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ORIGINAL PAPER

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Integrated abundance and biomass of sympagic meiofauna in Arctic and Antarctic pack ice

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Abstract The abundance and biomass of sympagic meiofauna were studied during three cruises to the Antarctic and one summer expedition to the central Arctic Ocean. Ice samples were collected by ice coring and algal pigment concentrations and meiofauna abundances were determined for entire cores. Median meiofauna abundances for the expeditions ranged from 4.4 to 139.5×10^3 organisms m^{-2} in Antarctic sea ice and accounted for 40.6×10^3 organisms m^{-2} in Arctic multiyear sea ice. While most taxa (ciliates, foraminifers, turbellarians, crustaceans) were common in both Arctic and Antarctic sea ice, nematodes and rotifers occurred only in the Arctic. Based on the calculated biomass, the potential meiofauna ingestion rates were determined by applying an allometric model. For both hemispheres, daily and yearly potential ingestion rates were below the production values of the ice algal communities, pointing towards non-limited feeding conditions for ice meiofauna year-round.

Introduction

As the importance of polar oceans to global change is recognized, the role of sea-ice associated (=sympagic) organisms in Arctic and Antarctic marine ecosystems is receiving increased attention (e.g., Arrigo et al. 1997; Gosselin et al. 1997; Legendre et al. 1992). It is known, for example, that ice algae contribute up to 57% of the total primary production in the central Arctic (Gosselin et al. 1997). This accumulated algal biomass is consumed by proto- and metazoans, living permanently (e.g. Arctic under-ice amphipods, Werner 1997) or temporarily (e.g. Antarctic krill *Euphausia superba*, Marschall 1988) in the ice or at the ice-water interface. Upon ice melt, the released algae may enhance phytoplankton growth (seeding hypothesis; Haecky et al. 1998) or sink (directly or mediated via faecal pellets) to the sea floor (e.g. Carey 1987) to sustain the benthos (Michel et al. 1996, 1997).

Ice algal growth dynamics has been studied in detail and now allows estimations of their production based on remote sensing data (Arrigo et al. 1997). Though knowledge of the occurrence of heterotrophic organisms inside the sea ice can be traced back to the first scientific expeditions to polar seas (e.g. Nansen 1906), their potential role in controlling algal production has been widely neglected (e.g. Meguro et al. 1967). Instead, physical and chemical parameters were thought to be of overwhelming importance in structuring and determining algal growth dynamics (e.g., Ackley and Sullivan 1994; Cota and Horne 1989; Cota et al. 1987; Eicken 1992) and were used to explain the general vertical and horizontal patchiness of Arctic and Antarctic ice biota. For example, variations in the brine salinity and temperature, snow thickness or fresh water flushing largely determine the accumulation of algal biomass (Palmisano and Garrison 1993; Smith et al. 1988) in certain ice layers characterized by differences in diversity, biomass and activity.

Previous studies on eucaryotic sympagic heterotrophs focused primarily on the taxonomy of proto- (e.g. Agatha et al. 1990, 1993; Corliss and Snyder 1986; Petz 1994; Thomsen et al. 1997) and metazoa (e.g. Chengalath 1985; Dahms and Dieckmann 1987; Dahms and Schminke 1992; Riemann and Sime-Ngando 1997; Tschesunov and Riemann 1995) and on their physiological adaptations to variable ice parameters (e.g. Dahms et al. 1990; Dieckmann et al. 1991; Gradinger and Schnack-Schiel 1998; Lee and Fenchel 1972; Spindler 1996). Detailed investigations on the composition of

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the in-ice metazoan communities are available mainly for Arctic locations (e.g. Cross 1982; Gradinger et al. 1991; Grainger et al. 1985; Kern and Carey 1983), while studies in Antarctica focused entirely on a few protozoan and crustacean taxa (e.g. Schnack-Schiel et al. 1998; Spindler et al. 1990; Stoecker et al. 1997, 1998; Tanimura et al. 1996; Thomsen et al. 1997). Consequently, knowledge of the occurrence of ice meiofauna (here defined as heterotrophs >20 µm) and their potential contribution to the carbon flux within polar sea ice is less than comprehensive. Direct measurements of grazing activities by protozoans and metazoans in sea ice do not exist at present. Vezina et al. (1997) incorporated protozoan activity (flagellates and ciliates) into a microbial carbon flow model for Arctic first-year sea ice; however, the contribution of metazoans was neglected although they may occur in considerable concentrations in this ice habitat (e.g. Riemann and Sime-Ngando 1997). The aim of this study was to estimate the potential meiofauna grazing activity in Arctic and Antarctic pack ice. Based on the biomass and composition of the Arctic and Antarctic ice meiofauna, their potential influence on ice algal accumulation was calculated on daily and yearly bases using allometric equations.

