major dimensions within the data from our 416

samples: differences between cruises and sample-depths. The 2D MDS projection of the data we have standardized upon represents cruises as differences in elevation within the data (Fig. 3a), and increasing depth moving from left to right with some curvature (Fig. 3b). It is notable that these trends appear clearest when one considers the three cruises (Fig. 3c, d) occurring primarily along the basin margins (Healy 2005, Polarstern 1993, 1995), while the cruises with samples toward the interior of the basins (Polarstern 1996, 1998) appear offset and compressed to the right, probably due to lower overall densities of zooplankton in surface and mesopelagic depths, but with closer similarity within the bathypelagic realm. This complication made visual interpretation of numerous distinct clusters within the data difficult, although nevertheless three major groups (epipelagic, mesopelagic, and bathypelagic) emerge at about 50-60% between-group similarity (data not shown). The similarity within each depth stratum (regardless of cruise) ranged from 60-70% except for the deepest strata (55%). However, when differences between cruises were accounted for (SIMPER two-way), similarity within each stratum increased by 6-10% (Table 4). Clustering by species produced consistent results, although most species are better characterized as unique in their distribution (Fig. 4). There is a relatively distinct assemblage of epi- and mesopelagic species, a more poorly defined assemblage of species with shelf or widespread (epipelagic) distribution, and an equally poorly clustered assemblage of meso-/bathypelagic species.

In terms of numerical importance, the classically epipelagic species are being replaced by mesopelagic ones with increased depth (Table 4). Clustering by species proves an alternate means of seeing these depth related patterns (Fig. 4). Again, visualization of mesopelagic community patterns is clearest if we reduce data to the 3 margin cruises (Healy 2005, Polarstern 1993, 1995 – Fig. 5) which represent 362 samples. From the cluster diagram one can see the change in abundance of the more dominant species in different depth strata. Surface waters are well represented by large-bodied copepod species: the three species of *Calanus*, *Metridia longa*, *Paraeuchaeta glacialis* and the small-bodied *Scolecithricella minor* (Fig. 6), with *C. finmarchicus* conspicuously absent in the Canada Basin. Numerically, however, small-bodied species such as *Oithona similis*, *Triconia borealis*, *Microcalanus*, and calanoid nauplii dominate the epipelagic mesozooplankton (Fig. 7). Mesozooplankton abundances decline significantly with depth for mesopelagic species, with distinct species-specific ranges obvious even within genera for the Aetideidae, Heterorhabdidae, *Scaphocalanus*, and *Spinocalanus* (Fig. 8). In contrast, most *Lucicutia* species occur only in the bathypelagic realm (Fig. 8). The relatively high numbers of *Mormonilla minor* (Fig. 7) that occur in these layers is interesting to note. Both larvaceans and
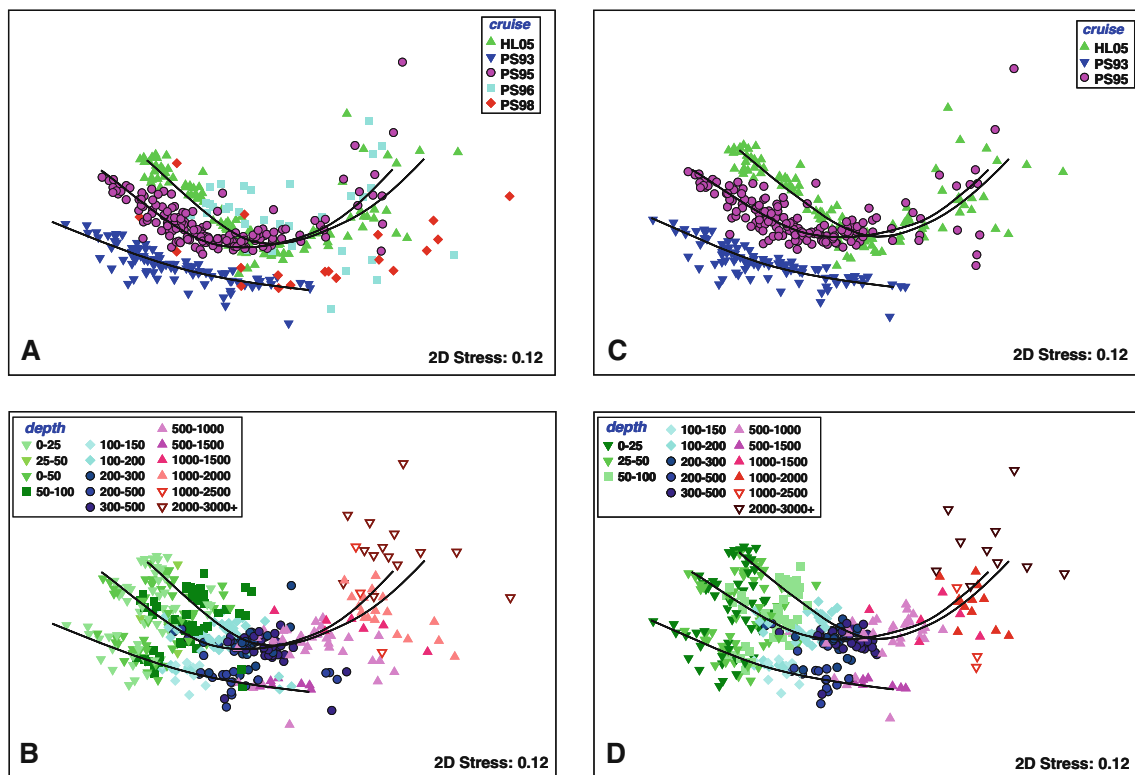
Fig. 3 a–d Multi-dimensional scaling (MDS) of Bray-Curtis similarities between zooplankton samples collected across the Arctic Ocean. MDS for all cruises coded by (**a**) cruise and (**b**) depth. MDS for the three basin margin cruise cruises coded by (**c**) cruise and (**d**) depth. Lines are fitted by eye to provide a reference for depth trajectory within *Healy* 2005, *Polarstern* 1993 and *Polarstern* 1995 cruises

thecosome pteropods (i.e. *Limacina helicina*) appear relatively confined to the epipelagic (Fig. 9, 7), while there are clear transitions in species associated with depth for the chaetognaths, the dominant cnidarians, and an assortment of prominent crustaceans (Fig. 9).

Diversity metrics

Although the total abundance of organisms declined exponentially with depth, the number of zooplankters counted per sample was relatively similar, because the thickness of the layers increased with depth (Fig. 10). This should reduce biases in the estimation of diversity indices that are calculated on a per sample basis. Nonetheless there were increasingly fewer samples available for analysis below 500 m. Diversity indices were consistent in showing diversity was lowest, less even, and less rich in surface waters (i.e., dominated by only a few species) and the most diverse and even at mid-depths (~200-500 m), while richness of species peaked slightly deeper (500-1,000 m). Species observed per sample and rarefied numbers showed similar patterns to the diversity indices, further indicating patterns were not strongly biased by sampling effort. In general, species accumulation curves (not shown) were close to asymptotic, as demonstrated by the close agreement between the total taxa observed in a layer (S_{Obs}), and the maximum predicted number of taxa predicted based on Michaelis-Menton curve fit (S_{Max}) at all depths except the deepest layer where the number of samples and counts within the samples were lowest. In contrast, the Chao2 estimator suggested there was still potential for the collection of additional rare species at most depths (i.e., 18-26% more then observed) except in surface waters. This discrepancy between species accumulation methods may be partially a reflection of the movement of a few individuals of species between their characteristic layers making them artificially rare, rather than an incomplete assessment of the planktonic species inhabiting the basins.

