

Abundance, biomass, composition and grazing impact of the sea-ice meiofauna in the North Water, northern Baffin Bay

Christian Nozais^{1,*}, Michel Gosselin¹, Christine Michel², Guglielmo Tita^{1,**}

¹Institut des sciences de la mer de Rimouski (ISMER), Université du Québec à Rimouski, 310 Allée des Ursulines, Rimouski, Québec G5L 3A1, Canada

²Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada

ABSTRACT: The abundance, biomass, composition and grazing impact of the bottom sea-ice meiofauna were investigated in the North Water, High Arctic, during April and May 1998. Sampling was conducted on both pack ice and land fast-ice. At the lowermost 2 to 4 cm of the sea ice, chlorophyll *a* reached a maximum concentration of 55.7 mg m⁻². Sea-ice meiofauna were observed only at the ice bottom, and were composed of nematodes, copepods (harpacticoids and cyclopoids), crustacean nauplii, polychaete larvae and turbellarians. Total abundance of sea-ice meiofauna ranged from 0 to 34 500 ind. m⁻² at the sampling stations. Nematodes were the most abundant taxon in the ice, with highest densities at a land fast-ice station. Highest abundances of copepods as well as crustacean nauplii were observed in the pack ice. The total sea-ice meiofauna biomass varied between 0 and 19.4 mg C m⁻². Potential ingestion rates, determined using allometric equations, indicated that sea-ice meiofauna never consumed more than 0.9% of the ice-algae standing stock and 5.7% of the daily ice-algae production. These calculations strongly suggest that the grazing impact of sea-ice meiofauna on ice algae was negligible in the North Water in early spring. The low standing stock of ice meiofauna also precludes their potential as an important food source for higher trophic levels. Meiofauna, therefore, appear to be a minor contributor to the overall carbon flow in the sea-ice biota of the North Water during spring.

KEY WORDS: Arctic polynya · Sea ice · Algae · Meiofauna · Grazing impact

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

In the Northern Hemisphere, sea-ice extent varies from a minimum of 7.0×10^6 km² in September to a maximum of 15.4×10^6 km² in March (Parkinson et al. 1999). Sea ice is recognized as playing a significant role in the biology and ecology of polar marine systems, supporting a productive community of microal-

gae as well as a diversity of heterotrophs ranging from bacteria to metazoa (Carey & Montagna 1982, Carey 1985, Laurion et al. 1995, Gradinger & Zhang 1997, Sime-Ngando et al. 1997). Most of the studies on the sea-ice biota in the Arctic Ocean and adjacent seas have been restricted to the coastal fast-ice, probably because of easier access compared to pack ice. With the recent development of highly sophisticated supports, investigations on ice floes have become feasible. Recently, studies of autotrophic and heterotrophic components of sea ice have been carried out on pack-ice systems in the Barents, Laptev, and Greenland Seas and in the central Arctic Ocean (Gradinger et al. 1992, 1999, Friedrich 1997, Melnikov 1997, Gradinger 1999).

*E-mail: christian_nozais@uqar.quebec.ca

**Present address: Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70808, USA

Sea-ice meiofauna predominantly inhabit the bottom layers of the sea ice and are comprised of both permanent and temporary residents (Carey 1985). Several field studies dealing with sea-ice meiofauna have focused on their composition, distribution, abundance and biomass (Carey & Montagna 1982, Cross 1982, Kern & Carey 1983, Grainger et al. 1985). Grainger & Hsiao (1990) were the first to study the diet of several components of sea-ice meiofauna. They concluded that some groups of ice meiofauna are major consumers of ice algae in Frobisher Bay, Canadian Arctic. Only 2 studies have provided estimates of the grazing impact of sea-ice meiofauna on ice algae. Gradingier (1999) reported that daily and yearly potential ingestion rates of sea-ice meiofauna were far below the values of ice-algae production in the central Arctic Ocean. In the Greenland Sea, however, Gradingier et al. (1999) showed

that grazing of sea-ice meiofauna controls biomass accumulation of primary producers in multi-year ice floes during summer and late autumn. Sea-ice meiofauna may therefore play an important role in controlling sea-ice algal development and could represent a link in the energy transfer from the ice to upper pelagic and benthic trophic levels.

There is, to our knowledge, no published information on the meiofauna inhabiting seasonal sea ice found in polynya regions. Arctic polynyas are defined as mesoscale areas (10 to 90 000 km²) of open water (or very little ice cover) surrounded by ice (Mysak & Huang 1992, Stirling 1997). The recurring North Water polynya of Smith Sound and northwestern Baffin Bay, the largest in the Canadian Arctic (Smith et al. 1990), is ice-covered during the coldest months and can have some open water in early spring (Stirling 1997). It is considered to be one of the most productive areas north of the Arctic circle (Stirling 1980, Lewis et al. 1996). The purpose of the present investigation was: (1) to document the composition, abundance and biomass of sea-ice meiofauna in first-year sea ice in the North Water during spring, and (2) to estimate the grazing impact of sea-ice meiofauna on the bottom ice-algae standing stock and primary production.

MATERIALS AND METHODS

Study area and sampling. This study was conducted on both land fast-ice and pack ice into the North Water, northern Baffin Bay, High Arctic, from 7 April to 29 May 1998, on board the icebreaker CCGS 'Pierre Radisson'. Ice-algae and meiofaunal sampling was carried out at 20 stations, located between 76°N and 78°N and between 73°W and 77°W (Fig. 1, Table 1). Only 1 station was located on the land fast-ice (Station 3); this station was repeatedly sampled during the season. Snow depth, ice thickness and incident and sub-ice irradiances (LI-COR PAR sensors) were measured at each station. From 5 to 8 ice cores were collected at each station, using a MARK II coring system (9 cm inner diameter; Kovacs Enterprise, Lebanon, New Hampshire). Three to 5 cores were used for the determination of salinity, particulate organic carbon (POC), pigment concentrations, and ice-algae production. The remaining 2 to 3 cores were sampled for abundance, biomass and composition of sea-ice meiofauna.

Laboratory analyses. The bottom 2 to 4 cm of the cores was cut and put together in a dark container for biological analyses. Then, the next 4 cm above were cut and melted for later determination of the salinity with an Autosal salinometer. In order to minimize osmotic stress during melting, the bottom-ice cores were rapidly mixed with surface water from the ice sta-

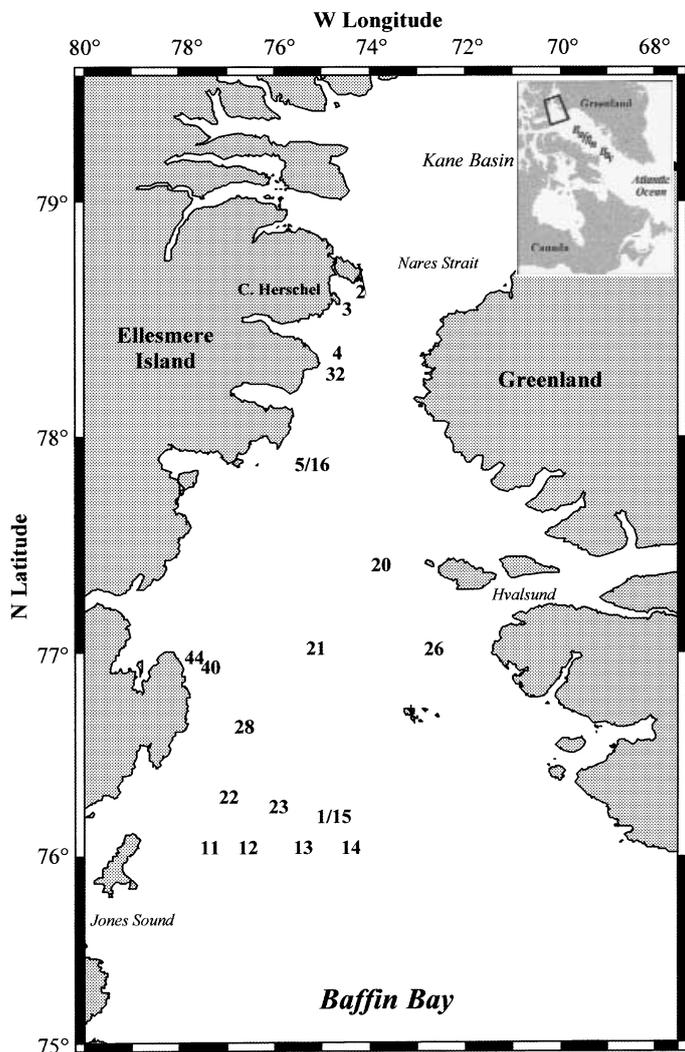


Fig. 1. Location of ice sampling stations in the North Water, High Arctic

Table 1. General characteristics of ice sampling stations and chlorophyll *a* (chl *a*) and POC concentrations in the bottom ice.
*Land fast-ice station (Stn 3), sampled on 4 occasions