Materials and methods

Sampling was carried out during three expeditions (Fig. 1) with RV *Polarstern* to the Weddell Sea, Antarctica (ANT 8/2: 6 September to 30 October 1989; ANT 9/3: 3 January to 28 March 1991; ANT 10/3: 27 March to 19 May 1992) and one expedition to the central Arctic Ocean (ARK 8/3: 1 August to 15 October 1991). Identical techniques were used for the determination of algal biomass and meiofauna composition during all cruises over the entire ice thickness. At each station two ice cores, having either 7.5 or 10 cm diameter, were taken. Ice cores were immediately cut into segments of 1–20 cm length and placed into cleaned polyethylene jars until further processing. Samples from the first core (for algal pigment determination) were melted in the dark at about 4°C, the volume then determined, and the samples were filtered onto Whatman GF/F filters. Algal pigments were extracted in 90% acetone and determined fluorometrically (Evans et al. 1987). The ice segments of the second core (for meiofauna abundance determination) were placed in larger containers and melted after addition of 200 ml 0.2 µm pre-filtered seawater per 1 cm core length (Garrison and Buck 1986). After complete melting, the volume was determined and ice meiofauna was concentrated over 20-µm gauze. Taxa were identified and organisms counted alive under a dissecting microscope immediately afterwards. During the expedition ANT 10/3, ciliates were not counted although they occurred frequently in the samples. Biomass of proto- and metazoans was estimated using individual biomass estimates of Friedrich (1997; based on computer-aided volume calculation of live video-recorded specimens) or by converting organism volume to carbon with a ratio of 0.11 pg C μm^{-3} (HELCOM 1989) (Table 1). Potential ingestion rates of the ice meiofauna were calculated using the allometric mass specific equations of Moloney and Field (1989) and assuming an ice temperature of −1°C and a Q_{10} value of 2 (typical for plankton metazoans): $I_{\max} = 63 \cdot M^{-0.25} \cdot 0.23326$ with $I_{\max}(\mathrm{day}^{-1})$ as daily mass-specific maximum potential ingestion rate and M (pg C, Table 1) as body mass of one organism.

Results

Ice thickness and algal pigment concentration

The ice cores taken for meiofauna analysis had thicknesses between 0.2 and 6.0 m (Fig. 2a). The ice thickness of Antarctic pack ice was significantly lower during ANT 8/2 compared to that sampled in summer (ANT 9/3: U-test $P < 0.005$) and autumn (ANT 10/3: U-test $P < 0.05$) while no difference existed between the summer and autumn data. The integrated algal biomass ranged from 0.1 to 72.6 mg chl a m^{-2} (Fig. 2b). In late winter/early spring (ANT 8/2), the pigment concentration had a median value of 2.5 mg chl a m^{-2}, which was significantly below the summer ($\mathrm{median}_{\mathrm{ANT\ 9/3}} =$ 22.3 mg chl a m^{-2}; U-test $P < 0.0001$) and autumn values ($\mathrm{median}_{\mathrm{ANT\ 10/3}} = 34.2$ mg chl a m^{-2}; U-test $P < 0.005$). The integrated pigment concentration in the Arctic sea ice in summer 1991 was similar to the ANT 8/2 data with a median of 1.4 mg chl a m^{-2}. Maximum Arctic values were low compared to Antarctic observations.

Abundance of Antarctic sea-ice meiofauna

The integrated abundances of the sympagic meiofauna, including ciliates, foraminifera and metazoans, varied between stations and expeditions (Fig. 3). In Antarctic sea ice, total abundances ranged between 0 and 320×10^3 organisms m^{-2}. Lowest median concentrations were observed during ANT 8/2 (median = 4.4×10^3 organisms m^{-2} ice) with protists (foraminifera and ciliates) as the largest fraction (Fig. 4; 65%). Copepods contributed only 12% to the total abundance, of which 47% were nauplii. Abundances increased during the summer (median = 14.5×10^3 organisms m^{-2} ice) and the relative contribution of protists decreased. Copepods were the dominant metazoans (39% of entire meiofauna) with a large fraction of nauplii (54% of all copepods). In autumn (ANT 10/3), a significantly higher concentration of ice meiofauna (median = 139.5×10^3 organisms m^{-2} ice) occurred compared to ANT 8/2 (U-test; $P < 0.0001$) and ANT 9/3 (U-test; $P < 0.001$), even though ciliates were not counted during this cruise. Foraminifera (44%) and copepods (29%, of which 50% were nauplii) were the most abundant taxa. Besides protists and copepods, turbellarians were regularly observed in nearly all ice cores. Their mean contribution to total abundance varied between 11% (ANT 8/2) and 27% (ANT 10/3).