Discussion

The current inventory represents the largest account of metazoan plankton fauna of the deep Arctic Ocean with a total of 174 species, containing the most detailed account of non-copepod species published to date (Tables 1, 2, and ESM), although it includes only species recorded within our original collections and by colleagues using divers and an ROV during the same expeditions (see Raskoff et al 2010). Of these 174 species, 134 species have been

Table 4 Similarity of communities within a depth layer and the top ten taxa contributing to those communities. The Bray-Curtis within group similarity is determined for a depth layer alone or a combination of depth and cruise

| Strata (m)	Factor (%)		Top species by rank									
	Depth	Depth & cruise	1	2	3	4	5	6	7	8	9	10
0-25	60.58	68.75	*Oithona similis*	Calanoida nauplii	*Calanus glacialis*	*Microcalanus* spp.	*Triconia borealis* CV-adults	*Pseudocalanus minutus*	*Metridia longa*	*Oncaea* spp. and *Triconia borealis* CI-IV	*Calanus hyperboreus*	*Calanus finmarchicus*
25-50	62.19	69.53	*Oithona similis*	Calanoida nauplii	*Microcalanus* spp.	*Triconia borealis* CV-adults	*Calanus glacialis*	*Metridia longa*	*Calanus hyperboreus*	*Calanus finmarchicus*	*Oncaea* spp. and *Triconia borealis* CI-IV	*Oikopleura vanhoeffeni*
50-100	63.86	73.41	*Oithona similis*	*Microcalanus* spp.	*Oncaea* spp. and *Triconia borealis* CI-IV	*Triconia borealis* CV-adults	*Metridia longa*	Calanoida nauplii	*Calanus glacialis*	*Eukrohnia hamata*	Copepoda eggs	*Calanus finmarchicus*
100-200	67.81	77	*Microcalanus* spp.	*Oithona similis*	*Triconia borealis* CV-adults	*Metridia longa*	*Oncaea* spp. and *Triconia borealis* CI-IV	Calanoida nauplii	Ostracoda	*Eukrohnia hamata*	Copepoda eggs	*Calanus glacialis*
200-300	71.64	77.24	*Microcalanus* spp.	*Oncaea* spp. and *Triconia borealis* CI-IV	*Metridia longa*	*Triconia borealis* CV-adults	*Oncaea parila*	Calanoida nauplii	*Spinocalanus* CI-III	*Oithona similis*	*Spinocalanus longicornis*	*Eukrohnia hamata*
300-500	70.74	78.53	*Microcalanus* spp.	*Oncaea* spp. and *Triconia borealis* CI-IV	*Spinocalanus* CI-III	Calanoida nauplii	*Metridia longa*	*Oncaea parila*	*Triconia borealis* CV-adults	*Mormonilla minor*	*Spinocalanus longicornis*	Ostracoda
500-1,000	64.42	75.06	*Microcalanus* spp.	*Oncaea* spp. CV-adults	Calanoida nauplii	*Spinocalanus* CI-III	*Mormonilla minor*	*Metridia longa*	*Eukrohnia hamata*	Copepoda eggs	Ostracoda	*Scaphocalanus brevicornis*
1,000-2,000	64.71	73.09	*Oncaea* spp. CI-IV	*Microcalanus* spp.	*Spinocalanus* CI-III	*Mormonilla minor*	*Spinocalanus elongatus*	Calanoida nauplii	*Scaphocalanus brevicornis*	*Oncaea* spp. CV-adults	*Spinocalanus horridus*	Ostracoda
2,000-3,000	54.96	61.28	*Oncaea* spp. CI-IV	Calanoida nauplii	*Spinocalanus polaris*	Ostracoda	*Spinocalanus* CI-III	*Microcalanus* spp.	*Scaphocalanus polaris*	*Disco* spp.	*Spinocalanus elongatus*	*Lucicutia polaris*
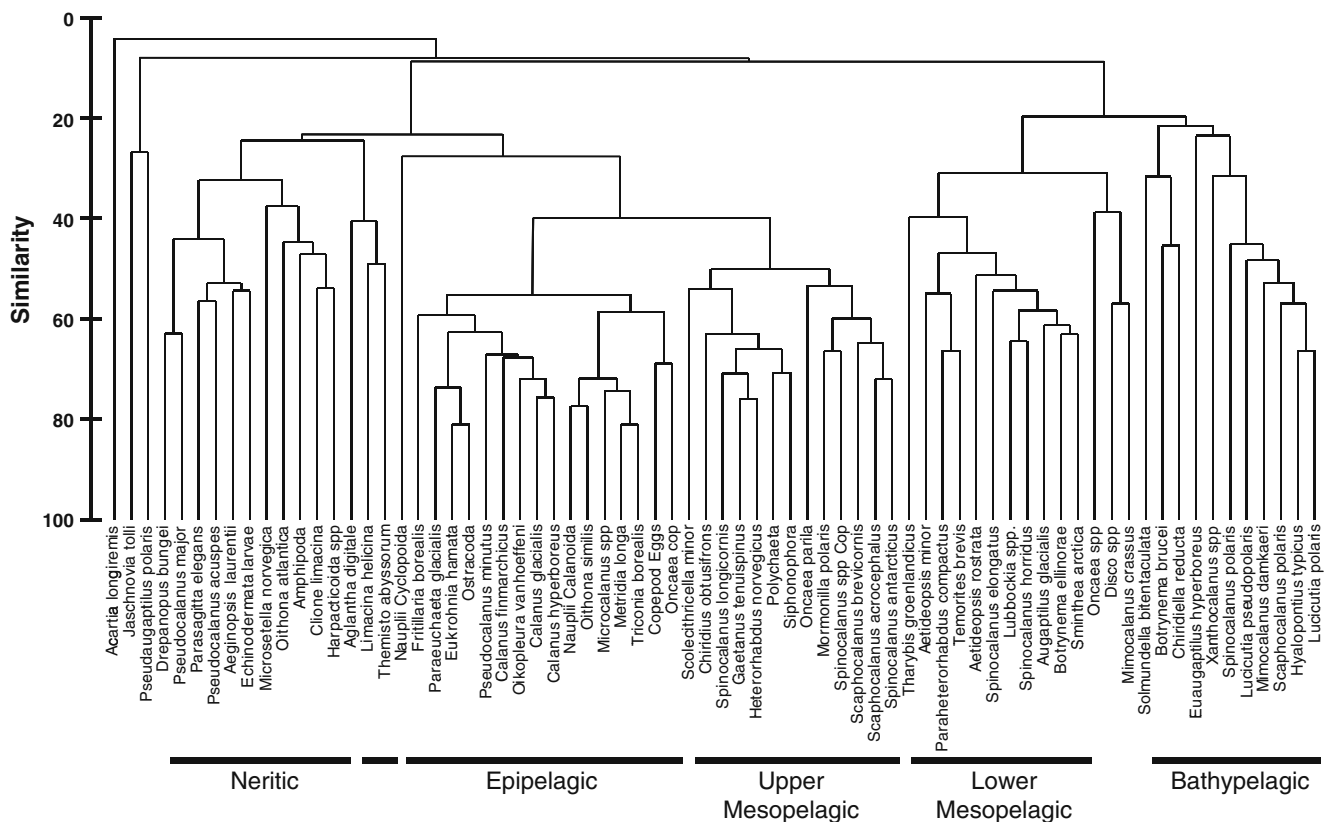
Fig. 4 Group-average hierarchical clustering of Bray-Curtis Similarity Index of taxa present with greater then 3% contribution to samples. Depth related clusters of are apparent for most species. Data from all cruises. *Cop* copepodite (non-adult) life stages

previously recorded in the Arctic Ocean (Table 1), while 21 are additions to the list based on previous work published on these collections (Kosobokova et al. 1998; Markhaseva and Kosobokova 1998, 2001; Kosobokova and Hirche 2000; Kosobokova and Hopcroft 2010; Raskoff et al. 2010). The remaining 19 species are novel species, recently

described from present collections, or currently under description.