Stn	Date	Latitude (N)	Longitude (W)	Ice salinity (‰)	Snow depth (cm)	Ice thickness (cm)	Chl <i>a</i> (mg m ⁻²)	POC (mg m ⁻²)
1	07 Apr	76° 17.0'	74° 45.0'	7.1	2.3	43.7	7.4	329.4
2	10 Apr	78° 36.0'	74° 20.6'	6.6	0	63.3	1.7	118.5
3A	13 Apr*	78° 35.9'	74° 29.5'	4.9	2.0	155.1	11.4	518.2
4	14 Apr	78° 21.5'	74° 42.4'	7.6	2.0	14.2	0.1	248.4
5	15 Apr	77° 50.0'	75° 33.0'	7.1	2.0	72.7	5.4	282.1
3B	16 Apr*	78° 35.9'	74° 29.5'	5.0	3.2	155	22.4	794.2
11	21 Apr	76° 03.0'	77° 25.0'	4.8	2.5	48.7	1.6	142.3
12	22 Apr	76° 03.0'	76° 20.0'	11.5	2.7	29	0.9	236.7
13	22 Apr	76° 03.0'	75° 20.0'	6.2	6.2	53.7	15.5	930.6
14	22 Apr	76° 03.0'	74° 20.0'	8.6	1.0	19.7	1.2	236.5
15	23 Apr	76° 17.0'	74° 45.0'	5.3	0.5	23.3	1.1	126
16	25 Apr	77° 50.0'	75° 33.0'	8.0	4.7	86.7	29.4	1594.7
3C	26 Apr*	78° 35.9'	74° 29.5'	4.6	5.2	155	18.8	875
20	26 Apr	77° 21.0'	73° 48.0'	5.4	5.0	40	10.6	698.7
21	28 Apr	77° 00.0'	75° 02.0'	3.7	4.3	59.7	25.0	1707.4
22	29 Apr	76° 19.4'	77° 24.7'	5.8	1.6	82	7.6	348.6
23	30 Apr	76° 19.1'	75° 53.0'	7.3	1.3	20.7	8.9	425.7
3D	01 May*	78° 35.9'	74° 29.5'	4.2	2.8	150.3	4.9	270.5
26	02 May	77° 00.0'	72° 25.4'	4.3	12.2	72	7.2	331.1
28	07 May	76° 36.2'	76° 29.6'	5.7	5.0	43.3	55.6	2880
32	13 May	78° 20.6'	74° 52.1'	2.8	6.3	50.3	7.1	235.3
40	23 May	76° 58.8'	77° 31.4'	4.0	1.1	24.8	7.4	970.5
44	29 May	76° 58.8'	77° 38.6'	4.7	10.4	60	50.9	3237.2

tion, which had been filtered through 0.22 µm hydrophilic Durapore membrane filters (Bates & Cota 1986, Garrison & Buck 1986). POC was determined on duplicate subsamples filtered on to precombusted Whatman GF/F glass-fiber filters, which were kept frozen until analysis on a Perkin Elmer Model 2400 CHN analyzer. Chlorophyll *a* (chl *a*) and pheopigment concentrations were determined fluorometrically on duplicate subsamples filtered on to Whatman GF/F glass fiber filters. Chl *a* and pheopigment concentrations were calculated using equations of Holm-Hansen et al. (1965) after measuring fluorescence with a R010 Turner Designs Fluorometer, following 24 h extraction in 90 % acetone at 5°C without grinding (Parsons et al. 1984). Particulate ice-algae production was measured using the ¹⁴C-assimilation method as described in Gosselin et al. (1997). Briefly, the photosynthetic rates versus irradiance were determined in a linear incubator (Babin et al. 1994). Water temperature was maintained at -1 to 0°C, using a thermoregulating bath. After 2 to 4 h incubation, samples were filtered on to Whatman GF/F glass-fiber filters. The filters were rinsed with non-radioactive filtered seawater before being removed from the filtration apparatus, after which they were dropped into borosilicate scintillation vials. Under the hood, 100 µl 0.5 N HCl was added to each vial in order to remove the non-incorporated ¹⁴C (Lean & Burnison 1979). Following the evaporation of the acid, Ecolume scintillation cocktail (ICN) was added. The activity was

measured on a Packard Tri-Carb 2100TR liquid scintillation analyzer. The daily production rate was estimated according to the model of Jassby & Platt (1976), using *in situ* irradiance.

Sea-ice meiofauna. The bottom 6 cm of 2 to 3 ice cores was cut into 3 sections of 2 cm (0–2, 2–4 and 4–6 cm). These sections were put in separate clean plastic bags and transported back to the ship. Each ice-core section was melted in 1 000 ml of surface water filtered through 0.22 µm hydrophilic Durapore membrane filters. After complete melting, each sample was then passed through 500 and 63 µm sieves, and the 63 µm screenings fixed in 4 % borax-buffered formaldehyde solution for subsequent analysis at home laboratory. Sea-ice meiofauna were sorted from the 63 µm fraction, after staining in Rose Bengal, and counted under a dissecting microscope.

Nematode composition was assessed at the land fast-ice station on 26 April (2 replicates) and 1 May (3 replicates). One-hundred nematodes were subsampled per replicate and mounted on glycerin slides (McIntyre & Warwick 1984) for species identification.

Biomass of the sea-ice meiofauna was estimated from size measurements of observed animals. The length and width of all organisms in each ice-core section were measured (except for Stn 3 where only 20 nematodes were measured on 26 April and 1 May), using a dissecting microscope. These measurements were used for further conversion into biomass, using conversion

factors corresponding to each taxonomic group, as follows:

Nematodes: The wet weight (WW in μg) of nematodes (393 individuals) was calculated according to Wieser (1960) and Warwick & Price (1979) as

$$WW = 530 \cdot L \cdot W^2 \cdot 1.13 \quad (1)$$

where 530 is a dimensionless conversion factor applied for nematodes, L is the total length (mm), W is the maximum width (mm) of a given individual, and 1.13 is the specific gravity ($\mu\text{g nl}^{-1}$) (Wieser 1960). Organic carbon content (C_{org}) was estimated assuming that C_{org} is equal to 12.4% of wet weight (Jensen 1984).

Copepods: The volume (V in nl) of copepods (186 individuals) was calculated according to Warwick & Gee (1984) with

$$V = L \cdot W^2 \cdot C \quad (2)$$

where L is the total length (mm), W is the width (mm), and C is a specific dimensionless conversion factor depending on the body form: semi-cylindrical ($C = 560$) and pyriform ($C = 400$). The wet weight (WW in μg) was calculated according to Riemann et al. (1990) as

$$WW = 0.9 \cdot V \cdot 1.13 \quad (3)$$

where 0.9 is a dimensionless conversion factor, V is the volume of a given individual (nl), and 1.13 is the specific gravity ($\mu\text{g nl}^{-1}$). The dry weight of copepods was estimated as 22.5% of wet weight according to Gradinger et al. (1999). Organic carbon content (C_{org}) was estimated as constituting 40% of dry weight (Feller & Warwick 1988).

Crustacean nauplii: The wet weight (WW in μg) of the nauplii (254 individuals) was calculated according to Gradinger et al. (1999) as

$$WW = 360 \cdot L \cdot W^2 \quad (4)$$

where 360 is a conversion factor ($\mu\text{g mm}^{-3}$), L is the length (mm) and W is the width (mm). Dry weight and organic carbon content were calculated as for copepods.

Polychaete larvae: The volume (V in nl) of the polychaete larvae (7 individuals) was determined using a program developed by Nozais & Duchêne (1996), which allows for a reconstruction of the body volume of polychaete larvae, according to a set of biometrical data. The biomass was estimated by converting the volume of a given individual into organic carbon with a value of $0.11 \text{ pg C } \mu\text{m}^{-3}$ (Gradinger 1999).

Turbellarians: The wet weight (WW in μg) of turbellarians (3 individuals) was obtained according to Gradinger et al. (1999) with

$$WW = 550 \cdot L \cdot W^2 \cdot 1.13 \quad (5)$$

where 550 is a dimensionless conversion factor, L is the

length (mm), W the width (mm), and 1.13 is the specific gravity ($\mu\text{g nl}^{-1}$). Dry weight and organic carbon content were calculated as described for copepods.

Potential maximum carbon ingestion rates of the sea-ice meiofauna taxa were calculated using the allometric equation given by Moloney & Field (1989) for planktonic organisms, and used for sea-ice organisms (Vézina et al. 1997, Gradinger et al. 1999), as

$$I_{\text{max}} = 63 \cdot M^{-0.25} \cdot e^{[0.0693 \cdot (T-20)]} \cdot B \quad (6)$$

where I_{max} is the potential maximum ingestion rate ($\text{mg C m}^{-2} \text{ d}^{-1}$), 63 is a rate coefficient (in $\text{pg C}^{0.25} \text{ d}^{-1}$), M is the size of a given individual (in pg C), B is the carbon biomass of the compartment (in mg C m^{-2}), and T is the temperature of the ice (in $^{\circ}\text{C}$). All rates were calculated assuming a Q_{10} value of 2 and an ice temperature of -1°C .

Ice-algae chlorophyll a concentration (in mg m^{-2}) was converted into autotrophic carbon (in mg C m^{-2}), using a POC:chl a ratio of 54 obtained by linear regression of POC versus chl a :

$$\text{POC} = 46.446 + (54.54 \cdot \text{chl } a), r^2 = 0.93 \quad (7)$$

Spearman's rank-correlation analysis was used to infer relationships between variables (Zar 1984).

