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Zooplankton communities of the Arctic's Canada Basin: the contribution by smaller taxa

Abstract Zooplankton was sampled at ten stations in the Canada Basin during August 2002 using both 53- and 236-μm mesh nets to examine the contribution by smaller and less studied species. Copepod nauplii, the copepods *Oithona similis*, *Oncaea borealis* and *Microcalanus pygmaeus*, and the larvacean *Fritillaria borealis typica* dominated the upper 100 m of the water column numerically, while biomass was dominated by the copepods *Calanus hyperboreus*, *Calanus glacialis* and *Paraeuchaeta glacialis*, and the chaetognath *Eukrohnia hamata*. Zooplankton biomass ranged from 3.7 to 14.5 mg AFDW m^{-3}, with a mean of 9.6 mg AFDW m^{-3}. While the three microcopepods contributed less than 5% of the biomass, estimates of their potential growth rates suggest they might contribute upwards of 25% of the metazoan zooplankton production. The true rates of growth and development of these microcopepods in the Arctic need to be determined to conclusively ascertain their importance.

Introduction

Relative to most of the world's oceans, our knowledge of zooplankton communities in the Arctic Ocean is deficient, especially so in the central basins due to their thick cover of multiyear ice. Over the past 50 years, zooplankton research in the basins has either taken the form of drifting ice stations that describe seasonal cycles or, more recently, ice-breaker transits that provide more extensive geographic coverage, but are generally confined to late summer when the ice is thinnest. Due to their high abundance and ease of capture, the taxonomic composition (Brodsky 1983; Sirenko 2001) and life history of the larger, more common copepods in the Arctic Ocean is now relatively well understood (see review by Smith and Schnack-Schiel 1990). The same cannot be said for the smallest copepod species that are variably missed by collection techniques (e.g. Auel and Hagen 2002), deep-water taxa (e.g. Kosobokova and Hirche 2000), or the more fragile gelatinous forms (see Raskoff et al. 2004).

Historically, effort has concentrated on copepods of the genus *Calanus* because they appear to dominate the zooplankton biomass (e.g. Smith and Schnack-Schiel 1990; Mumm et al. 1998; Thibault et al. 1999; Ashjian et al. 2003). They feed on algae and protozoa in the surface layers and accumulate surplus energy in the form of lipids. This chemical energy is utilized for over-wintering at depth and to fuel reproduction in the following spring. The life cycles of these species have been estimated to take 2–4 years (e.g. Hirche 1997; Kosobokova 1999). As in most oceans, smaller copepod taxa are actually numerically dominant (e.g. Conover and Huntley 1991; Kosobokova and Hirche 2000; Auel and Hagen 2002), yet only a few studies have used sufficiently fine meshes to fully assess their contribution (i.e., Kosobokova 1980; Pautzke 1979; Ashjian et al. 2003). These smallest species exhibit shorter generation time and more sustained reproduction (Ashjian et al. 2003), suggesting that their importance in ecosystem productivity could be greater than that implied by their biomass alone.

Although copepods are typically predominant in the basins, there is a broad assemblage of other holoplanktonic groups in the Arctic (e.g. Sirenko 2001) that are either ignored or briefly summarized (Thibault et al. 1999), and only occasionally reported in full detail (e.g. Kosobokova and Hirche 2000). Larvaceans

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(Appendicularians), for example, have been shown to be abundant in Arctic polynyas (Ashjian et al. 1995; Acuna et al. 1999) and common in the central Arctic (Kosobokova and Hirche 2000; Auel and Hagen 2002), although none of these studies has used sufficiently fine meshed nets to fully assess their importance. These soft-bodied filter-feeders are capable of much higher rates of ingestion, growth and reproduction than crustaceans (Hopcroft et al. 1998; Gorsky and Fenaux, 1998; R. R. Hopcroft, unpublished data), allowing them to respond more rapidly to shifts in primary productivity. During the times when larvaceans are numerically abundant, the efficiency with which primary production is exported to the benthos may be greatly increased compared to when copepods abound (Gorsky and Fenaux 1998).

Similarly, important and common predatory groups, such as the chaetognaths, amphipods, ctenophores and cnidarians, have received detailed reports in only a few surveys (Kosobokova and Hirche 2000; Auel and Hagen 2002). Arctic chaetognaths may represent considerable biomass (Kosobokova and Hirche 2000), have long life cycles (e.g. 2 years—Welsh et al. 1996) and are thought to be important in controlling *Calanus* populations (Falkenhaug and Sakshaug 1991). Hyperiid amphipods can also be common in Arctic waters (Mumm 1993; Auel and Werner 2003), with 2- to 3-year life cycles, and a similar potential to graze a notable proportion of the *Calanus* population (Auel and Werner 2003). The importance of ctenophores and cnidarians is under-appreciated. This is considered elsewhere in this issue (Raskoff et al. 2004).

In recent years, we have come to recognize that the Arctic may be more rapidly influenced by climate change than elsewhere on the globe (e.g. Sturm et al. 2003). Thus, there is a critical need for improved knowledge of its communities if any climatic effects are to be observed. To better understand the zooplankton communities of the Canada Basin, we employed both standard and fine-meshed nets to better establish the contribution of the smaller and less studied taxa.