Of the 174 species, 148 (85%) are true residents of the Arctic Ocean. The local reproduction of these species supports their populations, as obvious from the full range of life-stages in our and other collections from various areas

Fig. 5 Group-average hierarchical clustering of Bray-Curtis Similarity Index for samples from Polarstern 1993, 1995 and Healy 2005. *Black lines* connect statistically distinct clusters, while *red lines* indicate the intervals where clusters are not yet statistically distinct. Details for clusters with greater than 80% similarity, or lack of statistical distinction not shown, but the number and membership of samples clustering below these levels are represented by *depth-coded symbols*. Statistically distinct samples failing to cluster until less than 80% similarity are extended to axis
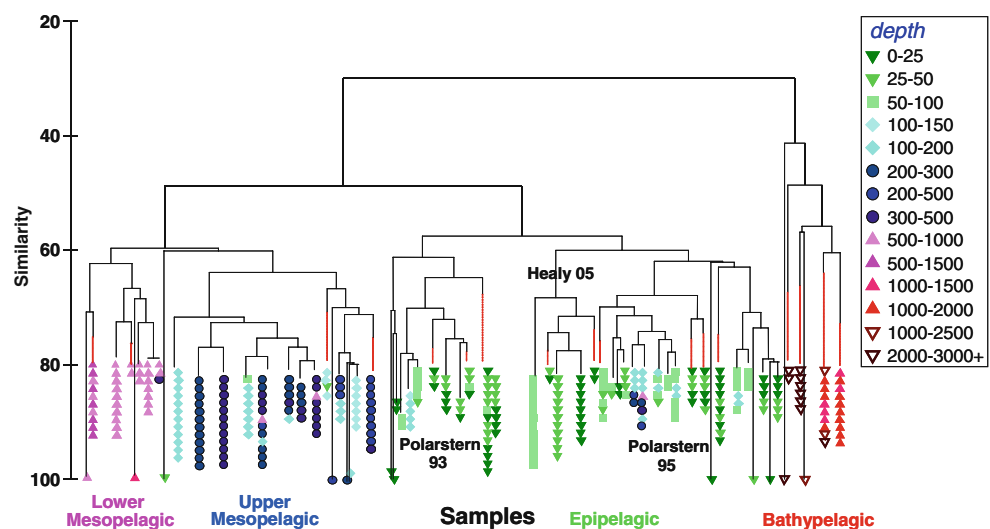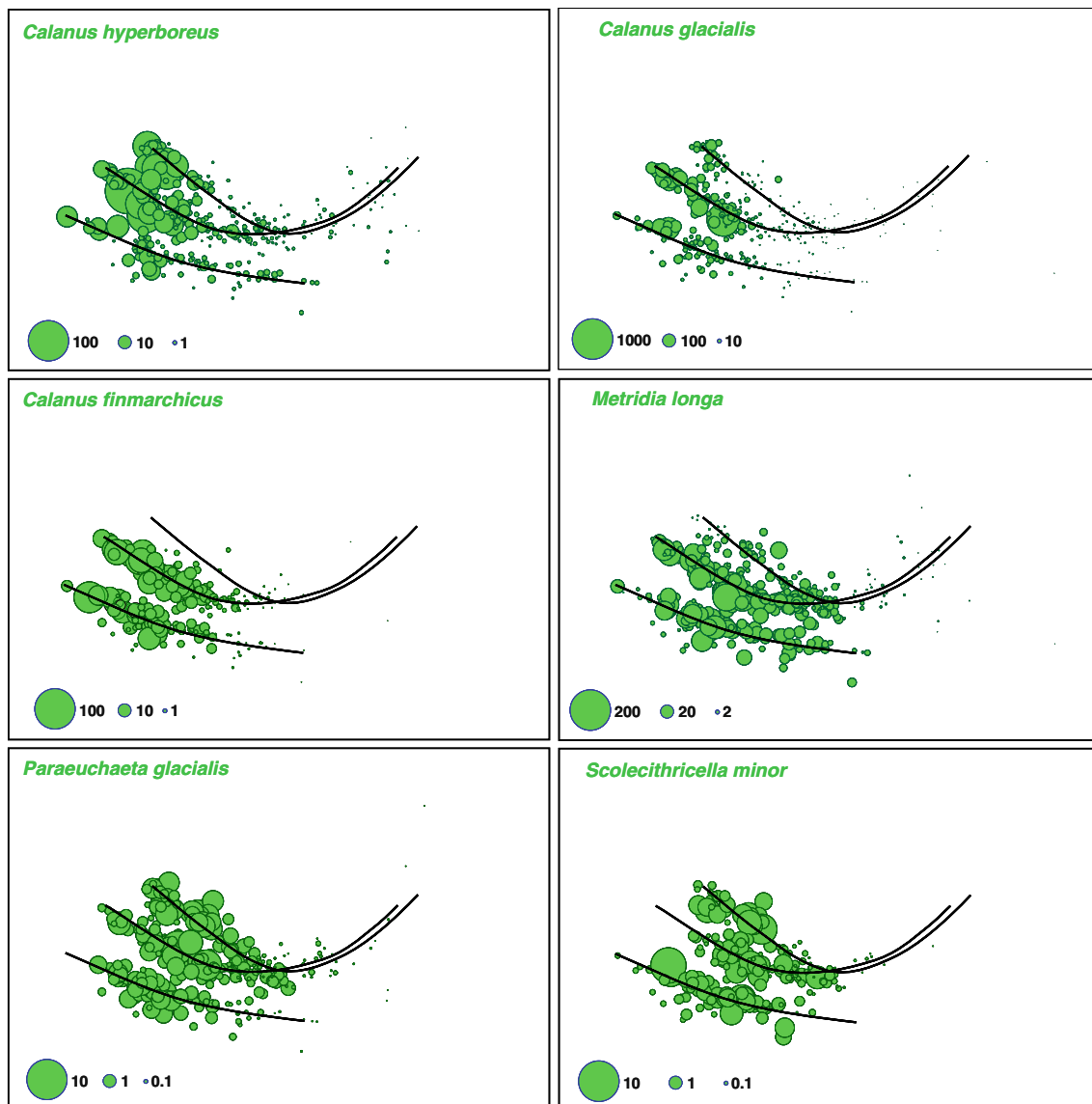
Fig. 6 Abundance (individuals m⁻³) of dominant large-bodied epipelagic and upper mesopelagic copepods superimposed on the location of their respective samples on the MDS plot. Reference lines provided for orientation to depth trajectory within *Healy* 2005, *Polarstern* 1993 and *Polarstern* 1995 cruises, with samples from shallower layers to the *left* and those from deeper layers to the *right*

all over the Arctic Ocean (Harding 1966; Dunbar and Harding 1968; Kosobokova et al. 1998; Ashjian et al. 2003; Stepanjants and Kosobokova 2006; Ota et al. 2008) and experimental observations on the reproductive biology and egg production of some of them (Kosobokova and Hirche 2001; Kosobokova et al. 2007; Kosobokova and Hopcroft 2007, 2008).