RESULTS

Physical variables showed large spatial variability in the North Water (Table 1). Snow depth varied between 0 and 12.2 cm and ice thickness ranged from 14.2 to 155 cm. Ice salinity ranged between 2.8 and 11.5‰. The concentrations of POC and chl a in the bottom 2 to 4 cm of the ice varied considerably in the pack ice, ranging from 118 to 3237 mg C m^{-2} and 0.1 to 55.6 mg m^{-2} , respectively. At the land fast-ice station, POC concentrations increased from 518 mg C m^{-2} on 13 April to 875 mg C m^{-2} on 26 April, and decreased thereafter to reach 271 mg C m^{-2} on 1 May. At the same stations, chl a concentrations were maximum on 16 April (22.4 mg m^{-2}) and minimum on 1 May (4.9 mg m^{-2}). Overall, high chl a concentrations were observed along the coast (Fig. 2). Pheopigment concentrations were always very low in the pack ice as well as at the land fast-ice station, ranging from 0 to 0.62 mg m^{-2} (data not shown).

Sea-ice meiofauna were found only in the lowermost 2 cm of sea ice in the North Water. Total abundance of the sea-ice meiofauna ranged from 0 to 34 500 ind. m^{-2} at the sampling stations (Fig. 3D, Table 2). Nematodes were the most numerous individuals in the ice, followed by copepods (harpacticoids and cyclopoids), crustacean nauplii, polychaete larvae, and turbellarians. At the pack-ice stations, copepods and crustacean nauplii often dominated in terms of abundance, exhibiting a

maximum of 11 080 ind. m^{-2} (Stn 21) and 4090 ind. m^{-2} (Stn 16), respectively (Fig. 3B,C). When present, copepods and nauplii contributed from 1.5 to 87.6%, and from 11.8 to 100% of the total meiofauna abundance, respectively (Fig. 4A). Highest densities of nematodes were observed in the land fast-ice at Cape Herschel (Fig. 3A), ranging from 1730 ind. m^{-2} (Stn 3A, 13 April) to 33 250 ind. m^{-2} (Stn 3C, 26 April) (Table 2). Overall, nematodes accounted for 80.5% (13 April) to 98.5% (26 April) of the total abundance of sea-ice meiofauna at the land fast-ice station (Fig. 4A).

The total sea-ice meiofauna biomass ranged between 0 and 19.4 mg C m^{-2} at the sampling stations (Fig. 5D, Table 3). The highest biomass was found at Stn 21, with copepods accounting for 98.5% of the total

biomass (Fig. 4B). At the land fast-ice station, the biomass of nematodes increased sharply from 13 to 26 April (from 0.17 [Stn 3A] to 3.39 mg C m^{-2} [Stn 3C]), and slightly declined thereafter to 3.31 mg C m^{-2} on 1 May (Fig. 5A, Table 3; Stn 3D). Nematodes comprised from 32.7% (13 April) to 91.7% (1 May) of the total biomass of sea-ice meiofauna at the land fast-ice station (Fig. 4B). Overall, sea-ice meiofauna contributed between 0.004 and 1.34% of the ice-bottom POC in the North Water (Table 3).

Using the carbon-based grazing model of Moloney & Field (1989), we estimated the potential grazing impact of sea-ice meiofauna in the North Water. Potential daily ingestion rates varied between 0.012 and 8.24 mg C m^{-2} for the total sea-ice meiofauna community in the pack ice (Table 4). Copepods had the highest maximum potential daily ingestion rate, followed by crustacean nauplii, nematodes, polychaete larvae, and turbellarians. When present in the pack ice, copepods and crustacean nauplii contributed 14.9 to 95.9%, and 1.5 to 55.8% of the potential daily ingestion rate, respectively (Fig. 4C). At the land fast-ice station, nematodes exhibited the highest maximum potential daily ingestion rate, followed by copepods, crustacean nauplii, polychaete larvae, and turbellarians. Nematodes were the main consumers, contributing 91.6% of the potential daily ingestion rate on 1 May (Stn 3D, Fig. 4C). During this study, ice-algae biomass and production ranged from 1.1 to 55.6 mg chl a m^{-2} and from 26 to 317 mg C m^{-2} d^{-1} , respectively (Table 4). The potential daily grazing impact of the different sea-ice meiofauna taxa remained low, ranging from <0.01 to 0.60% of bottom ice-algae standing stock and from <0.1 to 3.5% of bottom ice-algae production in the pack ice (Table 4). At the land fast-ice station, the potential daily grazing impact of the different sea-ice meiofauna taxa varied from 0.05% (Stn 3A, 13 April) to 0.92% (Stn 3D, 1 May) of bottom-ice algae standing stock and from 0.55% (13 April) to 5.7% (1 May) of bottom ice-algae production. Overall, the highest ice-meiofauna potential daily grazing impact on bottom-ice algae (1 to 5.7% of bottom-ice algae production) was found in the center of the North Water (Stn 21) and at the land fast-ice station, in conjunction with high abundances of copepods and nematodes, respectively (Tables 2 & 4).

No significant relationship was found between physical and biological variables measured at the land fast-ice station. At pack-ice stations, chl a concentration was positively correlated with snow depth (Table 5). Total ice meiofauna and copepod abundances and biomasses were positively correlated with chl a concentrations (Table 5). Total ice meiofauna and nauplii abundances and biomasses were also positively correlated with the ice thickness.

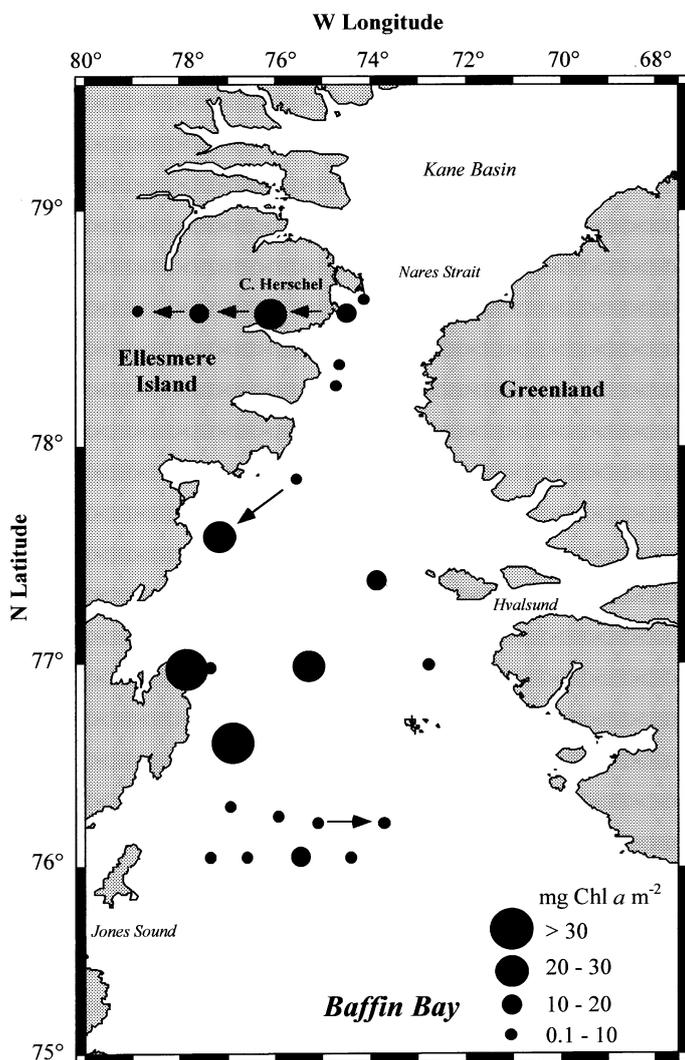


Fig. 2. Bottom-ice algae chlorophyll a concentrations ($mg\ m^{-2}$) in the North Water, in April and May 1998. Arrows indicate the temporal change of the studied variable at the land fast-ice station of Cape Herschel and at 2 pack-ice stations