Materials and methods

Zooplankton samples were collected from 21 August to 5 September 2003, between 0700 and 2100 hours by vertical hauls to 100 m depth of two separate sets of Bongo nets. Collections were made at a total of ten stations (Fig. 1), with sampling generally executed in ice-free zones to simplify deployment. Water temperatures in the upper 100 m varied between ∼0 and −1.5°C with salinity from 26 psu at the surface to ∼32 psu deeper (for details of physics, see McLaughlin et al. 2004). The larger Bongo set consisted of 60-cm-diameter black MARMAP-style nets of 236 µm mesh. The smaller set consisted of 22 cm diameter nets designed with a 1-m cylinder followed by a 1.6-m conical section, with one Bongo being of 150 µm mesh (used
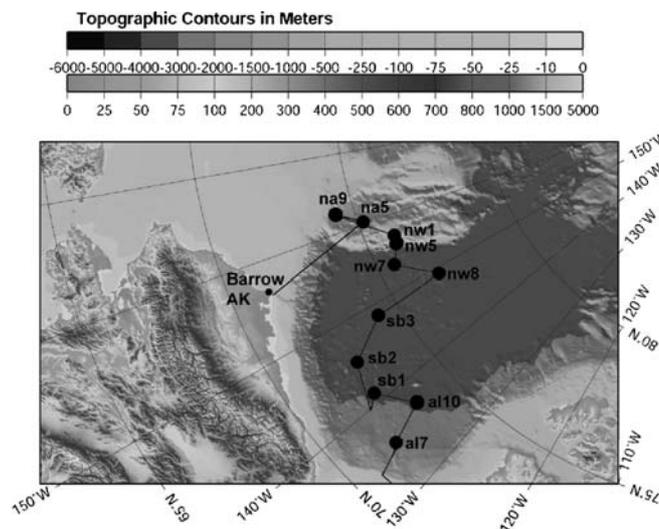

Fig. 1 Study region indicating sample stations and cruise track

for other purposes) and the other of 53 µm mesh. One of the larger nets was fitted with a Karl uni-directional flowmeter. Both nets in the smaller Bongo were fitted with GO flowmeters mounted such that the net immobilized the rotor during descent. Upon retrieval, the contents were preserved in 10% formalin.

Preserved samples were processed for quantitative determination of species composition using a combination of Folsom and Beaker splits. A maximum of 100 animals per species were identified and measured using a computer-assisted measuring system (Roff and Hopcroft 1986), with increasingly larger subsamples examined for the rarer taxa. For the copepods, the developmental stages and the sex of the adults was also noted, except for *Oncaea*, where staging of the subadults proved problematic. It is likely that for some congeneric species where earlier copepodites cannot be distinguished, they have been incorrectly grouped with the sibling species for which adults were identified. In the case of *Calanus*, the two species were distinguished largely by differences in prosome length (e.g. Unstad and Tande 1991; Hirche et al. 1994). The weight of each individual was predicted from species-specific relationships, or from those of a morphologically similar species (Table 1). Notably, although a relationship has been reported for *Oithona similis* (Sabatini and Kiørboe 1994), its slope is unusually shallow, and we have elected to use that for another congener. The data for smaller-bodied taxa were taken entirely from the 53-µm mesh nets, while data for larger-bodied taxa were taken from the 236-µm net because they filtered larger volumes and hence yielded better estimates of abundances (see Results).

Although it was not a goal of this study, where it could be easily observed, the reproductive condition of the various species was noted because such information is rare in the literature. In the case of the copepods, such observations are confined to egg-carrying species, where

Table 1 Relationships employed to predict weight from length for the taxa encountered in the study region

Species	Regression	Units	Source
Themisto abyssorum[a]	$DW = 0.0049 \cdot BL^{2.957}$	mm, µg	Ikeda and Shiga (1999)
Themisto libellula	$DW = 0.006 \cdot BL^{2.821}$	mm, µg	Auel and Werner (2003)
Calanus hyperboreus	$DW = 0.003 \cdot PL^{3.718}$	mm, mg	Ashjian et al. (2003)
Calanus glacialis	$DW = 0.010 \cdot PL^{3.414}$	mm, mg	Ashjian et al. (2003)
Scaphocalanus (acrocephalus)	$AFDW = 0.0107 \cdot PL^{3.0635}$	mm, mg	Mumm (1991)
Paraeuchaeta spp.	$AFDW = 0.0075 \cdot PL^{3.274}$	mm, mg	Mumm (1991)
Heterorhabdidae	$AFDW = 8.76 \cdot PL^{3.463}$	µm, µg	Yamaguchi and Ikeda (2000)
Oithona similis[b]	$\log AFDW = 3.16 \cdot \log PL - 8.18$	µm, µg	Hopcroft et al. (1998)
Oncaea spp.[b]	$\log AFDW = 3.16 \cdot \log PL - 8.18$	µm, µg	Hopcroft et al. (1998)
Oikopleura vanhoeffeni	$\log C = 3.20 \cdot \log TL - 8.93$	µm, µg	Deibel (1986)
Fritillaria borealis[c]	$\log DW = 3.21 \cdot \log TL - 9.11$	µm, µg	Fenaux (1976)
Metridia longa	$AFDW = 0.0101 \cdot PL^{3.0996}$	mm, mg	Mumm (1991)
Eucalanus bungii	$\log DW = 3.091 \cdot \log PL - 0.0026$	µm, µg	Hopcroft et al. (2002)
Large calanoids[d] (♀ > 1.5 mm)	$AFDW = 0.0089 \cdot PL^{3.4119}$	mm, mg	Mumm (1991)
Small calanoids	$\ln AFDW = 2.73 \cdot \ln PL - 16.41$	µm, µg	Chisholm and Rolf (1990)
Conchoecia borealis	$AFDW = 0.0228 \cdot PL^{2.3698}$	mm, mg	Mumm (1991)
Limacina helicina	$AFDW = 0.0390 \cdot PL^{3.5032}$	mm, mg	Mumm (1991)
Eukrohnia hamata	$DW = 0.00032 \cdot PL^{3.00}$	mm, mg	Matthews and Hestad (1977)
Sagitta elegans	$DW = 0.000064 \cdot PL^{3.30}$	mm, mg	Matthews and Hestad (1977)
Aglantha digitale	$DW = 0.00194 \cdot PL^{3.05}$	mm, mg	Matthews and Hestad (1977)