The remaining 26 species are functionally sterile expatriates (Ekman 1953) from adjacent regions: the North Atlantic, North Pacific, and the Arctic shelf seas either unable to reproduce in the Arctic Ocean proper, or unable to reproduce at sufficient rates to offset their mortality. All of them have restricted distribution in the Arctic Ocean, related to the intensity of water advection and abundance of

their populations in the source area. The other factors structuring their distribution are their life spans and survival potential under Arctic conditions versus transportation time/ speed. The most tolerant and abundant of these expatriates are spread by the respective advected waters over large part of the Arctic Basin, while others die off almost immediately after entering the basin proper. The most notable example is the copepod *Calanus finmarchicus*, a common and abundant member of plankton communities in the Eastern Arctic (Mumm 1993; Kosobokova and Hirche 2000; Hirche and Kosobokova 2007; Kosobokova and Hirche 2009), which fails to reproduce in the Arctic Ocean (Jaschnov 1970; Hirche and Kosobokova 2007; Kosobokova and Hirche 2009). Although huge numbers of *C. finmarchicus* are
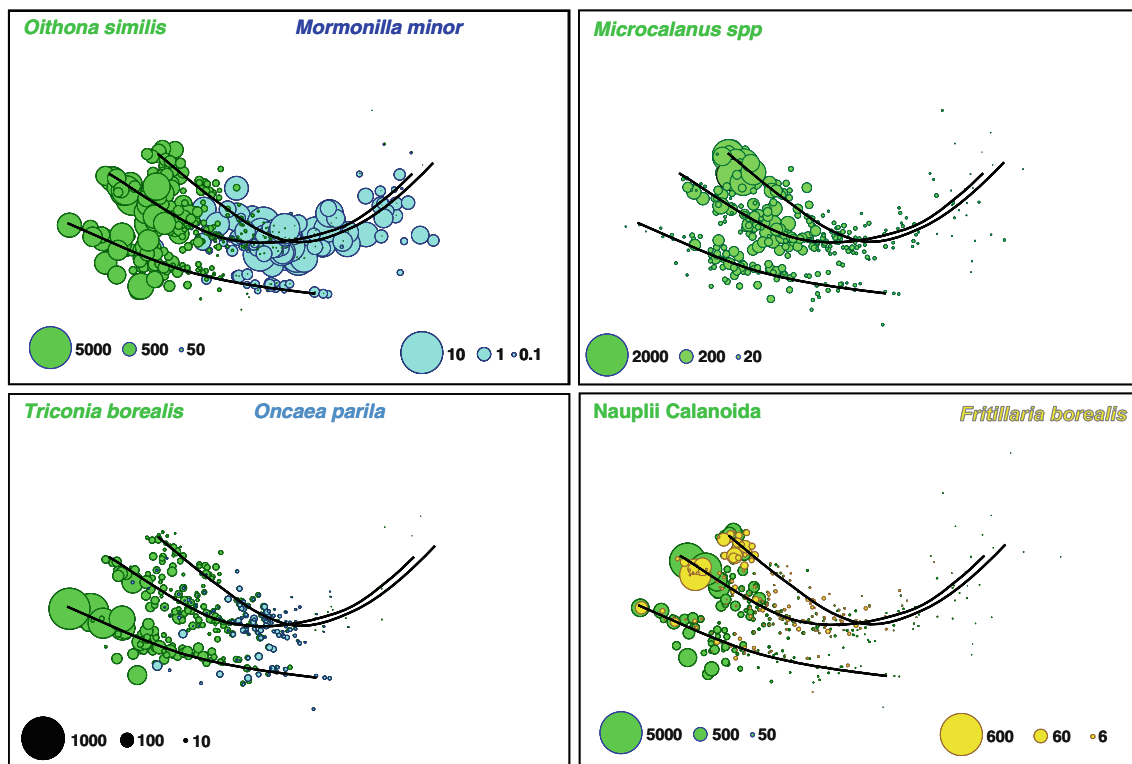
Fig. 7 Abundance (individuals m^{-3}) of dominant small-bodied epipelagic and upper mesopelagic copepods, and the small-bodied larvacean *Fritillaria borealis*, superimposed on the location of their respective samples on the MDS plot. Reference lines provided for orientation to depth trajectory within *Healy* 2005, *Polarstern* 1993 and *Polarstern* 1995 cruises, with samples from shallower layers to the *left* and those from deeper layers to the *right*

continuously advected into the Arctic via the Fram Strait and the Barents Sea shelf (Hirche and Mumm 1992; Kosobokova and Hirche 2009), their abundance decreases from the west to the east along the inflow of Atlantic water (Hirche and Kosobokova 2007; Kosobokova and Hirche 2009) and they disappear almost completely from the pelagic community in the Makarov Basin immediately east of the Lomonosov Ridge. Only a few specimens make it as far as the western Makarov Basin (Johnson 1963; Kosobokova 1981; Thibault et al. 1999; Kosobokova and Hirche 2000), but only to the area affected by the countercurrent of the Atlantic inflow (Rudels et al. 1994, 2000). In contrast to the Makarov Basin, in the Canada Basin *C. finmarchicus* is completely absent.

The distribution of another numerous Atlantic expatriate, the cyclopoid *Oithona atlantica*, strongly resembles that of *C. finmarchicus*. Such a wide distribution of both species leaves an open question of how, with a presumed 1-year life span, they make it that far east- and northward without successful reproduction in the Arctic. One can hypothesize that they either have longer life spans than currently believed in cold Arctic waters, or that the transport time from where they enter the Arctic Ocean is considerably shorter than estimations suggest (Treshnikov 1985). Neither

of these assumptions seem to be supported by field observations at present. Joint efforts of biological and physical oceanographers are required to reasonably explain mechanisms controlling the distribution of these Atlantic expatriates within the Arctic Ocean.

Among the other Atlantic expatriates, the carnivorous calanoid *Paraeuchaeta norvegica* is presumably not limited by feeding conditions (which may be the case for *C. finmarchicus*), but, nevertheless does not reproduce in the Arctic Ocean, and also occurs in the Nansen, Amundsen and Makarov, similar to *Calanus finmarchicus* and *Oithona atlantica*. Other expatriates from the Atlantic are present only close to where Atlantic water enters the Eurasian Basin or within the core of the Atlantic Boundary Current (Rudels et al. 1994, 2000; Schauer et al. 1997). None of them have yet been found in the Canadian Basin (Brodsky and Nikitin 1955; Johnson 1963; Harding 1966; Kosobokova 1981; Kosobokova and Hirche 2000; Kosobokova and Hopcroft 2010).