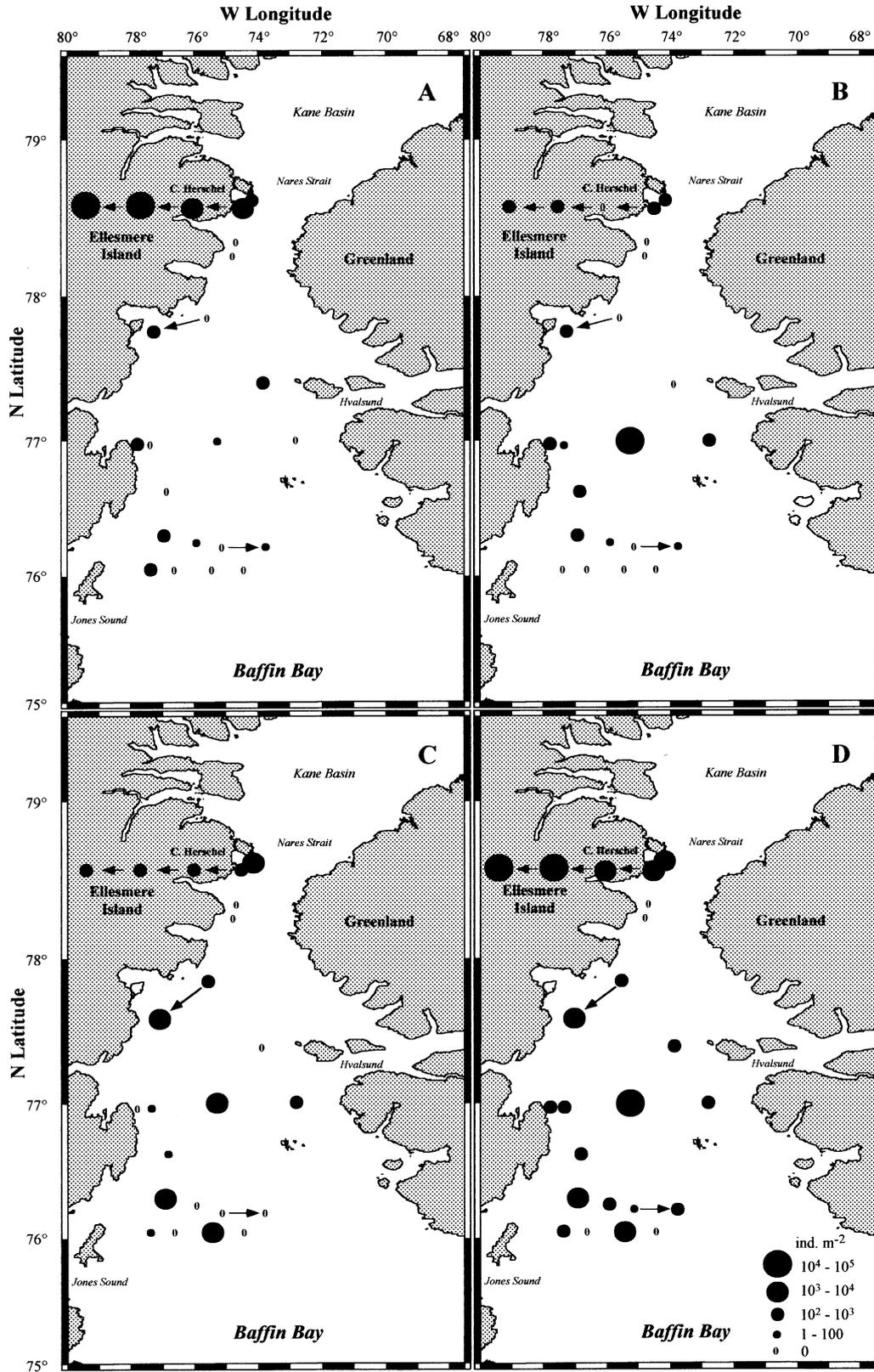


Fig. 3. Abundances (ind. m⁻²) of (A) nematodes, (B) copepods, (C) crustacean nauplii, and (D) total meiofauna in the bottom ice in the North Water in April and May 1998. Arrows indicate the temporal change of the studied variable at the land fast-ice station of Cape Herschel and at 2 pack-ice stations

Table 2. Abundance of sea-ice meiofauna taxa (mean \pm SD) in the bottom ice

Stn	Meiofauna abundance (10^3 ind. m^{-2})					
	Nematoda	Copepoda	Nauplii	Polychaeta (larvae)	Turbellaria	Total
1	0	0	0	0	0.05 \pm 0.09	0.05 \pm 0.09
2	1 \pm 0.51	0.05 \pm 0.09	2.36 \pm 1.60	0	0	3.41 \pm 1.74
3A	1.73 \pm 2.99	0.26 \pm 0.45	0.11 \pm 0.18	0	0.05 \pm 0.09	2.15 \pm 3.72
4	0	0	0	0	0	0
5	0	0	0.58 \pm 0.09	0.21 \pm 0.24	0	0.79 \pm 0.16
3B	3.38 \pm 1.44	0	0.31 \pm 0.22	0.08 \pm 0.11	0	3.77 \pm 1.33
11	0.11 \pm 0.18	0	0.05 \pm 0.09	0	0.05 \pm 0.09	0.21 \pm 0.09
12	0	0	0	0	0	0
13	0	0	3.77 \pm 2.04	0	0	3.77 \pm 2.04
14	0	0	0	0	0	0
15	0.05 \pm 0.09	0.05 \pm 0.09	0	0	0	0.11 \pm 0.09
16	0.31 \pm 0.16	0.11 \pm 0.09	4.09 \pm 0.98	0.05 \pm 0.09	0	4.56 \pm 0.96
3C	33.25 \pm 15.89	0.94 \pm 1.112	0.31 \pm 0.22	0	0	34.50 \pm 17.23
20	0.31 \pm 0.22	0	0	0	0	0.31 \pm 0.22
21	0.08 \pm 0.11	11.08 \pm 3.00	1.49 \pm 1.00	0	0	12.65 \pm 2.11
22	0.31 \pm 0.22	0.16 \pm 0	1.10 \pm 0.22	0	0	1.57
23	0.05 \pm 0.09	0.05 \pm 0.09	0	0.05 \pm 0.09	0	0.16 \pm 0.27
3D	31.12 \pm 3.31	0.31	0.16 \pm 0.27	0	0	31.60 \pm 3.30
26	0	0.16	0.16	0	0	0.31
28	0	0.16	0.079 \pm 0.111	0	0	0.24 \pm 0.11
32	0	0	0	0	0	0
40	0	0.08 \pm 0.11	0.079 \pm 0.111	0	0	0.16 \pm 0.22
44	0.11 \pm 0.09	0.37 \pm 0.40	0	0	0	0.47 \pm 0.47

Table 3. Biomass of the different sea-ice meiofauna taxa (mean \pm SD) and contribution of the total meiofauna biomass to total ice POC

Stn	Biomass (mg C m^{-2})						% POC
	Nematoda	Copepoda	Nauplii	Polychaeta (larvae)	Turbellaria	Total	
1	0	0	0	0	0.02 \pm 0.04	0.02 \pm 0.04	0.006
2	0.19 \pm 0.08	0.1 \pm 0.17	0.37 \pm 0.22	0	0	0.66 \pm 0.34	0.555
3A	0.17 \pm 0.29	0.33 \pm 0.57	0.004 \pm 0.007	0	0.02 \pm 0.04	0.52 \pm 0.90	0.101
4	0	0	0	0	0	0	
5	0	0	0.08 \pm 0.02	0.07 \pm 0.08	0	0.14 \pm 0.06	0.051
3B	0.22 \pm 0.08	0	0.06 \pm 0.04	0.03 \pm 0.04	0	0.31 \pm 0.08	0.039
11	0.04 \pm 0.07	0	0.01 \pm 0.02	0	0.02 \pm 0.04	0.07 \pm 0.04	0.049
12	0	0	0	0	0	0	
13	0	0	0.64 \pm 0.28	0	0	0.64 \pm 0.28	0.069
14	0	0	0	0	0	0	
15	0.02 \pm 0.03	0.13 \pm 0.23	0	0	0	0.15 \pm 0.22	0.121
16	0.09 \pm 0.05	0.27 \pm 0.23	0.79 \pm 0.18	0.02 \pm 0.03	0	1.16 \pm 0.17	0.073
3C	3.39 \pm 1.60	1.96 \pm 2.19	0.05 \pm 0.04	0	0	5.40 \pm 3.83	0.617
20	0.03 \pm 0.02	0	0	0	0	0.03 \pm 0.02	0.004
21	0.002 \pm 0.003	19.15 \pm 11.05	0.29 \pm 0.20	0	0	19.44 \pm 10.86	1.139
22	0.03 \pm 0.02	0.14	0.21 \pm 0.03	0	0	0.37 \pm 0.01	0.106
23	0.004 \pm 0.008	0.05 \pm 0.08	0	0.02 \pm 0.03	0	0.07 \pm 0.08	0.016
3D	3.31 \pm 0.48	0.27	0.03 \pm 0.05	0	0	3.61 \pm 0.47	1.336
26	0	0.14	0.03	0	0	0.17	0.051
28	0	0.14	0.01 \pm 0.02	0	0	0.15 \pm 0.02	0.005
32	0	0	0	0	0	0	
40	0	0.07 \pm 0.1	0.04 \pm 0.02	0	0	0.11 \pm 0.15	0.011
44	0.01 \pm 0.01	0.31 \pm 0.33	0	0	0	0.32 \pm 0.33	0.010