Where necessary, dry weight (DW) was converted to ash-free dry weight (AFDW) assuming 10% ashCarbon was assumed to be 40% of AFDW

[a] Relationship from *Themisto japonica*

[b] Relationship from *Oithona nana*

[c] Relationship from *Fritillaria pellucida*

[d] Relationship from *Chiridius/Gadius* spp.

the eggs and egg sacs remain characteristically identifiable, even after separation from the female.

Results

A total of 24 species of copepods and 13 non-copepod taxa were collected during the cruise (Table 2). In general, most taxa were adequately collected by the 236-µm net, with the notable exception of copepods (and nauplii) whose prosome length was less than 500 µm (Fig. 2). Curiously, after the rapid drop in abundance of copepod size classes to ~1,000 µm prosome length, the abundance spectra remained surprisingly flat. In terms of biomass, the 236-µm net missed relatively little of the total, with the overall spectra characterized by a depressed region between ~600 and 3,000 µm and a peak between 6,000 and 7,000 µm that corresponds to the size of *Calanus hyperboreus* females.

On average, the 53-µm net captured 1,447 copepods m^{-3} (including nauplii), while the 236-µm net captured only 149 m^{-3}. In terms of composition, this difference was due largely to the extrusion of virtually all nauplii, all stages of *Oncaea borealis*, *Microcalanus pygmaeus* below stage C5, and *Oithona similis* below C5. In terms of the non-copepods, the 53-µm net on average captured 43.9 individuals m^{-3}, while the 236-µm net captured 32.6 m^{-3}, with this difference due in part to better retention of larvaceans by the finer mesh. In terms of corresponding biomass, the 53-µm net on average captured 6.7 and 1.4 mg AFDW m^{-3} of copepods and non-copepods, respectively, while the 236-µm net captured 8.39 and 1.3 mg AFDW m^{-3} of copepods and non-copepods, respectively. These biomass differences arise in part because at two stations (al10 and nw1) 53-µm nets were not collected, and also due to the greater accuracy of the larger net in estimating the biomass of larger organisms. Ultimately, these biomass differences are not statistically significant between the nets (t-test and Mann–Whitney Rank). From this point forward we will, therefore, combine the data on all stages of these smaller species taken exclusively from the 53-µm net, while all other data will be employed from the 236-µm net, with the exception of the missing samples for which the 236-µm data will be employed for those species where the bias is less extreme. Once the data from the two nets are combined, total zooplankton biomass ranges from 3.7 to 14.5 mg AFDW m^{-3} (Figs. 3, 4), with a mean of 9.6 mg AFDW m^{-3}. Although calanoid nauplii (average 76 m^{-3}) and non-calanoid nauplii (average 984 m^{-3}) contributed significantly to the community, due to the difficulty in identifying them to the species, and their low biomass (0.02 and 0.08 mg AFDW m^{-3}, respectively), they shall not be considered further.