The Pacific expatriates, to the contrary, are restricted to the Canadian Basin (Table 3). They enter the Arctic Ocean with Pacific water through the Chukchi Sea (Stepanova 1937a, b; Jaschnov 1940; Brodsky and Nikitin 1955; Johnson 1963; Harding 1966; Dunbar and Harding 1968;
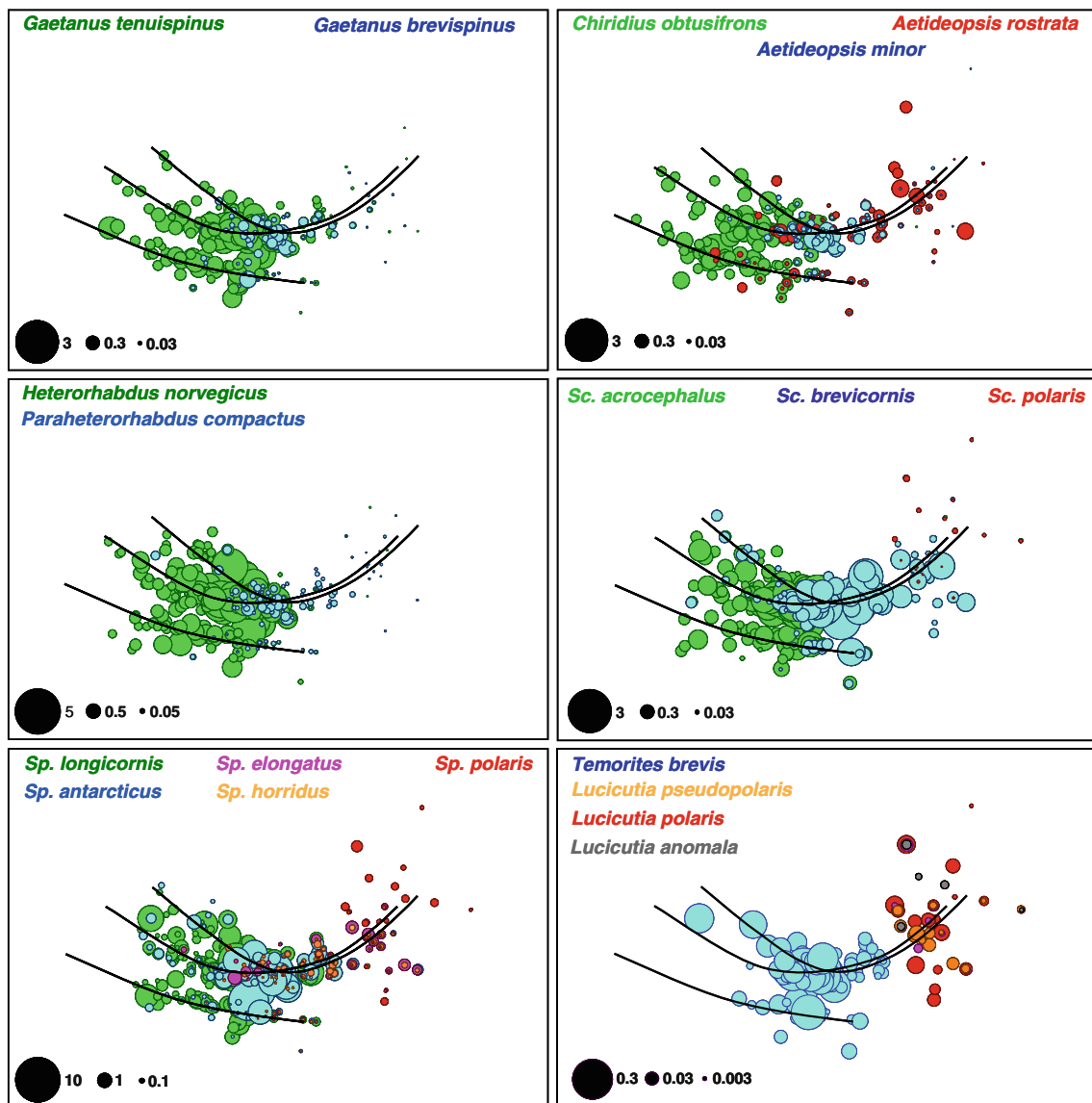
Fig. 8 Abundance (individuals m⁻³) of dominant mesopelagic and bathypelagic copepods superimposed on the location of their respective samples on the MDS plot. Reference lines provided for orientation to depth trajectory within *Healy* 2005, *Polarstern* 1993 and *Polarstern* 1995 cruises, with samples from shallower layers to the *left* and those from deeper layers to the *right*. *Sp. = Spinocalanus, Sc. = Scaphocalanus*

Pavshtiks 1971; Hopcroft et al. 2010; Kosobokova and Hopcroft 2010). However, the high numbers observed for some Atlantic expatriates in the Eurasian Basin are never found in the Canadian Basins proper, perhaps because the long-distance transport across the shallow Bering and Chukchi shelves does not favor survival of Pacific oceanic species.

This large data set clearly demonstrates that apart from differences in the distribution of these expatriates and a few rare bathypelagic species with poorly understood occurrence (see below), species composition in the Eurasian and Canadian Basins is very similar, indicating successful faunistic exchange across the underwater ridges (Kosobokova and Hirche 2000; Kosobokova and Hopcroft 2010). This refutes previous suggestions 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 (Brodsky and Pavshtiks 1977). Recent oceanographic observations further suggest the deepwater exchange from the Canada Basin to the Eurasian Basins may be stronger than appreciated (Björk et al. 2010).

A striking feature of the resident zooplankton fauna of the Arctic Ocean is the respectable degree of endemism (Harding 1966; Dunbar and Harding 1968; Kosobokova and Hirche 2000). All the 19 common endemic species listed here, have been known from the Arctic for decades or longer (Brodsky 1950, 1967; Dunbar and Harding 1968; Shirley and Leung 1970) and have not been found in any
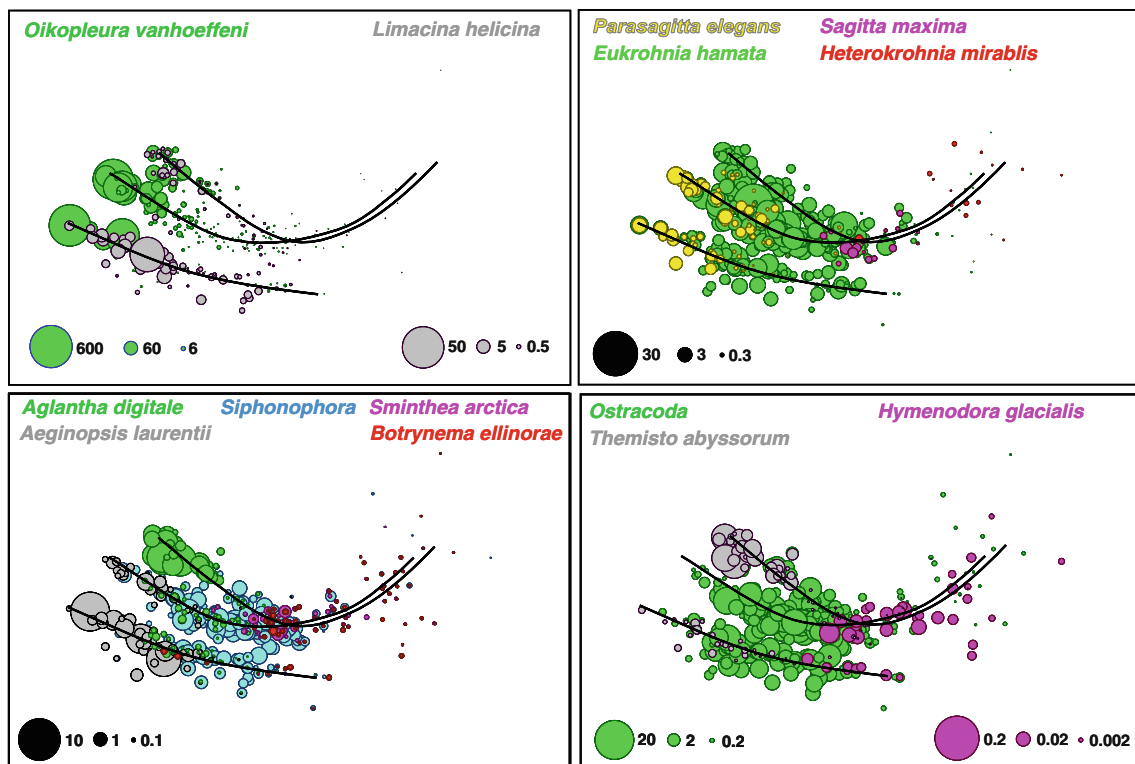
Fig. 9 Abundance (individuals m⁻³) of dominant non-copepod taxa superimposed on the location of their respective samples on the MDS plot. Reference lines provided for orientation to depth trajectory within *Healy* 2005, *Polarstern* 1993 and *Polarstern* 1995 cruises, with samples from shallower layers to the *left* and those from deeper layers to the *right*

other region since their description. It is not surprising that a proportion of the Arctic endemics (about one-third) are ice-associated fauna. More notable is that almost two-thirds of these common endemics are the bathypelagic species with a clear preference for depths below 1,000 m (Kosobokova and Hirche 2000; Kosobokova and Hopcroft 2010). The evolution of these deep-water species is without doubt related to the geological history of the Arctic Ocean, whose deep-water habitat was cut-off from other deep oceans until

the opening of Fram Strait 17.5 million years ago (Jakobsson et al. 2007). In recent decades quite a number of rare bathypelagic species have been added to the list. Unfortunately, all recent additions were not equally collected and studied in the four deep basins, which may contribute to the apparent differences of species composition between Eurasian and Canadian Basins and the basins within them. For example, the new copepod species from the family Xanthocalanidae (*Byrathis laptevorum*, *Phaennocalanus*