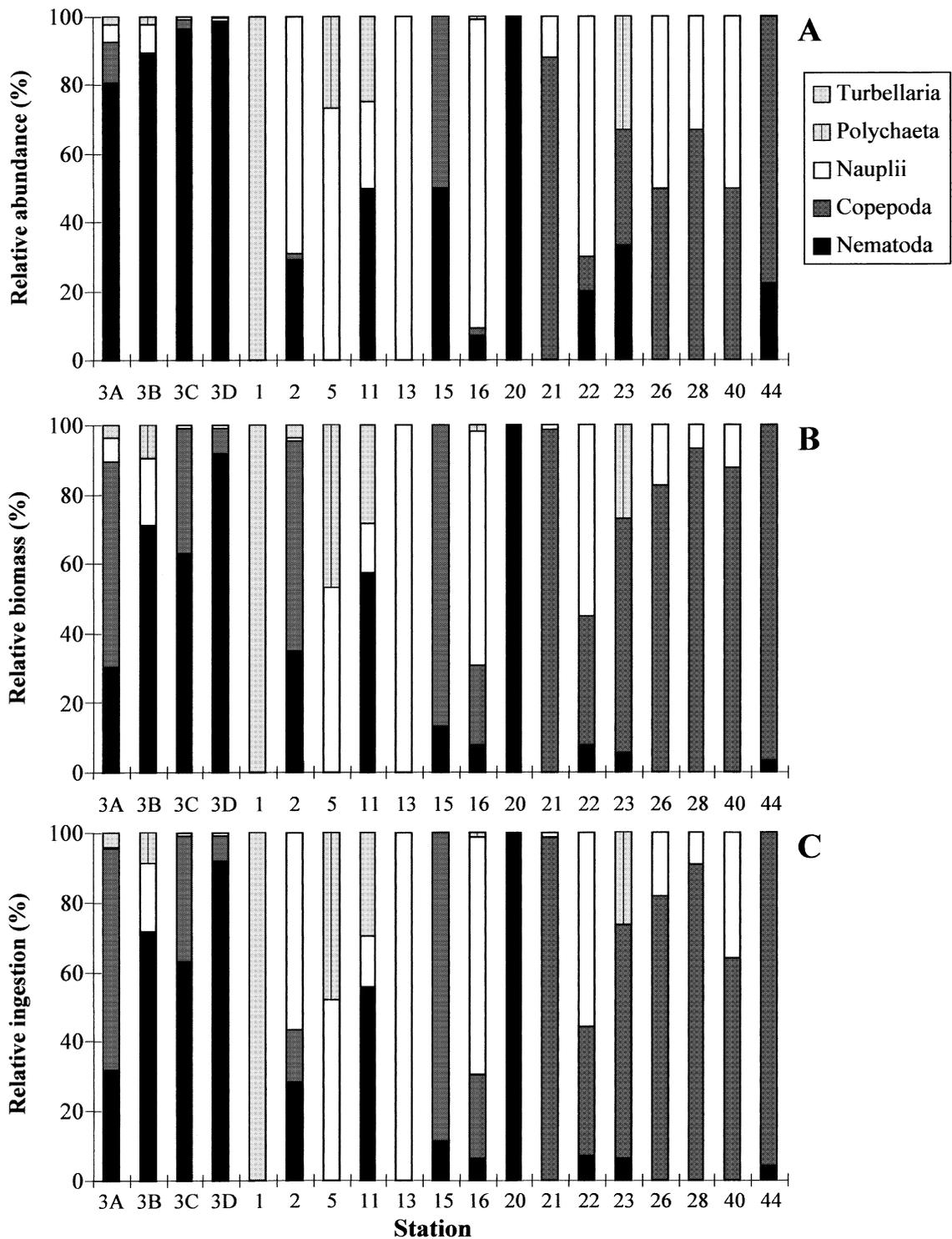


Fig. 4. Relative contributions of different taxa to (A) total abundance, (B) total carbon biomass, and (C) total potential ingestion rates of the bottom ice meiofauna

The mean values of the carbon biomass, potential daily ingestion rate, and grazing impact of the different sea-ice meiofauna taxa have been calculated for

thin (thickness <0.5 m) and thick (thickness \geq 0.5 m) pack ice. On average, total carbon biomass and potential daily ingestion rate of sea-ice meiofauna under

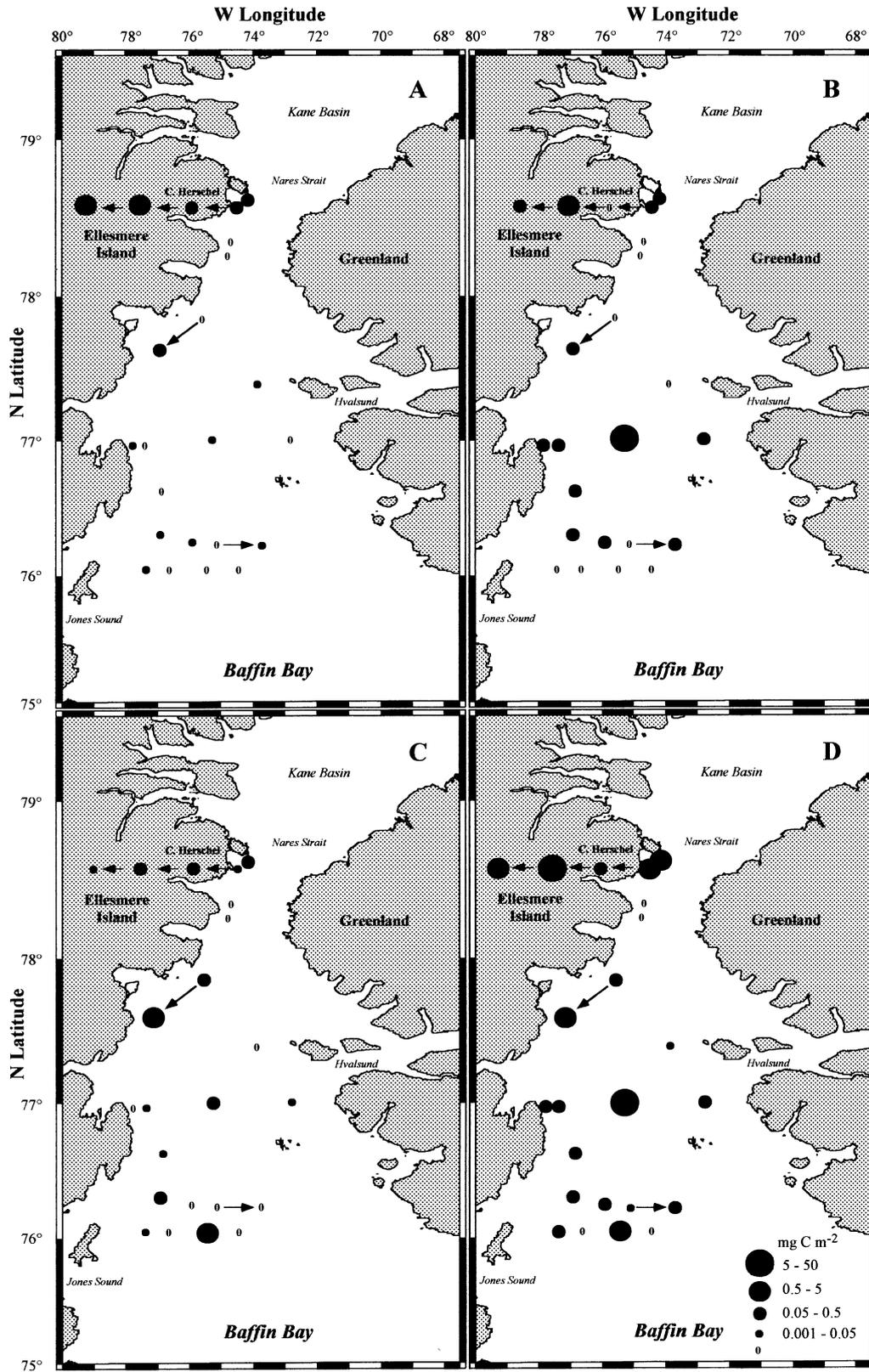


Fig. 5. Biomasses (mg C m^{-2}) of (A) nematodes, (B) copepods, (C) crustacean nauplii, and (D) total meiofauna in the bottom ice in the North Water in April and May 1998. Arrows indicate the temporal change of the studied variable at the land fast-ice station of Cape Herschel and at 2 pack-ice stations

Table 4. Bottom ice-algae biomass, production, potential maximum ingestion rates and grazing impact of sea-ice meiofauna. Nem.: Nematoda; Cop.: Copepoda; Naup.: nauplius; Pol.: Polychaeta; Turb.: Turbellaria

Stn	Chl <i>a</i> (mg m ⁻²)	Primary production (mg C m ⁻² d ⁻¹)	Potential ingestion rate (mg C m ⁻² d ⁻¹)					Potential daily grazing impact		
			Nem.	Cop.	Naup.	Pol.	Turb.	Total	% ice algal biomass	% production
1	7.4	51.9	0	0	0	0	0.012	0.012	0.003	0.023
2	1.7	No data	0.141	0.039	0.275	0	0	0.455	0.506	–
3A	11.4	55.5	0.139	0.152	0.004	0	0.012	0.307	0.050	0.553
5	5.4	126.6	0	0	0.061	0.022	0	0.083	0.028	0.066
3B	22.4	52.9	0.231	0	0.043	0.016	0	0.290	0.024	1.701
11	1.6	30.2	0.035	0	0.007	0	0.012	0.054	0.063	0.179
13	15.5	125.2	0	0	0.533	0	0	0.533	0.063	0.426
15	1.1	33.7	0.011	0.050	0	0	0	0.060	0.100	0.178
16	29.4	193.2	0.055	0.099	0.552	0.011	0	0.717	0.045	0.004
3C	18.8	167.4	3.034	0.780	0.037	0	0	3.850	0.375	2.3
20	10.6	133.8	0.026	0	0	0	0	0.026	0.004	0.0002
21	25.0	233	0.002	8.036	0.206	0	0	8.243	0.604	3.538
22	7.6	26	0.022	0.066	0.146	0	0	0.234	0.057	0.9
23	8.9	206.7	0.004	0.022	0	0.011	0	0.037	0.008	0.0001
3D	4.9	43.6	2.334	0.131	0.021	0	0	2.486	0.921	5.702
26	7.2	83.8	0	0.066	0.021	0	0	0.087	0.022	0.104
28	55.6	317.3	0	0.066	0.010	0	0	0.076	0.003	0.024
40	7.4	99.4	0	0.033	0.011	0	0	0.044	0.011	0.044
44	50.9	63.6	0.010	0.149	0	0	0	0.159	0.006	0.25