Biomass and ingestion rates of Antarctic meiofauna

The integrated meiofaunal biomass in Antarctic sea ice ranged from 0 to 118.2 mg C m^{-2} ice (Fig. 3). The biomass during ANT 10/3 (median = 24.3 mg C m^{-2}) was significantly higher than during the other two

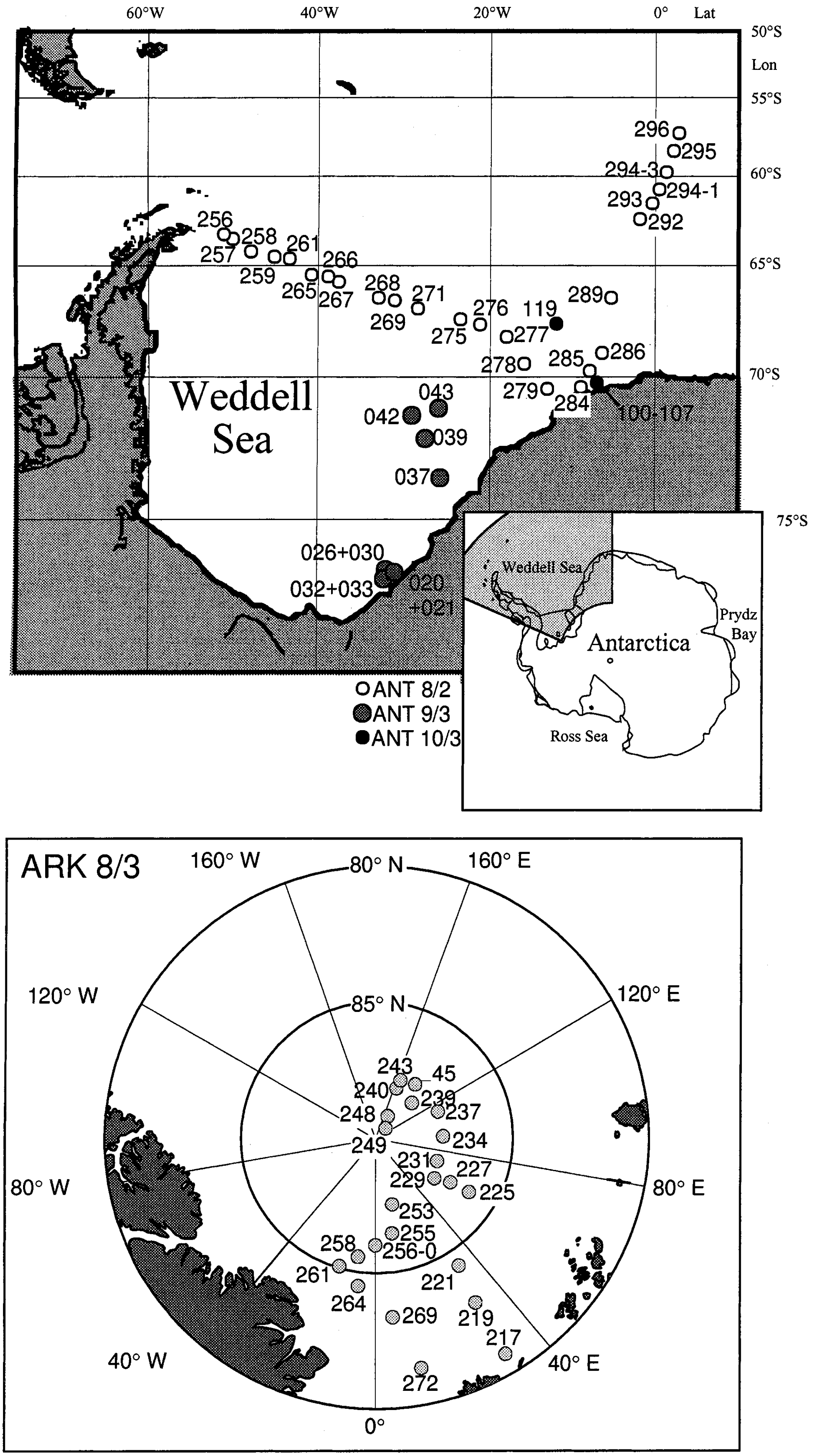

Fig. 1 Station maps for the Arctic and Antarctic expeditions (*station number* = day of the year)