Fig. 10 Number counted in each sample, standardized abundance (individuals m⁻³), and number of samples. Diversity indices: evenness (*J′*), Shannon (*H′*) as log(e), and Margalef's richness (*d*). Taxa in each sample (*S*), total taxa observed in layer (*S*_Obs), *ES (1000)* rarefaction, the maximum predicted number of taxa based on Michaelis-Menton curve (*S*_Max) and *Chao2* estimation; 95% confidence intervals of means presented
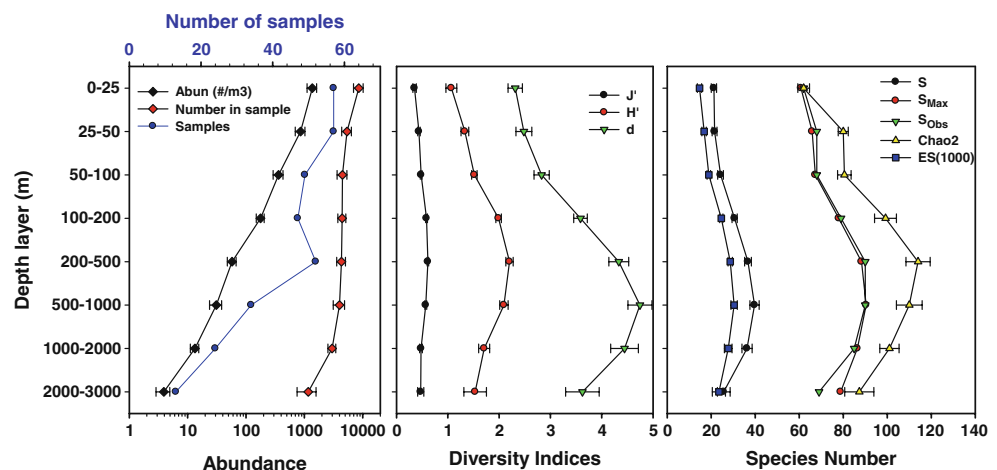
unispinosus, *Xanthocalanus polarsternae*, *X. spinodenticulatus*) were collected only in the Amundsen and Nansen Basins (Markhaseva 1998), using a benthopelagic trawl (Sirenko et al. 1996), while copepods from the families Tharybidae and Discoidae (*Brodskius* sp. n., Discoidea sp. n. 1, Discoidea sp. n. 2, Discoidea sp. n. 3), the ostracod *Boroecia* sp. n. and several cidippid ctenophores were studied only in the collections from the Makarov and Canada Basins (Andronov and Kosobokova, personal communication; Angel, personal communication; Raskoff et al. 2010). It remains to be clarified if these newer species are also endemics arising as a result of the Arctic's deep-water isolation, or if they are unknown from elsewhere due to limited or inappropriate sampling effort.

As for the other geographical components of the non-endemic resident plankton fauna, it was long believed that at least one-half of zooplankton species in the Arctic Ocean were of North Atlantic origin (Brodsky 1956; Brodsky and Pavshtiks 1977; Grainger 1989). Our distributional data show, however, that the North Atlantic fauna contributes only 19% to the copepod fauna and 25% to all taxa in the Arctic Ocean zooplankton. The rest, almost a half of all resident species, have wider distribution ranges (Fig. 2). The majority is represented by widely distributed and bipolar meso- and bathypelagic species. The deep-water species until recently were generally believed to be largely cosmopolitans because of the lack of major gradients in the deep sea (Grice and Hulseman 1967). While some bathypelagic organisms inhabiting deep water of the Arctic Ocean apparently have extensive distributional ranges, molecular genetic studies may, however, find that not all of these species are monotypic (Ward and Shreeve 2001).

Depth is the major structuring element for species distribution in the Arctic Ocean basins, and consequently for the communities that they collectively form. Typical vertical distribution ranges, depth preferences of the majority of copepod species, and the fact that overall diversity increases with depth, have been reported elsewhere (e.g., Kosobokova 1989; Mumm et al. 1998; Auel 1999; Kosobokova and Hirche 2000; Laakmann et al. 2009; Kosobokova and Hopcroft 2010). This study demonstrates the robustness of these conclusions using a wider suite of diversity metrics and non-copepod species. The important point here is that most Arctic residents have characteristic but wide vertical distribution ranges (Harding 1966; Dunbar and Harding 1968; Grainger 1989), inhabiting two or more of the conventionally defined water masses of the Arctic Ocean (Coachman and Aagaard 1974). Many mesopelagic species with highest abundances in the Atlantic layer also occupy waters both above and below this layer. This is reflected by the extension of their vertical range into the intermediate water (100-200 m) and the surface layers up to 50-100 m depths. Other species with

clear preference for the Atlantic layer may be found in small numbers in the Arctic Bottom Water below 1,000 m. The bathypelagic species, most abundant below 1,000 m, may occur as well in the lower portion of Atlantic layer. These patterns appear consistent throughout the Arctic, and although the absolute abundance of epipelagic and upper mesopelagic species shows some variation that drove the distinction between this study's cruises in our multivariate analysis, the lower mesopelagic and bathypelagic environment seem much more similar across all deep basins. Although some species showed significant differences in their prevalence between the Canadian and Eurasian Basins, it is unclear to what extent this may be a reflection of differences in seasonal timing of the cruises, inter-annual variability, or geographic location per se [i.e., proximity to Atlantic inflow (Kosobokova and Hirche 2009)]. These questions cannot be resolved without consistent multi-year observations in each region.

In contrast to the copepods, the vertical distribution of other groups has seldom been well defined, and even then only for the most abundant species (e.g., Scott 1969; Kosobokova 1989; Kosobokova and Hirche 2000; Raskoff et al. 2010). It is notable that such under-studied groups contain a substantial fraction of total species number observed (i.e., cnidarians contribute 16%, amphipods 9%). While we have presented depiction for the more abundant non-copepod species, the extent of our observations makes it possible to present the first generalized depth distribution of species of much lower occurrence (Table 2). Clearly, the non-copepod species are vertically structured in ways similar to that observed in the copepods. The relatively low abundance of many of these non-copepods in deeper waters results in them being under-presented in plankton nets, even though they may be large in size. This point has been made abundantly clear by recent ROV observations (Raskoff et al. 2010), suggesting we have much to learn about both biodiversity at these depths, as well as the potentially significant ecological role of some of these species. Similarly, the smallest crustacean species (e.g., Heron and Damkaer 1984), and the hyperbenthic habitat, to which many of the recently described copepod species have affinity, remain virtually unsampled within the basins (Sirenko et al. 1996; Markhaseva 1998). As indicated by the relatively large number of recently collected "new" species reported here, there is much still to be resolved and discovered with the Arctic's zooplankton, despite its seemingly low diversity.

References

Ashjian CJ, Campbell RG, Welch HE, Butler M, Van Keuren D (2003) Annual cycle in abundance, distribution, and size in relation to hydrography of important copepod species in the western Arctic Ocean. Deep Sea Res I 50:1235–1261

Auel H (1999) The ecology of Arctic deep-sea copepods (Euchaetidae and Aetideidae). Aspects of their distribution, trophodynamics and effect on the carbon flux. Ber Polarforsch 319:1–97

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

Björk G, Anderson LG, Jakobsson M, Antony D, Eriksson B, Eriksson PB, Hell B, Hjalmarsson S, Janzen T, Jutterström S, Linders J, Löwemark L, Marcussen C, Olsson KA, Rudels B, Sellén E, Sølvsten M (2010) Flow of Canadian Basin deep water in the Western Eurasian Basin of the Arctic Ocean. Deep Sea Res I 57:577–586

Bogorov VG (1946) Zooplankton from the collections of the expedition of the ice breaker "G. Sedov" 1937-1939. In: Trudy dr. eksp. Glavsevmorputi l/p "G.Sedov" in 1937-1940 3:336-370 [in Russian]

Brodsky KA (1950) Copepoda Calanoida of the far eastern seas of the USSR and the Polar Basin. In: Pavlovsky EN (ed) Identification keys to the fauna of the USSR 35. Akademia Nauk USSR, Moscow-Leningrad [in Russian]

Brodsky KA (1956) Deep-sea life in the Arctic Basin. Priroda 5:41–48, Transl No. 242 Am Meteorol Soc

Brodsky KA (1967) Calanoida of the far eastern seas and Polar Basin of the USSR. In: Pavlovsky EN (ed) Keys to the fauna of the USSR. Israel Program for Scientific Translation. 35, Jerusalem.