Of the 24 copepod taxa observed (Table 2), 14 species were present at more than half the stations. Seven of these copepods warrant further attention (Fig. 3) because they dominated in terms of abundance (*Oithona similis*, *Oncaea borealis* and *Microcalanus pygmaeus*) or biomass (*Calanus hyperboreus*, *C. glacialis*, *Paraeuchaeta glacialis* and *Metridia longa*). The cyclopoid *Oithona similis* was the most abundant copepod on average (142 m^{-3}), displaying no trends across the study area. All stages were well represented in the collections, with their readily identifiable egg sacs found loose in the collections at all stations (Table 3). The poecilostomatoid *Oncaea borealis* was the next most abundant taxon throughout the study area (average 129 m^{-3}) at all but
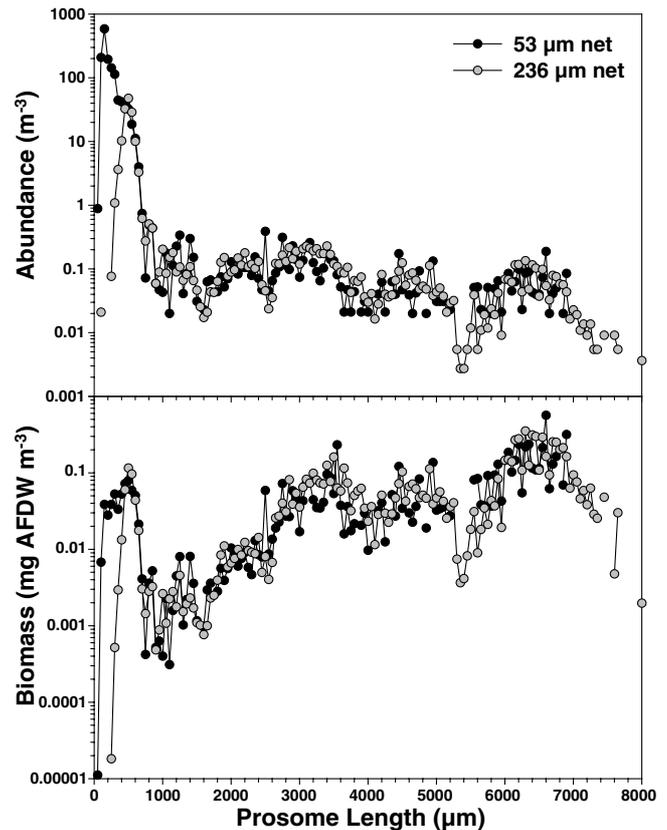
Table 2 Abundance and biomass of taxa collected, averaged over the study region

Taxa	Abundance no. (m^{-3})	Biomass (mg AFDW m^{-3})
Acartia danae	R	–
Calanus hyperboreus	4.61	5.531
Calanus glacialis	2.62	1.232
Chiridius obtusifrons	0.04	0.014
Eucalanus bungii	0.04	0.012
Paraeuchaeta glacialis	0.87	0.748
Gaetanus tenuispinus	R	–
Heterorhabdus norvegicus	0.18	0.001
Heterorhabdus compactus	R	–
Metridia longa	1.96	0.217
Microcalanus pygmaeus	88.56	0.220
Neocalanus cristatus	R	–
Pseudocalanus minutus	2.54	0.015
Pseudocalanus mimus	R	–
Scaphocalanus brevicornis	0.09	0.024
Scolecithricella ovata	R	–
Scolecithricella minor	0.26	0.005
Spinocalanus longicornis	1.00	0.005
Spinocalanus antarcticus	R	–
Oithona similis	142.15	0.152
Oncaea borealis	128.90	0.068
Oncaea notopus	R*	–
Microsetella norvegica	0.52	0.001
Mormonilla sp.	R	–
Calanoid nauplii	76.30	0.019
Non-calanoid nauplii	984.07	0.084
Oikopleura vanhoeffeni	4.05	0.009
Fritillaria borealis typica	32.23	0.005
Limacina helicina	2.89	0.007
Eukrohnia hamata	1.34	0.969
Sagitta elegans	0.14	0.084
Conchoecia borealis	1.97	0.088
Themisto abysorrum	0.07	0.055
Themisto libellula	0.01	0.022
Aglantha digitale	0.13	0.088
Radiolarians	1.35	–
Hymenodora glacialis	R	–
Clione limacina	R	–
Dimophyes arctica	R	–

R Rare taxa, with fewer than two individuals observed; *R** rare relative to congener

Fig. 2 Size spectra of copepods in the Canada Basin during August 2002 in terms of abundance and biomass, as ash-free dry-weight. All size bins are 50 μm wide. Data represent average of all stations

nated, but both tended to be more prevalent over the central Basin, while C3 and younger were most common near and over the Northwind Ridge (Fig. 5). *Calanus glacialis* (average 2.6 m^{-3}, 1.2 mg AFDW m^{-3} —Table 2) ranked second for biomass and tended to be slightly more common at the most shoreward stations. Female *C. glacialis* were not as common as C5 throughout the study area, although like *C. hyperboreus*, C3 and younger were most common near and over the Northwind Ridge (Fig. 5). Like the calanids, *Metrida longa* (average 2.0 m^{-3}, 0.2 mg AFDW m^{-3} —Table 2) showed no spatial trends in terms of abundance, but the biomass was higher over the Northwind Ridge. This was related to an increase from east to west in average developmental stage (Fig. 5). Despite lower abundances, *Paraeuchaeta glacialis* (average 0.9 m^{-3}, 0.7 mg AFDW m^{-3}—Table 2) ranked third in terms of biomass. The numbers were too low and variable to establish an across-region stage distribution, but all stages were present (Table 3), and a number of females were observed carrying egg sacs. Notably, *Microcalanus pygmaeus* tied *Metrida longa* in terms of biomass, and both were followed closely by *Oithona similis*.