cruises (ANT 8/2: 0.4 mg C m^{-2}; *U*-test; $P < 0.005$; ANT 9/3: 1.1 mg C m^{-2}; *U*-test: $P < 0.05$). Turbellaria contributed on average between 25 and 41% of the total mean meiofauna biomass of each expedition, crustaceans between 35 and 62% and foraminiferans between 5.5 and 28.3% (Fig. 4). Calculated potential ingestion rates (Fig. 3) varied between 0 and 58 mg C m^{-2} day^{-1} with a significantly higher median during ANT 10/3 (8.2 mg C m^{-2} day^{-1}) compared to ANT 8/2 (0.3 mg C m^{-2} day^{-1}; $P < 0.005$) and ANT 9/3 (1.0 mg C m^{-2} day^{-1}; $P < 0.05$) (Fig. 3).

Table 1 Individual biomass estimates for Arctic and Antarctic meiofauna

Taxon	Biomass (µg C $specimen^{-1}$)	Comments
Rotatoria	0.023	See Friedrich (1997)
Nematoda	0.13	See Friedrich (1997)
Ciliata	0.011	See Friedrich (1997)
Acoela	0.39	See Friedrich (1997)
Copepoda	0.60	See Friedrich (1997)
Nauplii	0.02	See Friedrich (1997)
Neogloboquadrina pachyderma	0.031	Own estimate, based on cell volume

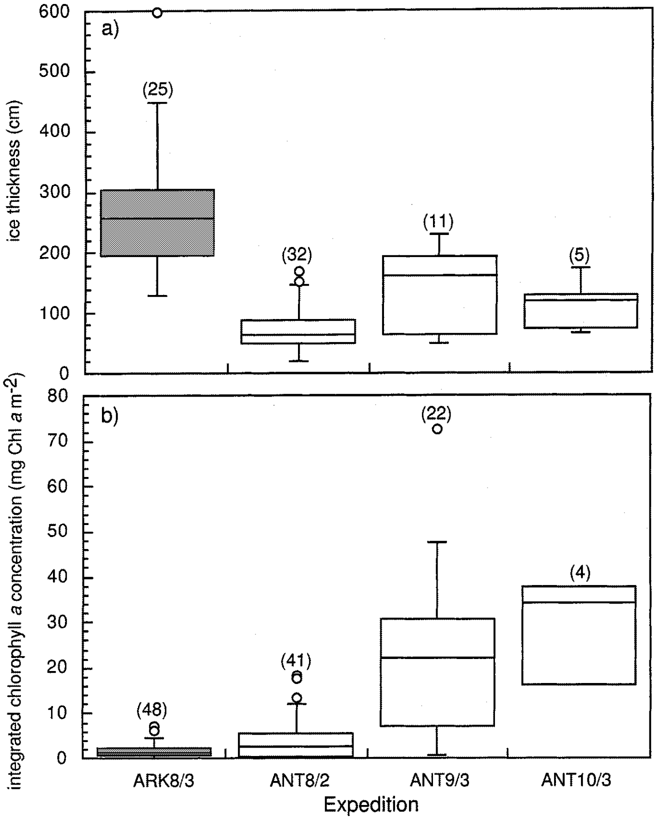

Fig. 2 Box plots of **a** the ice thickness of the meiofauna ice cores, and **b** integrated chlorophyll *a* concentrations in Arctic and Antarctic sea ice. In the box plots, the total data range and the 25–75% quartile range (*box*) are shown. Single data points are marked as *outliers*, when they are above/below a value of $V = UQ + 1.5 \cdot IQD$ or $V = LQ - 1.5 \cdot IQD$ (LQ = lower quartile, UQ = upper quartile, IQD = interquartile distance)

Abundance of Arctic sea-ice meiofauna

The integrated abundance of the sea-ice meiofauna ranged from 1.3 to 221.3×10^3 organisms m^{-2} ice (Fig. 3). Rotifers and nematodes were the only groups that were exclusive to Arctic sea ice. All other taxa were found in both polar areas (except for tintinnids, which were only seen during ANT 9/3). The most abundant taxa (Fig. 4) were ciliates (53%), followed by nematodes (15%). Crustacea contributed only 5% to total abundance.

Biomass and ingestion rates of Arctic sea-ice meiofauna

The integrated biomass ranged between <0.1 and 7.4 mg C m^{-2} (median = 3.0 mg C m^{-2}). Most important contributors were acoel turbellarians (27%), followed by crustaceans (22%), nematodes (20%) and ciliates (15%). Potential ingestion rates varied between <0.1 to 7.9 mg C m^{-2} day^{-1} (median = 1.8 mg C m^{-2} day^{-1}). Largest fractions were ingested by protists (36%), turbellarians (22%), nematodes (20%) and crustaceans (17%).