Brodsky KA, Nikitin MN (1955) Observational data of the scientific research drifting station of 1950-1951. Hydrobiological work. Morskoy Transport 1:404–410 [in Russian]

Brodsky KA, Pavshtiks EA (1977) Plankton of the central part of the Arctic Basin. Pol Geogr 1:143–161 (Transl. from Voprosy Geographii, 101:148-157; 1976)

Clarke KR, Warwick RM (1999) The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. Mar Ecol Prog Ser 184:21–29

Clarke KR, Warwick RM (2001a) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E, Plymouth

Clarke KR, Warwick RM (2001b) A further biodiversity index applicable to species lists: variation in taxonomic distinctness. Mar Ecol Prog Ser 216:265–278

Clarke KR, Warwick RM (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth

Coachman LK, Aagaard K (1974) Physical oceanography of arctic and subarctic seas. In: Herman Y (ed) Marine Geology and Oceanography of the Arctic Seas. Springer, Berlin Heidelberg New York, pp 1-72.

Dawson JK (1971) Taxonomic guides to Arctic zooplankton (III): species of Arctic Ocean Chaetognaths. Univ South California, Dept Biol Sciences Tech Rep 3:6–23

Dunbar MJ, Harding G (1968) Arctic Ocean water masses and plankton—a reappraisal. In: Sater JE (ed) Arctic Drifting Stations: a report on activities supported by the Office of Naval Research. Arctic Institute of North America, Washington D.C., pp 315-326

Ekman S (1953) Zoogeography of the Sea. Fox HM (ed) Sidgwick and Jackson, London

Groendahl F, Hernroth L (1986) Vertical distribution of copepods in the Eurasian part of the Nansen Basin, Arctic Ocean. In: Schriever G, Schminke HK, Shih C-T (eds) Proc Sec Int Conf Copepoda Ottawa, Syllogeus 58, pp 311-320

Grainger EH (1965) Zooplankton from the Arctic Ocean and adjacent Canadian waters. J Fish Res Board Can 22:543–564

Grainger EH (1989) Vertical distribution of zooplankton in the central Arctic Ocean. In: Rey L, Alexander V (eds) Proc 6th Conf Comité Arctique International, pp 48–60

Grice GD (1962) Copepods collected by the nuclear submarine Seadragon on a cruise to and from the North Pole, with remarks on their geographic distribution. J Mar Res 20:97–109

Grice GD, Hulseman K (1967) Bathypelagic calanoid copepods of the western Indian Ocean. Proc US Nat Mus 122:1–67

Harding GC (1966) Zooplankton distribution in the Arctic Ocean with notes of life cycles. MS Thesis, McGill University, Montreal

Heron GA, Damkaer DM (1984) Arctic Ocean Copepoda of the genera Lubbockia, Oncaea and Epicalymma (Poecilostomatoida: Oncaeidae) with remarks on distributions. J Crustac Biol 4:448–490

Hirche HJ, Kosobokova KN (2007) Distribution of Calanus finmarchicus in the northern North Atlantic and Arctic Ocean—expatriation and potential colonization. Deep Sea Res II 54:2729–2747

Hirche HJ, Mumm N (1992) Distribution of dominant copepods in the Nansen Basin, Arctic Ocean, in summer. Deep Sea Res A 39 (Suppl 2):S485–S505

Hirche HJ, Hagen W, Mumm N, Richter C (1994) The Northeast Water Polynya, Greenland Sea. III. Meso- and macrozooplankton distribution and production of dominant herbivorous copepods during summer. Pol Biol 14:491–503

Hopcroft RR, Kosobokova KN (2010) Distribution and egg production of Pseudocalanus species in the Chuckchi Sea. Deep Sea Res II 57:49–56

Hopcroft RR, Kosobokova KN, Pinchuk AI (2010) Zooplankton community patterns in the Chukchi Sea during summer 2004. Deep Sea Res II 57:27–39

Hopcroft RR, Clarke C, Nelson RJ, Raskoff KA (2005) Zooplankton communities of the Arctic's Canada Basin: the contribution by smaller taxa. Pol Biol 28:197–206

Hughes KH (1968) Seasonal vertical distribution of copepods in the Arctic water in the Canadian basin of the North Polar Sea. MSc Thesis, University of Washington, Seattle

Jaschnov VA (1940) Plankton productivity of the northern seas of the USSR. Moscovskoe Obshestvo Ispytatelei Prirody Press, Moscow [in Russian]

Jaschnov VA (1970) Distribution of Calanus species in the seas of the northern hemisphere. Intern Rev der Gesamt Hydrobiol 55:197–212

Jakobsson M, Backmann J, Rudels B, Nikander J, Frank M, Mayer L, Jokat W, Sangiorgi F, D'Oregan M, Brinkhuis H, King J, Moran K (2007) The early Miocene onset of a ventilated circulation regime in the Arctic Ocean. Nature 447:986–990

Jennings RM, Bucklin A, Pierrot-Bults A (2010) Barcoding of arrow worms (Phylum Chaetognatha) from three oceans: genetic diversity and evolution within an enigmatic phylum. PLoS ONE 5(4):e9949. doi:10.1371/journal.pone.0009949

Johnson MW (1963) Zooplankton collections from the high polar basins with special reference to the Copepoda. Limnol Oceanogr 8:89–102

Kosobokova KN (1981) Zooplankton of the Arctic Ocean. PhD Thesis, Institute of Oceanology. Akademy of Sciences, Moscow [in Russian]

Kosobokova KN (1989) Vertical distribution of plankton animals in the eastern part of the central Arctic Basin. Explorations of the Fauna of the Seas, Marine Plankton, Leningrad 41:24–31 [in Russian]

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

Kosobokova KN, Hirche HJ (2001) Reproduction of Calanus glacialis in the Laptev Sea, Arctic Ocean. Pol Biol 24:33–43

Kosobokova KN, Hirche HJ (2009) Biomass of zooplankton in the eastern Arctic Ocean—a baseline study. Prog Oceanogr 82:265–280

Kosobokova KN, Hopcroft RR (2007) Population structure and reproduction of the chaetognath Eukrohnia hamata in the Canada Basin, Arctic Ocean. Abstr 4th Zoopl Prod Symp, Hiroshima, 141

Kosobokova KN, Hopcroft RR (2008) Population structure and egg production of Metridia longa in the Arctic Ocean. Abstr 10th Intern Conf Copepoda, Pattaya, p 159

Kosobokova KN, Hopcroft RR (2010) Diversity and vertical distribution of mesozooplankton in the Arctic's Canada Basin. Deep Sea Res II 57:96–110

Kosobokova KN, Hirche HJ, Hopcroft RR (2007) Reproductive biology of deep-water calanoid copepods from the Arctic Ocean. Mar Biol 151:919–934

Kosobokova KN, Hanssen H, Hirche HJ, Knickmeier K (1998) Composition and distribution of zooplankton in the Laptev Sea and adjacent Nansen Basin during summer, 1993. Pol Biol 19:63–76

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

Leung YM (1970a) Taxonomic guides to Arctic zooplankton (I): Euphausiids of the Central Arctic. and peripheral seas. In: Kobayashi HA (ed) Univ South California, Dept Biol Sciences Tech Rep 2:38-49

Leung YM (1970b) Taxonomic guides to Arctic zooplankton (II): Siphonophores of the Central Arctic. Ctenophores of the Central Arctic. In: Kobayashi HA (ed) Univ South California, Dept Biol Sciences. Tech Rep 3:19-51.