Nine species of non-copepods warrant attention (Fig. 4) because of their abundance (*Oikopleura vanhoeffeni*, *Fritillaria borealis*, *Limacina helicina*) or biomass (*Eukrohnia hamata*, *Sagitta elegans*, *Conchoecia*

the shallowest stations on the Northwind Ridge (i.e. na5, nw1, nw5). Its absolute numbers were greatest over the deepest waters of the basin. Although this species was not staged routinely, lengths suggest a mix of all developmental stages. The calanoid *Microcalanus pygmaeus* was third in abundance (average 89 m^{-3}) and, like *Oncaea*, its numbers tended to be greater over the deeper parts of the study area. All stages were present in the samples, but notably adults were relatively scarce, with C4 and C5 dominating at most stations (Fig. 5). Despite their high abundances, these three "micro"-copepods contributed relatively little to biomass (Fig. 2) due to their size even though they rank fifth through seventh in terms of copepod biomass.
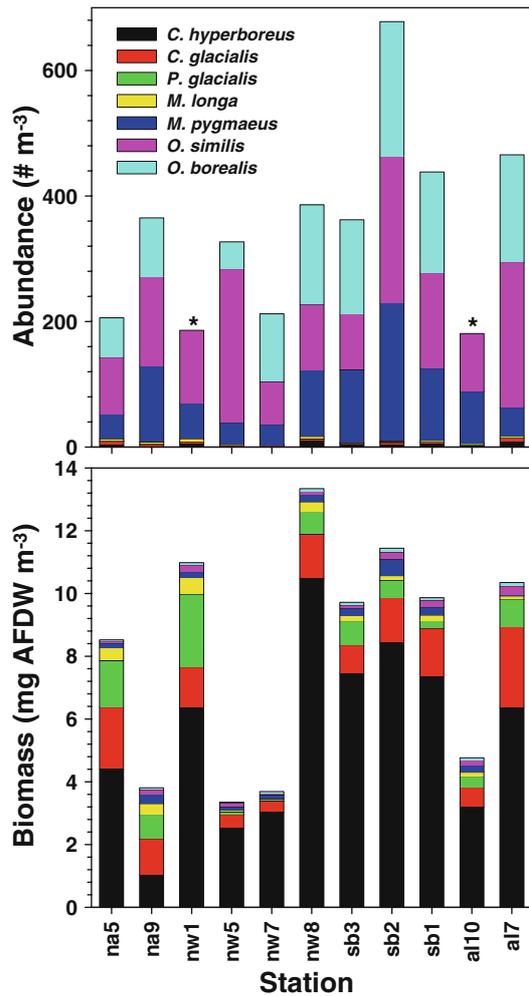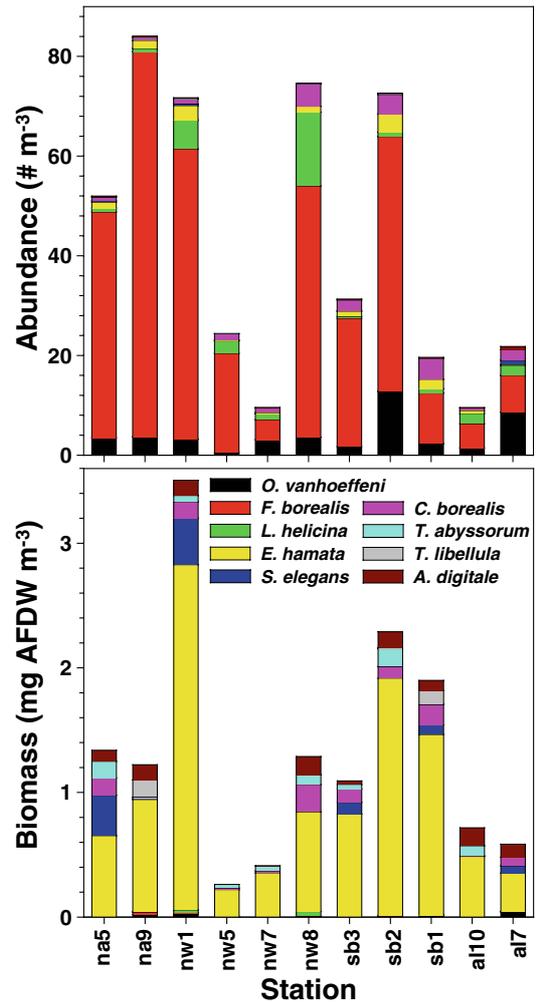
In contrast, *Calanus hyperboreus* (average 4.6 m^{-3}, 5.5 mg AFDW m^{-3} —Table 2) represented the majority of the copepod community biomass. There were no spatial trends in its abundance or biomass (Fig. 3). Females, and to a lesser extent C5s, generally predomi-

Fig. 3 Abundance and biomass, as ash-free dry-weight, of the dominant copepod taxa (excluding nauplii) in the Canada Basin, August 2002. *Asterisks* indicate stations for which the 53-μm mesh collection was not available

Fig. 4 Abundance and biomass, as ash-free dry-weight, of the dominant non-copepod taxa in the Canada Basin, August 2002

borealis, *Themisto abysorrum*, *Themisto libellula*, *Aglantha digitale*). The larvacean *F. borealis* clearly dominated the abundance of non-copepods at all stations, but contributed little to biomass due to its small size (mean trunk length 400–500 μm). The larvacean *O. vanhoeffeni* was present as two distinct size classes, predominately juveniles with trunks < 700 μm, and limited numbers of individuals of 2–4 mm trunk length. Unlike *F. borealis*, which frequently had well-developed gonads, gonads in even the largest *O. vanhoeffeni* were virtually undeveloped (see Shiga 1976). The pteropod *L. helicina* was present at all stations only as small juveniles (< 1 mm). The chaetognath *E. hamata* dominated the non-copepod biomass at all stations, with notable contribution from *S. elegans* at the two shallowest stations on the Northwind Ridge. The majority of the chaetognaths were larger than 10 mm body length, and on several occasions female *E. hamata* were observed to have broods carried in their marsupium. Similarly, the ostracod *C. borealis* (0.6–3 mm carapace) was found at all stations in low numbers, and on several occasions with a clutch of large eggs