Relation between algal biomass and meiofauna abundance, biomass and ingestion rates

The non-parametric Spearman rank correlation test revealed significant positive correlations between the integrated algal biomass (mg chl *a* m^{-2}) and meiofauna abundance $\rho = 0.3$; $P < 0.05$), biomass ($\rho = 0.4$; $P < 0.01$) and potential ingestion ($\rho = 0.3$; $P < 0.01$) for all cruises. For the Arctic data, significant relationships were found between chlorophyll *a* concentration and meiofauna carbon biomass and potential ingestion, respectively ($\rho = 0.5$; $P < 0.05$ each). The Antarctic ice algal biomass was significantly correlated with meiofauna abundance ($\rho = 0.5$; $P < 0.01$) and biomass ($\rho = 0.4$; $P < 0.05$).

Discussion

The abundance of sympagic meiofauna has been studied mainly in the Arctic (Table 2). A comparison with these Arctic studies is difficult due to methodological differences, which hinder quantitative comparisons of the published data. Ice was sampled using different techniques, from brine sampling (Garrison and Buck 1991), sub-ice coring and pumping (Grainger 1991) to coring

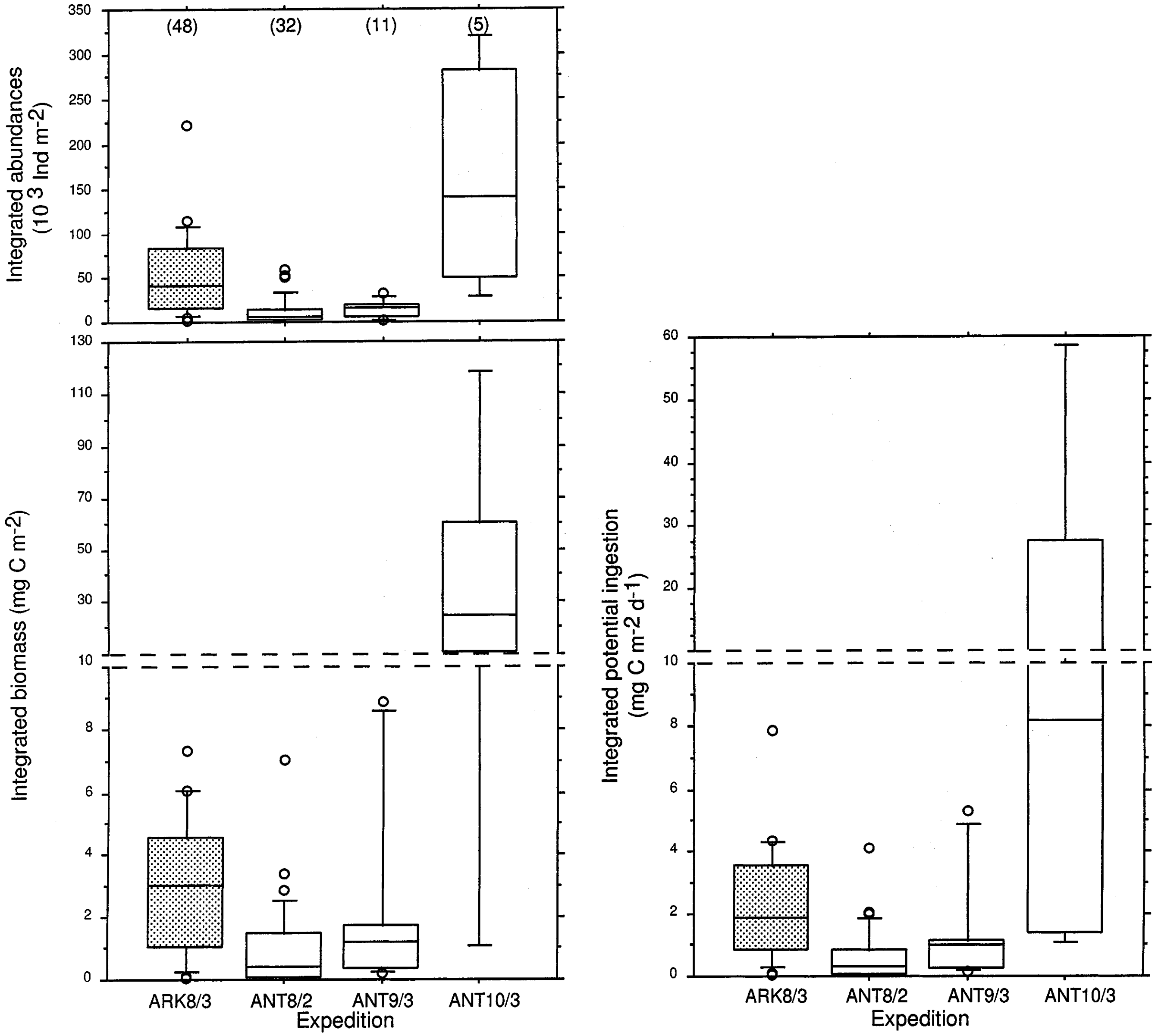

Fig. 3 Box plots of the integrated meiofauna abundances, biomass and potential ingestion rates. For explanation of box plots see Fig. 2