Leung YM (1971) Taxonomic guides to Arctic zooplankton (III): Pteropods of the Central Arctic. In: Kobayashi HA (ed) Univ South California, Dept Biol Sciences Tech Rep 4:24-28

Leung YM (1972) Taxonomic guides to Arctic zooplankton (VI): Appendicularians of the Central Arctic. Mysids of the Arctic Ocean and confluent seas. Field Guide to Arctic Zooplankton Crustaceans. Ostracods of the Central Arctic Ocean. In: Kobayashi HA (ed) Univ South California, Dept Biol Sciences Tech Rep 2:1-41

Leung YM, Havens A, Rork W (1971) Taxonomic guides to Arctic zooplankton (III): Decapods of the Central Arctic. In: Kobayashi HA (ed) Univ South California, Dept Biol Sciences Tech Rep 4:29-45

Magurran AE (2004) Measuring biological diversity. Blackwell Science, Malden

Markhaseva EL (1998) New species of the genus Xanthocalanus (Copepoda, Calanoida, Phaennidae) from the Laptev Sea. J Mar Syst 15:413–419

Markhaseva EL (2002) Phaennocalanus unispinosus (Copepoda, Calanoida, Phaennidae): new genus, and new species from the bathypelagial Arctic Basin. Sarsia 87:312–318

Markhaseva EL, Kosobokova KN (1998) New and rare species of calanoid copepods from the central Arctic Basin (Crustacea, Copepoda). Zoosystematica Rossica 7:45–53

Markhaseva EL, Kosobokova KN (2001) Arctokonstantinus hardingi (Copepoda, Calanoida: Arctokonstantinidae): new family, new genus and new species of from the bathypelagial Arctic Basin. Sarsia 86:319–324

Minoda T (1967) Seasonal distribution of Copepoda in the Arctic Ocean from June to December, 1964. Rec Oceanogr Works Jpn 9:161–168

Mumm N (1993) Composition and distribution of mesozooplankton in the Nansen Basin, Arctic Ocean, during summer. Pol Biol 13:451–461

Mumm N, Auel H, Hanssen H, Hagen W, Richter C, Hirche HJ (1998) Breaking the ice: large-scale distribution of mesozooplankton after a decade of Arctic and transpolar cruises. Polar Biol 20:189–197

Ota Y, Hattori H, Makabe R, Sampei M, Tanimura A, Sasaki H (2008) Seasonal changes in nauplii and adults of Calanus hyperboreus (Copepoda) captured in sediment traps, Amundsen Gulf, Canadian Arctic. Pol Sci 2:215–222

Pautzke CG (1979) Phytoplankton primary production below the Arctic Ocean pack ice, an ecosystems analysis. PhD Thesis, University of Washington, Seattle

Pavshtiks EA (1971) Hydrobiological characteristics of waters of the Arctic Basin in the drifting area of "North Pole 17". Trudy Arkticheskogo Antarcticheskogo Instituta 30:63–69 [in Russian]

Raskoff KA (2010) Bathycorus boulloni: a new genus and species of deep-sea jellyfish from the Arctic Ocean (Hydrozoa, Narcomedusae, Aeginidae). Zootaxa 2361:57–67

Raskoff KA, Purcell JE, Hopcroft RR (2005) Gelatinous zooplankton of the Arctic Ocean: in situ observations under the ice. Pol Biol 28:207–217

Raskoff KA, Hopcroft RR, Kosobokova KN, Purcell JE, Youngbluth M (2010) Jellies under ice: ROV observations from the Arctic 2005 hidden ocean expedition. Deep Sea Res II 57:111–126

Razouls C, de Bovee F, Kouwenberg J, Desreumaux N (2005-2009) Diversity and Geographic distribution of marine Planktonic Copepods, http://copepodes.obs-banyuls.fr/en

Rudels B, Jones P, Anderson L, Kattner G (1994) On the intermediate depth waters of the Arctic Ocean. In: Johannessen OM, Muench RD and Overland JE (eds) The Polar Oceans and Their Role in Shaping the Global Environment. Geoph Monogr 85:33–46.

Rudels B, Muench RD, Gunn J, Schauer U, Friedrich HJ (2000) Evolution of the Arctic boundary current north of the Siberian Shelves. J Mar Syst 25:77–99

Sars GO (1900) V. Crustacea. In: Nansen F (ed) The Norwegian North Polar Expedition 1893-1896. Scientific Results, 1-5.

Scott DA (1969) Seasonal and vertical distributions of zooplankton in the Canadian Basin of the Arctic Ocean. MS Thesis, University of Washington, Seattle

Schauer U, Muench RD, Rudels B, Timokhov L (1997) Impact of eastern shelf waters on the Nansen Basin intermediate layers. J Geophys Res 02C2:3371–3382

Shirley WD, Leung Y-M (1970) Taxonomic Guides to Arctic Zooplankton: Medusae of the Central Arctic. In: Kobayashi HA (ed) Univ South California, Dept Biol Sciences Tech Rep 3:1-18.

Shirshov PP (1938) Oceanographical observations. Dokl Akad Nauk SSSR 17:569–580 [in Russian]

Sirenko BI (2001) List of species of free-living invertebrates of Eurasian Arctic Seas and adjacent deep waters. Russian Academy of Science, Exploration of the Fauna of the Sea 51:1-129

Sirenko BI, Markhaseva EL, Buzhinskaya GN, Golikov AA, Menshutkina TV, Petryashov VV, Semenova TN, Stepanjants SD, Vassilenko SV (1996) Preliminary data on suprabenthic invertebrates collected during RV Polarstern cruise in the Laptev Sea. Pol Biol 16:345–352

Stepanjants SD, Kosobokova KN (2006) Medusae of the genus Rhabdoon (Hydrozoa: Anthoathecata: Tubularioidea) in the Arctic Ocean. Mar Biol Res 2:388–397

Stepanova VS (1937a) Biological indicators of currents in the northern Bering and southern Chukchi Seas. Issledovanija Morei SSSR 25:175–216 [in Russian]

Stepanova VS (1937b) Distribution of Bering Sea water in the Chukchi Sea (from data of the analysis of zooplankton from a cruise on the icebreaker Krasin in 1935). Tr Arkticheskogo Nauchno Issledovatel'skogo Inst 82:113–143 [in Russian]

Tencati JR (1970) Taxonomic guides to Arctic zooplankton (I). Amphipods of the central Arctic. In: Kobayashi HA (ed) Univ South California, Dept Biol Sciences Tech Rep 2:1-37

Thibault D, Head EJH, Wheeler PA (1999) Mesozooplankton in the Arctic Ocean in summer. Deep Sea Res I 46:1391–1415

Timofeev SF (1998) Reproduction of chaetognath *Eukrohnia hamata* (Möbius, 1875) in the Arctic Ocean. Rep Pol Res 287:70–73

Treshnikov AF (1985) Atlas of the Arctic.The State Maps Department, Moscow, pp 1-204 [*in Russian*].

Virketis MA (1957). Some data on the zooplankton from the central part of the Arctic Basin. Materials of scientific observations of the drift stations "North Pole 3" and "North Pole 4" 1954/55 1, Moscow, pp 238-311 [*in Russian*]

Ward P, Shreeve RS (2001) The deep-sea copepod fauna of the Southern Ocean: patterns and processes. Hydrobiologia 453 (454):37–54

Yingst DR (1972) Pelagic Polychaetes of the Central Arctic Basin. In: Kobayashi HA (ed) Univ South California, Dept Biol Sciences Tech Rep 1