incubated within the valves of the larger individuals. Both the amphipods *T. abysorrum* and *T. libellula* were more variable in terms of presence and size (3–10 mm), with the former being more common. The reproductive condition could not be judged for either species because of the limited number of animals and the potential liberation of juveniles within the marsupium upon preservation. *A. digitale* (3–13 mm axial length) was the only cnidarian found in the nets, and it occurred at all but one of the stations. Gonadal development was variable, but never extensive in this hydromedusae.

Discussion

In general, the species observed in this study are simply characteristic of those reported by other studies working in the deeper waters of the Arctic (e.g. Mumm 1991; Kosobokova et al. 1998; Kosobokova and Hirche 2000; Auel and Hagen 2002). Consistent with these studies, *Calanus* species dominate the biomass, followed by the *Metridia longa* and then *Paraeuchaeta* species, while

smaller species dominate numerically. Furthermore, the number of unique species observed, and their relative abundance/biomass (accounting for mesh-size biases), are also relatively similar to those described for the upper 100 m by taxonomically detailed studies (Mumm 1991; Kosobokova et al. 1998; Kosobokova and Hirche 2000; Auel and Hagen 2002) in deeper waters. The most

notable differences in species composition between those studies that emphasize the Eurasian Basins and this study is the absence of the Atlantic *Calanus fimarchicus*, which is not normally present in the Amerasian Basins (e.g. Kosobokova 1982; Smith and Schnack-Schiel 1990). Reciprocally, single individuals of the Pacific *Eucalanus bungii* and *Neocalanus cristatus* were not

Table 3 Percentage at each copepodite developmental stage for the dominant copepod species averaged across the study region

Species	C1	C2	C3	C4	C5	C6f	C6m
Calanus hyperboreus	3	2	15	16	26	38	0
Calanus glacialis	4	4	4	9	54	25	0
Paraeuchaeta glacialis	5	15	25	15	30	11	0
Metrida longa	17	8	6	9	24	36	0
Pseudocalanus minutus	0	9	15	21	34	12	0
Microcalanus pygmaeus	13	12	16	33	22	4	1
Oithona similis	31	19	18	10	5	15	1

Fig. 5 Stage frequency distribution of dominant copepods in the Canada Basin, August 2002
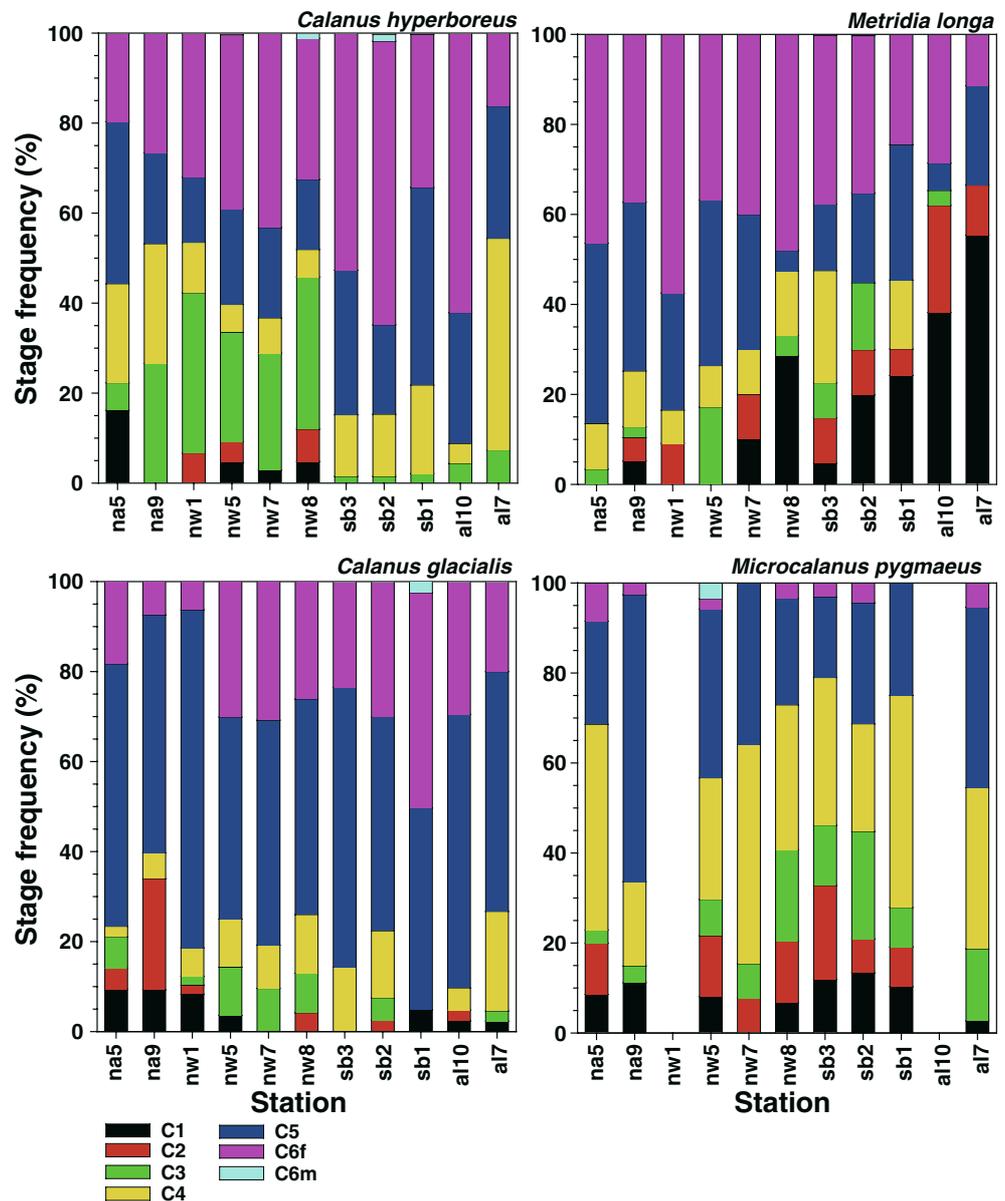
normally observed in the Eurasian Basins but were found as far into the Canada Basin as sb2 and sb1, respectively.