Table 5. Correlation matrix using Spearman's r_s between ice salinity, snow depth, ice thickness, chlorophyll *a* concentration, and chlorophyll *a* concentration and sea-ice meiofauna abundance and biomass. Significance levels are: *0.01 < p ≤ 0.05; **0.001 < p ≤ 0.01; ***p ≤ 0.001

	Salinity	Snow depth	Ice thickness	Chl <i>a</i>
Chl <i>a</i>	-0.302	0.498*	0.416	
Total meiofauna (abundance)	-0.189	0.218	0.770***	0.631**
Nematoda (abundance)	-0.085	-0.138	0.398	0.273
Copepoda (abundance)	-0.421	0.176	0.396	0.601**
Nauplii (abundance)	-0.069	0.294	0.725***	0.382
Polychaeta (abundance)	0.415	-0.108	0.253	0.162
Turbellaria (abundance)	-0.043	-0.059	-0.030	-0.164
Total meiofauna (biomass)	-0.270	0.111	0.703***	0.559*
Nematoda (biomass)	-0.051	-0.198	0.331	0.171
Copepoda (biomass)	-0.359	0.159	0.442	0.577**
Nauplii (biomass)	-0.076	0.033	0.701***	0.378
Polychaeta (biomass)	0.415	-0.108	0.253	0.162
Turbellaria (biomass)	-0.031	-0.063	-0.031	-0.157

thin pack ice were about 1 to 2 orders of magnitude lower than those under thick pack ice (Fig. 6, Table 6). Copepods contributed the largest fraction of meiofauna biomass under both thin (64.3%) and thick (87.8%) pack ice. The potential daily ingestion rate of sea-ice meiofauna varied on average, from 0.028 mg C m⁻² under thin pack ice to 1.31 mg C m⁻² under thick pack ice (Table 6). These rates accounted for a potential consumption of 0.017 and 0.17% of the total ice-algae biomass (chl *a*), and for 0.044 and 0.81% of the primary production for thin and thick ice, respectively.

Table 6. Bottom ice-algae biomass, production, potential maximum ingestion rates of sea-ice meiofauna and grazing impact (mean ± SD) under thin (thickness < 0.5 m) and thick (thickness ≥ 0.5 m) pack ice

	Chl <i>a</i> (mg m ⁻²)	Primary production (mg C m ⁻² d ⁻¹)	Potential ingestion rate (mg C m ⁻² d ⁻¹)	Potential daily grazing impact % ice algal biomass	% production
Thin ice	9.3 ± 4.8	98.1 ± 30.3	0.028 ± 0.01	0.017 ± 0.01	0.044 ± 0.02
Thick ice	17.8 ± 5.9	121.6 ± 27.4	1.31 ± 0.99	0.170 ± 0.09	0.81 ± 0.46

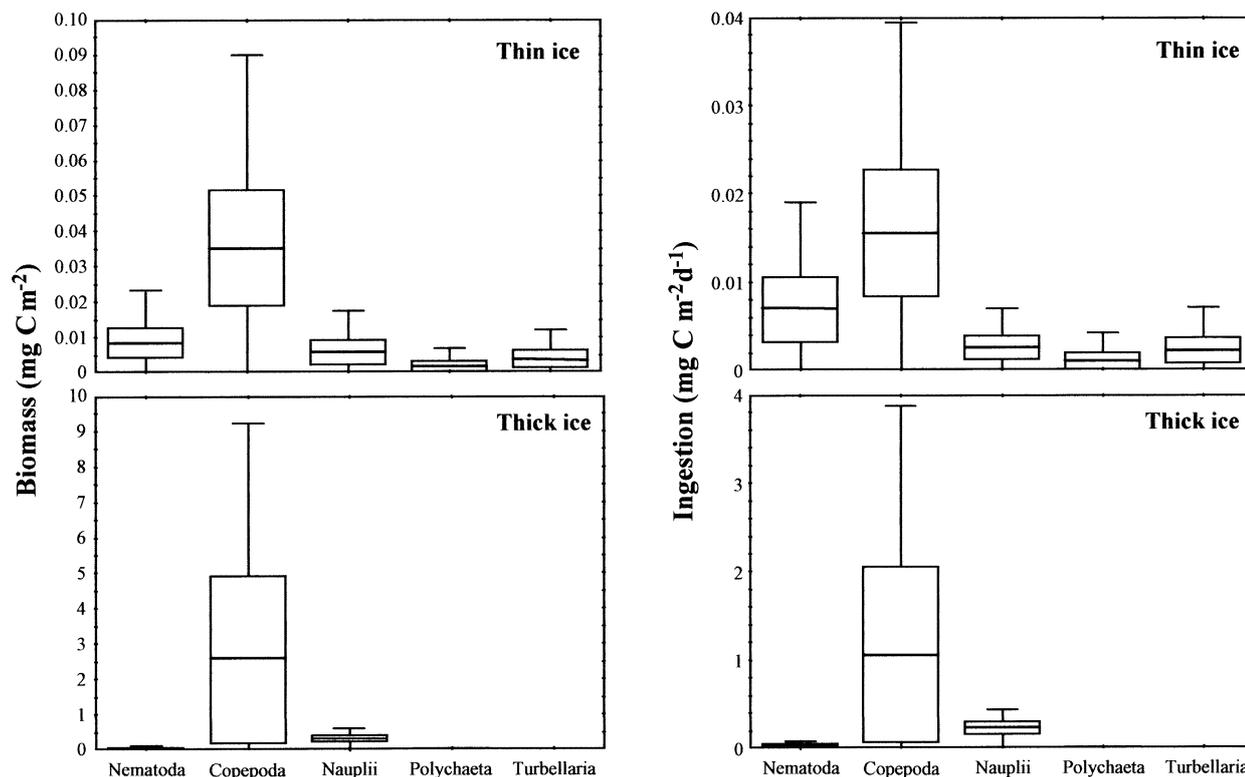


Fig. 6. Biomasses and potential maximum ingestion rates of sea-ice meiofauna under thin (ice thickness < 0.5 m, $n = 10$) and thick (ice thickness ≥ 0.5 m, $n = 9$) pack ice. Medians, standard deviations and standard errors are shown

Three nematode species were found at the land fast-ice station, all belonging to the superfamily Monhysteroida. The most abundant species corresponded to the description of *Monhysterid* sp. 'alpha' given by Riemann & Sime-Ngando (1997). This species accounted for 90% of the total abundance of nematodes and was only represented by juveniles. The other 2 species were *Cryonema tenue* Tchesunov & Riemann 1995, and *Theristus melnikovi* Tchesunov 1986. For each species, only 1 adult individual (female) per each species was found, the remaining individuals being juveniles.

DISCUSSION

The bottom ice-algae biomass was variable in the North Water, with values ranging from 0.1 to 55.6 mg chl *a* m^{-2} . These values are lower than those found by Smith et al. (1988) in the coastal fast-ice of Resolute Passage during spring (max. > 250 mg chl *a* m^{-2}), but comparable to concentrations reported by Cota et al. (1987) in Barrow Strait (0 to 79.8 mg chl *a* m^{-2}) and by Gosselin et al. (1986) in southeastern Hudson Bay (0.1 to 39.7 mg chl *a* m^{-2}). Consistent with other studies (Smith et al. 1988, 1993), higher ice-algae biomasses

were found under thicker snow cover. It is possible that thick snow cover provided protection from photoinhibition (Gosselin et al. 1986).

Sea-ice meiofauna were observed only in the bottom 2 cm of sea ice in the North Water. These observations contrasted with those of Friedrich (1997), who reported that highest densities of meiofauna could occur in the interior parts of sea ice (i.e. in the lower 30 to 40 cm). However, our results agree with those of Gradinger et al. (1999), who observed highest densities of sea-ice meiofauna in the lowermost 2 cm of ice, coinciding with highest chl *a* concentrations. However, these authors also reported the presence of metazoa more than 1 m above the bottom of the ice. Since highest chl *a* concentrations were observed in the bottom 2 to 4 cm of the sea ice in our study, it is likely that maximum abundances of sea-ice meiofauna were related to highest concentrations of chl *a*.