from the surface (this study). In addition, some studies only focused on certain layers of the ice cores, in the Arctic mainly on the bottom few centimetres, despite the fact that ice meiofauna is also found in the interior parts of Arctic sea ice (Friedrich 1997). Therefore sampling of only the bottom layers does not adequately provide data on integrated sympagic abundances and biomass. Further artefacts were introduced by direct melting of the ice, as it was used in many studies (see Gradinger et al. 1991). The use of salinity-buffered melting techniques led also, in coastal locations, to high abundances of ciliates (Sime-Ngando et al. 1997), similar to my observations. Therefore I assume that the low contribution of ciliates from many Arctic locations is an artefact caused by inadequate melting techniques (Table 2). Bearing in mind these limitations, three general trends are shown by comparing the compiled data.

Crustacea, ciliates and acoel turbellarians live in sea ice of both polar regions, while nematodes and rotifers occur only in the Arctic. To my knowledge, planktic nematodes are not described from polar seas, while rotifers are common in Arctic plankton (e.g. DeSmet 1995), but are probably absent in the Antarctic (Knox 1994). In contrast to the likely planktic origin of rotifers, a different hypothesis has been formulated for nematodes by Tschesunov and Riemann (1995), who described taxa which lived either in sediment or in the baleen of whales as possible ancestors of endemic ice nematodes. Until now, foraminiferans were considered to be regular components only of Antarctic sea-ice biota (Spindler 1990), where the polar species *Neogloboquadrina pachyderma* is incorporated into the developing ice sheet and may grow inside the brine channel network

Fig. 4 Relative contribution of ice meiofauna taxa to integrated abundance, biomass and potential ingestion rates