It is much harder to compare the composition, abundance and biomass of the non-copepods because they are not often reported in detail, or the sampling depth strata are not directly comparable to this study. Nonetheless, other studies in Arctic Basins have indicated that *Eukrohnia hamata* dominates the biomass of the non-copepods, contributing 7–18% of the epipelagic biomass (Kosobokova et al. 1998; Kosobokova and Hirche 2000). It is replaced by the neritic *Sagitta elegans* as one moves into shallower waters (Kosobokova et al. 1998). This study does indicate a higher abundance of larvaceans than previously reported for the basins, although this may be due to the use of the 53-µm net that sampled *Fritillaria borealis* relatively undamaged. At times when larger *Oikopleura vanhoeffeni* are common, larvacean biomass may be relatively more important in the Basins than observed here (e.g. Kosobokova and Hirche 2000). Interestingly, while *F. borealis* populations appeared to be reproductively active, *O. vanhoeffeni* appeared to exist as two distinct cohorts, the larger of which appeared to be in an arrested reproductive development that is as yet undocumented for this group. The standard growth mode in larvaceans involves simultaneous development of both somatic and reproductive tissue (Fenaux 1998), such that gonads are extremely obvious in larger individuals. Aside from basic information on abundance and biomass (e.g. Kosobokova et al. 1998; Kosobokova and Hirche 2000; Auel and Hagen 2002), and occasionally detailed information on size–structure (Mumm 1991; Richter 1994), information on the reproductive patterns of most of these non-copepod groups is absent from the literature.

Overall, the abundance and biomass of most metazoan zooplankton species, and the community in aggregate, was surprisingly stable over the entire region of the study (>1,000 km), and similar to that of a number of other deeper-water Arctic studies previously cited. Nonetheless, there exists a significant range in the observations between these studies, and given the concerns about climate change impacts in the Arctic, it is worth considering if these are regional, year-to-year, or systematic differences. Given that the biomass peak may be relatively brief in the Arctic (e.g. Pautzke 1979), and that species and biomass can be extremely stratified (e.g. Kosobokova 1982; Kosobokova and Hirche 2000; Auel and Hagen 2002; Ashjian et al. 2003), it becomes critical that inter-study comparisons be made from the same depth intervals and the same seasonal periods. Although mesh size can also represent a significant bias in biomass estimates in most ecosystems (Hopcroft et al. 2001), the bias resulting from differences in mesh sizes below 236 µm is relatively small in the central Arctic, and therefore not of major consequence in comparing studies. Notably, the values from this study are three to fourfold lower than those observed in the upper 100 m during August 1994 on, and north of, the Chukchi Plateau (Thibault et al. 1999), and those from August 1998 on the Chukchi Plateau (Ashjian et al. 2003). Despite this, the stage distributions of the dominant copepods are very similar to those observed in August 1998 (Ashjian et al. 2003). The biomass values reported in this study are, however, often very similar to the central basin values reported for August 1995 (Mumm et al. 1998), and the summer of 1975 (Kosobokova 1982; Kosobokova and Hirche 2000). Like all of these more contemporary studies, historical biomass values of 1 mg DW m^{-3} reported for the Canada Basin in August 1966 (Hopkins 1969) and August 1975 (Pautzke 1979) are not supported. Both these latter ice-camp studies surveyed a region similar to those of this study. Notably, in both cases, unmetered nets of 62–73 µm were employed, and overestimation of the volume filtered could account for their low numbers. Interestingly, when unmetered 223-µm mesh nets were employed during August 1970–1973, the biomass was estimated as 2–8 mg DW m^{-3} (Pautzke 1979) overlapping the values observed within this study. Without a more standardized set of locations, more regular occupation of them and more standardized methods, it would be impossible to disentangle the effect of location and year.