Sea-ice meiofauna were composed of nematodes, copepods (harpacticoids and cyclopoids), crustacean nauplii, polychaete larvae and turbellarians. A similar composition has been reported within the bottom layers of sea ice in other arctic and subarctic ecosystems (Carey 1985). Data on the relative abundance and composition of sea-ice meiofauna from different parts of the Arctic are summarized in Table 7. Due to consid-

Table 7. Relative abundance (%) of sea-ice meiofauna taxa from various Arctic seas. 'Others' includes: amphipods, pelecypod larvae, gastropod larvae, *Balanus* larvae, Tunicate larvae. Cil.: Ciliata; Prot.: Protozoa; Nem.: Nematoda; Ac.: Acoela; Turb.: Turbellaria; Rot.: Rotatoria; Cop.: Copepoda; Naup.: Nauplius; Pol.: Polychaeta

Region, Time of the year	Ice layer studied	Mesh size used (µm)	Cil./Prot.	Nem.	Ac./Turb.	Rot.	Cop.	Naup.	Pol.	Others	Mean ab. (ind. m ⁻²)	Source
Stefansson Sound, March 1979	No data	63	0.7	0.7		0.7	9.1	22.1	67.3		8 000	Carey & Montagna (1982) ^b
Stefansson Sound, May 1979	No data	63	76.9	76.9		0	18	5.1	0		4 500	"
Pond Inlet, May 1979	Bottom 0.5–1 cm	76	58.8	58.8			39.7	1.5			9 776	Cross (1982) ^b
Beaufort Sea, April 1980	Bottom few cm	64	3.2	3.2	2.7		45.7	45.9	2.5	2.5	11 138	Kern & Carey (1983) ^b
Beaufort Sea, May 1980	Bottom few cm	64	47.4	47.4	9.4		34.8	5.2	3.3	3.3	19 784	"
Beaufort Sea, June 1980	Bottom few cm	64	51.9	51.9	31.4		14.5	1.7	0.5	0.5	48 235	"
Frobisher Bay, February 1981	Bottom 3 cm	10	0.5	10.1		0.04	2.3	86.6	0.4	0.06	105 020	Grainger et al. (1985) ^b
Frobisher Bay, March 1981	Bottom 3 cm	10	51.4	51.4		0.4	3.6	44.2	0.2	0.3	59 040	"
Frobisher Bay, 1 May 1981	Bottom 3 cm	10	56.3	56.3		1.1	2.5	11.4	21.9	4.9	36 780	"
Frobisher Bay, 27 May 1981	Bottom 3 cm	10	0.01	98.6		0.01	0.2	0.7	0.03	0.4	110 336	"
Frobisher Bay, June 1981	Bottom 3 cm	10	0.2	92.3		2.7	0.1	4.6		0.1	17 340	"
Frobisher Bay, February 1982	Bottom 3 cm	10	1.1	13.6		0.1	6.1	79		0.1	60 951	"
Frobisher Bay, March 1982	Bottom 3 cm	10	0.1	7.3		6.1	43.4	29.5	13	0.6	26 727	"
Frobisher Bay, May 1982	Bottom 3 cm	10	0.6	55		10.1	0.4	33.5	0.3	0.1	26 573	"
Fram Strait, May 1988	Total core	20	29.0	5.0	51.0	<1.0	ca 1.0	13.0			29 600	Gradinger et al. (1991)
Barents Sea, August 1993	Bottom 30 cm	20	25.0	25.0	4.0	25.0	2.8	3.1			68 719	Friedrich (1997)
Laptev Sea, August/September 1993	Bottom 30 cm	20	48.9	1.8	3.2	16.3	8.3	21.5			54 367	"
Greenland Sea, July/August 1994	Bottom 30 cm	20	70.0	19.8	6.7	1.4	2.0	0.1			83 039	"
Central Arctic, August–October 1991	Bottom 1 to 20 cm	20	53.0	15.0	5.0	9.0				4 ^a	40 600	Gradinger (1999)
North Water (pack ice), April–May 1998	Bottom 2 cm	63	8.1	8.1	0.4		42.6	47.8	1.1		1 514	This study
North Water (land fast-ice), April–May 1998	Bottom 2 cm	63	96.5	96.5		2.1	2.1	1.2	0.1		18 005	This study

^aIncludes Harpacticoida, Polychaeta and Amphipoda; ^bAuthors did not melt the ice cores in filtered seawater

erable differences in the sampling procedures and methodologies as well as the seasons and locations involved (see Gradinger et al. 1991 for further comments), the resolution of these studies varies widely. Nevertheless, the data are amenable to preliminary comparisons. Average abundance of sea-ice meiofauna observed in the North Water was generally low, but nevertheless comparable to those available in the literature from different parts of the Arctic Ocean (Table 7). Free-living nematodes usually represent the dominant meiofauna group in Arctic sea ice (Carey 1985, Grainger et al. 1985), especially in coastal fast-ice. They represented from 7.3 to 98.6% of the total abundance of sea-ice meiofauna in Frobisher Bay, Canadian Arctic (Table 7). Consistent with these results, nematodes accounted for 96.5% of the total abundance of sea-ice meiofauna at the land fast-ice station of Cape Herschel. Given that our land fast-ice station is representative of the coastal fast-ice in the North Water, the coastal sea-ice meiofaunal community composition in the North Water would appear to be similar to other arctic areas. All nematodes found at the land fast-ice station belonged to the superfamily Monhysterioidea, for whom representatives are described as living in extreme habitats (Tchesunov & Riemann 1995). Until now, the most abundant species identified as Monhysterid sp. 'alpha' has never been reported in sediments, although close relatives are found in the benthic environment (Riemann & Sime-Ngando 1997). The origin of these ice nematodes remains unclear. It is assumed that the monhysterid ice nematodes represent an allochthonous organism in the ice biota (Riemann & Sime-Ngando 1997). The fact that we observed a temporal increase of abundance of juveniles of nematodes, together with an extremely low number of females at the land fast-ice station,

might support this view. Carey & Montagna (1982) hypothesized that the bottom layers of coastal fast-ice could represent a recruitment area for benthic meiofauna of shallow waters during spring. Carey (1992) reported that nematodes can be enclosed in the ice after they have been passively lifted together with sediment from the bottom. During the present study, we did not sample the sediment at the land fast-ice station. Therefore, we cannot exclude an interaction between ice and the benthic environment. However, we did not observe any trace of sediments within the ice, suggesting that benthic animals were not incorporated in the land fast-ice through sediment resuspension. Other processes that have been proposed to explain the occurrence of nematodes in the ice include sowing of newly formed ice by pieces of multi-year ice (Tchesunov 1986), and transport by other animals such as amphipods (Tchesunov & Riemann 1995), some species of Decapoda Natantia (Steiner 1958), or whales by means of their baleen (Lorenzen 1986). These 2 hypotheses cannot be rejected, since multi-year ice is observed in the North Water and transport by animals is unknown.

In the pack ice, crustacean nauplii were, on average, the second most abundant component of the sea-ice meiofauna, followed by copepods. Carey (1992), studying the reproduction of sympagic harpacticoid copepods in the Arctic, reported that ice metazoa are capable of producing several generations per year with a more or less continuous reproduction. Similarly, the occurrence of nauplii at most stations of the North Water suggests that the ice copepods were reproducing actively at the bottom surface of the ice during spring. Polychaete larvae were observed both in the pack ice and in the land fast-ice but were poorly represented. Carey & Montagna (1982) reported the presence of polychaete larvae in coastal fast-ice. Larvae of benthic animals, such as polychaetes, are known to migrate in shallow coastal areas into the ice-brine channel network of first-year ice (Carey 1985). In our study, all polychaete larvae belonged to the spionid family and were nectochaetes. Their occurrence has already been reported in Canadian Beaufort sea ice (Pett et al. 1983).

Overall, the biomass of sea-ice meiofauna in the North Water during spring ranged between 0 and 19.4 mg C m^{-2} , with a median of 1.75 mg C m^{-2} . This value is low compared to those recorded in drifting pack of the Greenland Sea (5.6 mg C m^{-2}), but higher than those observed in the Barents and Laptev Seas (0.5 and 0.6 mg C m^{-2} , respectively) (Friedrich 1997). Sea-ice meiofauna weakly contributed to the total ice particulate organic matter ($<1.4\%$).

Few studies have specifically considered the significance of grazing by ice fauna as a factor structuring

sea-ice biota in Arctic areas. Laurion et al. (1995) reported first estimates on grazing rates of nanoflagellated protozoa on ice bacteria. Werner (1997) investigated the grazing impact of under-ice amphipods on ice algae and concluded that food was not a limiting factor in the Laptev and Greenland Seas. To date, very little is known about the grazing impact of sea-ice meiofauna on bottom ice-algae production. The only thorough studies of this type have been undertaken in the central Arctic Ocean and in the Greenland Sea (Gradinger 1999, Gradinger et al. 1999). By comparing calculated total potential ingestion rates with published estimates of annual primary production for Arctic multi-year sea ice, Gradinger et al. (1999) concluded that sea-ice meiofauna were able to control the ice-algae standing stock of drifting multi-year ice floes occurring in the Greenland Sea in summer. In the central Arctic Ocean, however, the ice meiofauna did not appear to be limited all year round (Gradinger 1999). To our knowledge, the present study provides the first estimate of the grazing impact of sea-ice meiofauna inhabiting seasonal arctic sea ice. Moreover, in contrast to these previous studies, measurements of ice-algae production at the stations studied allowed for more accurate determination of the grazing impact of sea-ice meiofauna. Assuming that allometric equations provided a reasonable estimate of daily maximum ingestion rates (Moloney & Field 1989), the total bottom-ice meiofauna (63 to $500 \text{ }\mu\text{m}$) had, on average, a daily potential ingestion rate of 0.96 mg C m^{-2} . This is low compared to the value of $5.5 \text{ mg C m}^{-2} \text{ d}^{-1}$ reported by Gradinger et al. (1999). The discrepancy between our results and those obtained by these authors can at least be partly explained by differences in methodologies. We defined meiofauna as animals $>63 \text{ }\mu\text{m}$ (Giere 1993) and thus used a mesh size of $63 \text{ }\mu\text{m}$, while Gradinger et al. (1999) included animals $<63 \text{ }\mu\text{m}$ in their estimates. Hence, our estimates did not comprise smaller metazoan meiofauna. Maximum daily sea-ice meiofauna grazing impact was observed in the land fast-ice, but represented only 0.9% of the ice-algae standing stock and 5.7% of primary production. When considering ice thickness, it appeared that highest sea-ice meiofaunal daily-grazing impact on sea-ice algae standing stock and production was observed in the thick ($\geq 0.5 \text{ m}$) pack ice. Whether grazing pressure by sea-ice meiofauna in the land fast-ice differs significantly from that in pack ice cannot be ascertained here, because an insufficient number of stations has been sampled in the land fast-ice. Nevertheless, results of the present study clearly indicate that sea-ice meiofauna were not food-limited and that grazing on bottom-ice algae was negligible in the North Water during spring. This low grazing pressure by sea-ice meiofauna was also supported by the very low proportion of pheopigments in the ice

at all stations, likely indicating a low grazing pressure (Shuman & Lorenzen 1975) in the ice.