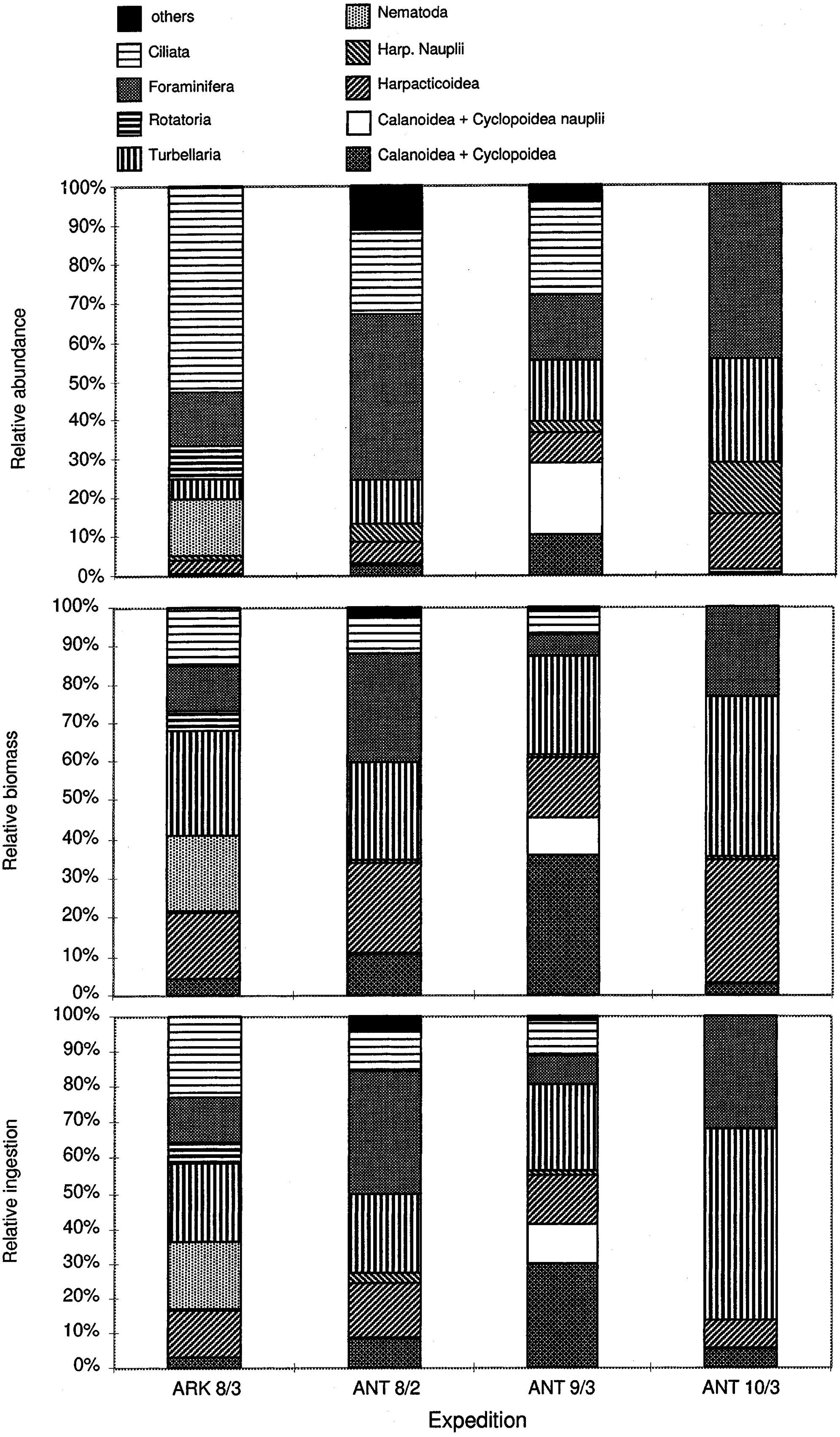

Table 2 Relative abundances (%) of ciliates and metazoa in sea ice from different Arctic and Antarctic areas. Others include: harpacticoids, copepods, polychaetes, amphipods. Authors in *italics* indicate direct melt of the ice cores

Author/expedition	Region	Foraminifers	Ciliates	Nematodes	Turbellarians	Rotifers	Nauplii	Others
Arctic								
Cross (*1982*)	Pond Inlet	–	–	59	–	–	41	
Carey and Montagna (*1982*)	Stefanson Sound	–	–	77	–	–	–	23
Kern and Carey (*1983*)	Beaufort Sea	–	–	47	16	–	–	37
Grainger et al. (*1985*)	Frobisher Bay	–	< 1	51	-	1	45	2
Gradinger et al. (1991)	Fram Strait (field N)	0	29	5	51	< 1	13	1
ARK 8/3	Arctic Ocean	14	53	15	5	9	1	4
Antarctic								
ANT8/2	Weddell Sea	43	22	0	11	0	5	19
ANT9/3	Weddell Sea	17	24	0	16	0	21	21
ANT10/3	Weddell Sea	44	No data	0	27	0	14	15

(Dieckmann et al. 1991; Spindler et al. 1990). The frequent occurrence of *N. pachyderma* during the ARK 8/3 cruise is a rare observation. During previous (ARK 5/1: Gradinger et al. 1991) and later cruises (ARK 10/1: Friedrich 1997) to the Greenland or Laptev Seas (Friedrich 1997), no living or dead foraminiferans were found in Arctic sea ice using identical techniques. Reasons for the absence of sympagic Arctic foraminiferans are probably related to the formation of Arctic sea ice in coastal shallow sea areas with low salinities on the Russian shelves, which makes the incorporation of oceanic foraminiferans unlikely. Although interannual variability in the composition and abundance of ice biota can be expected and is documented for coastal locations (Grainger et al. 1985), the findings of large numbers of foraminiferans during ARK 8/3 cannot be explained.

Immigration of larvae of benthic taxa (e.g. gastropods or polychaetes), which locally dominate coastal shallow water fast-ice meiofauna in the Arctic (Carey 1992), was not observed in either Arctic or Antarctic pack ice. However, immigration of larvae of pelagic calanoid copepods is common in Antarctica (Kurbjeweit et al. 1993; Schnack-Schiel et al. 1998; Tanimura et al. 1996) and contributes to the high abundance of nauplii in the pack ice. Studies of the reproduction of sympagic harpacticoid copepods, carried out in both in the Arctic (Carey 1992) and the Antarctic (Bergmans et al. 1991), revealed that these sympagic metazoans are capable of producing several generations per year with reproduction uninterrupted during winter. This agrees with my observed high nauplii concentrations during all expeditions.