What has not been previously well established is the actual contribution of these smaller species to community biomass because a substantial proportion, if not the bulk, of these species has been extruded through the collection nets. Pautzke (1979) reached conclusions similar to those of this study, in terms of which stages of *Microcalanus*, *Oncaea* and *Oithona* were missed by his 223-µm mesh compared to the 62- or 73-µm nets, but did not estimate the impact on biomass. Our data, which collected even the smallest metazoans, support the longstanding belief that during Arctic summer, the biomass of these smaller taxa in the epipelagic realm is trivial in comparison to the larger taxa. This appears to be a feature unique for Arctic waters, because in most other pelagic systems zooplankton biomass tends to decline with increasing size (Quinones et al. 2003, and references therein). This pattern appears to hold even when restricted to just the copepods for both tropical and temperate waters (Hopcroft et al. 2001). It is therefore remarkable that over deep waters in the Arctic, abundance in the upper 100 m remains relatively flat across much of the spectra, while biomass actually increases with size along the spectra. The curious depression in the biomass spectra between 600 and 3,000 µm is, however, likely not a permanent or consistent feature of Arctic waters, because earlier in the year it would be better occupied by earlier stages of larger species. In coastal waters, this gap would also be filled by medium-bodied species such as *Pseudocalanus* (Conover and Huntley 1991), and perhaps by a greater contribution of *Metridia longa* (Conover and Huntley 1991; Ashjian et al. 2003), which although generally characterized as a strong diel migrator, is commonly observed during summer in the Arctic's upper 100 m (Pautzke 1979; Kosobokova and Hirche 2000; Auel and Hagen 2002).

Seasonally, the *Calanus* species will migrate from the upper mixed layer to enter diapause at depth, and during such times *Microcalanus*, *Oncaea* and *Oithona* will contribute more significantly to the biomass spectra. These small species continue active, albeit reduced, growth and recruitment outside of the summer period, as suggested by their stage distribution in this and other studies (e.g. Pautzke 1979; Ashjian et al. 2003). Thus, some of our impression of biomass and production patterns in the Arctic may be biased by emphasis on the late summer periods. It would therefore be interesting to see what a seasonally averaged size spectra of biomass and production actually looks like during future efforts.

Elsewhere, it has been argued that the biomass present in these smaller zooplankton size fractions may be misleading because smaller animals tend to grow faster than larger ones (Hirst and Lampitt 1998; Hirst and Bunker 2003). To explore such a premise in the Arctic, it is useful to undertake a crude estimation of the growth rates and productivity of the *Calanus* species that dominate the biomass, and with *Oithona similis* that dominates numerically. The simplest approach is to take the weight of the egg and the adult female and the typical generation time it takes to move between the two (Huntley and Lopez 1992), ignoring the fact that some species undergo diapause periods. *C. hyperboreus* appears to have a 3- to 4-year life cycle (Conover 1967; Hirche 1997), has eggs that weigh 1.4 µg DW (Conover 1962) and are up to 5 mg DW as adult females in the Canada Basin (Ashjian et al. 2003). In a genus such as *Calanus*, where diapause occupies a large proportion of the year, the growth rate will be much greater during the active periods, and zero (or negative) during diapause. However, we can calculate an average instantaneous growth rate over their lifetime of $\sim$0.006 day^{-1} (i.e. 0.6% day^{-1}), which compares nicely to an independent specific egg production rate estimate of 0.7% day^{-1} (Hirche and Niehoff 1996).

Oithona similis eggs are $\sim$60 µm in diameter (Nielsen et al. 2002), so assuming an egg density of 0.14 pg C µm^{-3} (Kiørboe and Sabatini 1994), and carbon as 40% AFDW, the eggs weigh 0.04 µg AFDW, while females in this study would weigh 2.6 µg AFDW on average. The generation lengths of *Oithona*, *Oncaea* and *Microcalanus* in the Arctic are not well established, with the suggestion from field observations being that only one generation occurs per year (McLaren 1969; Kosobokova 1980). The broad representation of all stages, including females carrying sacs and high numbers of nauplii, in this and other studies (e.g. Ashjian et al. 2003) is, however, suggestive of multiple overlapping generations per year. If we assume that as many as three generations occur per year, the instantaneous growth rate would be $\sim$0.035 day^{-1} for *O. similis*. This also agrees with the maximum reproductive rate of 7.1% at 15°C (Hirst and Bunker 2003), which corrected by his Q_{10} of 1.49 for sac spawning adults, would predict a rate of 0.039 day^{-1} at 0°C, although caution is warranted in extrapolating his relationships below 5°C. Thus, growth rates in *O. similis* could be approximately sixfold greater than that those of *C. hyperboreus*.

Assuming that these crude estimates of growth rate are correct, this raises the aggregate importance of the three smallest species from $\sim$5% of the total copepod biomass to $\sim$25% of the total copepod production. Although the production by the *Calanus* species would still predominate, the production of these smaller genera (i.e. *Microcalanus*, *Oncaea* and *Oithona*) would be worth serious consideration. If such high productivity by small species is in fact true, it implies that these small species must be under intense predatory pressure, which keeps them from making more substantial contributions to community biomass as is common in most other oceanic regions. This would help explain the unusual biomass size spectra we have observed. Alternatively, the growth in small species is not disproportionately faster than larger species, and their importance in terms of both biomass and production is therefore not significant. This suggests that future efforts would be well spent determining the true rates of growth and development of these smaller Arctic species to distinguish between these possibilities.

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