The potential grazing pressure of sea-ice meiofauna is low compared to daily primary production rates during the polar summer in both hemispheres. Median potential grazing rates in the central Arctic were below 2 mg C m^{-2} day^{-1}, similar to previous observations in pack ice of the Greenland Sea (Gradinger et al., in press). This value is, however, at least 1 order of magnitude less than the mean primary production estimates of 57 mg C m^{-2} day^{-1} (Gosselin et al. 1997) and 83 mg C m^{-2} day^{-1} (SubbaRao and Platt 1984) of Arctic sympagic algae. The same holds true for Antarctic sea ice, where primary production measurements range between 0.5 and 240 mg C m^{-2} day^{-1} (Knox 1994), while potential maximum grazing rates were of the order of 0.3–8.2 mg C m^{-2} day^{-1}. This difference becomes even more pronounced when other nutritional sources of ice meiofauna are included. While ingestion of primary producers (mainly diatoms and chlorophytes) is well documented for ice ciliates, crustaceans and turbellarians (Friedrich 1997; Grainger and Hsiao 1990; Gradinger et al., in press; personal observations), the nutrition of nematodes is less clear. Grainger and Hsiao (1990) observed diatoms in nematodes' guts, while

Table 3 Estimated daily (mg C m^{-2} day^{-1}) and yearly (g C m^{-2} $year^{-1}$) maximum ingestion rates of Arctic and Antarctic sea-ice meiofauna in comparison to sympagic primary production rates (g C m^{-2} $year^{-1}$). Winter values were calculated based on previous measurements assuming an ice temperature of −5°C and a Q_{10} of 2

Season/author	Duration (days)	Arctic	Weddell Sea
Spring	92	0.27 (ARK 8/3)	0.96 (ANT 8/2)
Summer	91	0.27 (ARK 8/3)	8.15 (ANT 9/3)
Autumn	91	0.21 (76% of summer value)	1.91 (ANT 10/3)
Winter	91	0.21 (76% of summer value)	1.45 (76% of autumn value)
Yearly ingestion rate		0.1	1.1
Yearly primary production rates			
Kirst and Wiencke (1995)		0.7	1.9
Arrigo et al. (1997)			6.7 (for 7 months)
Gosselin et al. (1997)		4.0	

Tschesunov and Riemann (1995) proposed an osmotrophic uptake of dissolved organic matter as the most probable mode of nutrition for three ice nematode taxa. Furthermore, bacteria (Gradinger and Zhang 1997; Grossmann and Dieckmann 1994) and protozoans are potential food sources for ice meiofauna. None of these other sources are taken into account by only relating meiofauna grazing to algal production.

In general, sea-ice meiofauna does not appear to be food limited and probably will not control ice algal accumulation during the polar summer, although selective feeding might influence prey diversity. This conclusion is also supported by the weak relations between algal biomass and meiofauna abundance and biomass presented here. The calculated median maximum ingestion rates for the four expeditions ranged between 0.27 mg C m^{-2} day^{-1} for Arctic and 0.96–8.15 mg C m^{-2} day^{-1} for Antarctic pack-ice meiofauna (Table 3). On a yearly basis, the decreased winter temperatures will reduce the meiofauna activity considerably. Winter ice temperatures of −5°C will lower the potential maximum ingestion rate to 76% of the rate at $T = -1$°C assuming a Q_{10} of 2. I estimated the yearly carbon consumption by the sea-ice meiofauna, assuming such winter conditions for 6 months in the Arctic and 3 months in the Antarctic (Table 3), which leads to ingestion values of 0.1 g C m^{-2} $year^{-1}$ for Arctic and 1.1 g C m^{-2} $year^{-1}$ for Weddell Sea pack ice, which are only about 3% (Arctic) and 16% (Antarctic) of the sympagic algal production. These rough estimations show that the ice primary production is sufficient to fulfil the carbon demand of the sea-ice meiofauna both in Arctic and Weddell Sea pack ice year-round. However, other trophic levels of the microbial food web, such as bacteria or heterotrophic flagellates, were not taken into account as potential food sources. Also, the three dimensional structure of the brine channel network will form spatial niches where larger predators are excluded and phototrophs experience reduced grazing pressure. Besides these obvious restrictions, my data highlight the potential impact of meiofauna on other sympagic organisms. First measurements (Laurion et al. 1995) and model development (Vezina et al. 1997) on the sympagic microbial food web in Arctic first-year sea ice demonstrated the significant contribution of protozoans to biological carbon cycling. However, these studies ignored the contribution of sympagic meiofauna. The Arctic meiofauna ingestion rates are similar to the modelled microbial carbon demand of bacterial grazers (0.1–3.5 mg C m^{-2} day^{-1}) in Arctic first-year ice (Vezina et al. 1997). Therefore, the in-situ determination of grazing rates of ice meiofauna and the incorporation of these results into model simulations to estimate the net carbon production by polar sea ice are the next steps in our journey to understand the biology of this environment.

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