In our study we assumed that the sea-ice meiofauna exploited only bottom-ice algae as a food source (Grainger et al. 1985, Grainger & Hsiao 1990, Grainger 1991). Turbellarians have been described as omnivores (McIntyre 1969), and have been shown to feed on ice algae (Gradinger et al. 1999). Conover & Siferd (1993) hypothesized that nauplii, hatching close to the bottom of the ice, directly graze on ice algae, while Grainger & Hsiao (1990) reported the presence of *Atthya septentrionalis* and *Nitzschia* sp. in the diet of copepod nauplii. Similarly, harpacticoid and cyclopoid copepods are known to feed on ice algae (Grainger & Hsiao 1990, Friedrich 1997). Although nematodes living in the sediment are reported to feed on algae, bacteria and small metazoa (Boaden 1964, Giere 1993), little is known about the nutrition of ice nematodes. Grainger & Hsiao (1990) reported the occurrence of diatoms in their intestines, while Gradinger & Zhang (1997) suggested bacteria and protozoa as their potential food items. Despite the abundance of diatoms in the land fast-ice, there was no clear indication for this food uptake by nematodes. Tchesunov & Riemann (1995) suggested dissolved organic matter as a possible contributor to the nutrition of nematodes. Recently, Moens et al. (1999) demonstrated that adoncholaimid nematodes were able to feed on dissolved organic matter. Indeed, high concentrations of dissolved organic carbon (up to 40 mg C l⁻¹) were measured in the bottom ice in Frobisher Bay (Bunch & Harland 1990) and Resolute Passage (Smith et al. 1997) in the High Canadian Arctic. Whether ice nematodes feed on dissolved organic matter and/or ice algae would be an important topic for future research.

Sea ice is known as an environment of limited and patchily distributed food sources (Poltermann 1998). Hence, food availability is likely to be one of the main factors influencing the distribution of the sea-ice meiofauna in terms of abundance and biomass. Interestingly, we observed a significant increase in the abundance of nematodes in response to the increased chl *a* concentration in the land fast-ice station. One might assume that increase to be a response to the food sources. Along the same line, both biomass and abundance of copepods correlated well with chl *a* concentration in the pack ice. Lastly, the relationships between the abundance and biomass of different components of the sea-ice meiofauna and the ice thickness of the pack ice suggest that the horizontal distribution of sea-ice meiofauna is probably governed by ice type, formation and melting processes.

This study clearly shows that sea-ice meiofauna do not control bottom ice-algae standing stock nor its production during spring in the North Water. However,

sea-ice meiofauna are certainly not the only consumers of ice algae. For instance, sea-ice amphipods are known to successfully exploit this food source (Werner 1997) as well as several pelagic species of copepods (Cross 1982, Conover et al. 1986, Runge & Ingram 1988, Tremblay et al. 1989). Therefore, the most important part of the bottom ice-algae stock remains available for trophic competitors of sea-ice meiofauna during spring. Whether or not sea-ice meiofauna control ice-algae standing stock and production in autumn and winter is not known. This question needs further attention, because ice algae may play a major role as a principal primary producer in ice-covered seas in autumn (Hoshiai et al. 1996).

Acknowledgements. This research, as part of the International North Water Polynya Study (NOW), was supported by grants from the Natural Sciences and Engineering Research Council (NSERC) of Canada to M.G. C.N. was supported by a post-doctoral stipend from NSERC grant to M.G. We are grateful to the Polar Continental Shelf Project and the Canadian Coast Guard officers and crews of the 'Pierre Radisson' for their skilful support during the expedition. We are especially indebted to M. Gagnon for his logistic and moral support, Gaston Desrosiers, Daniel Dubé, Marie-Ève Garneau, Meike Holst, Pierre Larouche, Peter Lee, Christopher Mundy, Mohammed Skohr, and Andrea Weise for technical assistance in the field or in the laboratory. We thank Diane Bérubé for CHN analyses, Neil Price for use of his liquid scintillation counter, Rolf Gradinger for providing information on the allometric equations, Elizabeth Spencer and 3 anonymous reviewers for useful comments. This is a contribution to the research programs of the Institut des Sciences de la Mer de Rimouski.

LITERATURE CITED

- Babin M, Morel A, Gagnon R (1994) An incubator designed for extensive and sensitive measurements of phytoplankton photosynthetic parameters. *Limnol Oceanogr* 39: 694–702
- Bates SS, Cota GF (1986) Fluorescence induction and photosynthetic responses of arctic algae to sample treatment and salinity. *J Phycol* 22:421–429
- Boaden PJS (1964) Grazing in the interstitial habitat: a review. In: Crisp DJ (ed) *Grazing in terrestrial and marine environments*. Blackwell, Oxford, p 299–303
- Bunch JN, Harland RC (1990) Bacterial production in the bottom surface of sea ice in the Canadian subarctic. *Can J Fish Aquat Sci* 47:1986–1995
- Carey AG (1985) Marine ice fauna. In: Horner RA (ed) *Sea-ice biota*. CRC Press, Boca Raton, p 173–190
- Carey AG (1992) The ice fauna in the shallow southwestern Beaufort Sea, Arctic Ocean. *J Mar Syst* 3:225–236
- Carey AG, Montagna PA (1982) Arctic sea ice faunal assemblages: first approach to description and source of the underice meiofauna. *Mar Ecol Prog Ser* 8:1–8
- Conover RJ, Siferd TD (1993) Dark-season survival strategies of coastal zone zooplankton in the Canadian Arctic. *Arctic* 46:303–311
- Conover RJ, Herman AW, Prinsenberg SJ, Harris LR (1986) Distribution of and feeding by the copepod *Pseudocalanus*

- under fast-ice during the Arctic spring. *Science* 232: 1245–1247
- Cota GF, Prinsenberg SJ, Bennett EB, Loder JW, Lewis MR, Anning JL, Watson NHF (1987) Nutrient fluxes during extended blooms of Arctic ice algae. *J Geophys Res* 92: 1951–1962
- Cross WE (1982) Under-ice biota at the Pond Inlet ice edge and adjacent fast ice areas during spring. *Arctic* 35:13–27
- Feller RJ, Warwick RM (1988) 13. Energetics. In: Higgins RP, Thiel H (eds) Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, DC, p 181–196
- Friedrich C (1997) Ecological investigations on the fauna of the Arctic sea-ice. *Rep Polar Res* 246:1–211
- Garrison DL, Buck KR (1986) Organisms losses during ice melting: a serious bias in sea-ice community studies. *Polar Biol* 6:237–239
- Giere O (1993) Meiobenthology—the microscopic fauna in aquatic sediments. Springer-Verlag, Berlin
- Gosselin M, Legendre L, Therriault JC, Demers S, Rochet M (1986) Physical control of the horizontal patchiness of sea-ice microalgae. *Mar Ecol Prog Ser* 29:289–298
- Gosselin M, Levasseur M, Wheeler PA, Horner RA, Booth BC (1997) New measurements of phytoplankton and ice algal production in the Arctic Ocean. *Deep-Sea Res Part II Top Stud Oceanogr* 44:1623–1644
- Gradinger R (1999) Integrated abundance and biomass of sympagic meiofauna in Arctic and Antarctic pack ice. *Polar Biol* 22:169–177
- Gradinger R, Zhang Q (1997) Vertical distribution of bacteria in Arctic sea ice from the Barents and Laptev seas. *Polar Biol* 17:448–454
- Gradinger R, Spindler M, Henschel D (1991) Development of Arctic sea-ice organisms under graded snow cover. *Polar Res* 10:295–307
- Gradinger R, Spindler M, Weissenberger J (1992) On the structure and development of Arctic pack ice communities in Fram Strait: a multivariate approach. *Polar Biol* 12: 727–733
- Gradinger R, Friedrich C, Spindler M (1999) Abundance, biomass and composition of the sea ice biota of the Greenland Sea pack ice. *Deep-Sea Res Part II Top Stud Oceanogr* 46: 1457–1472
- Grainger EH (1991) Exploitation of Arctic sea ice by epibenthic copepods. *Mar Ecol Prog Ser* 77:119–124
- Grainger EH, Hsiao IC (1990) Trophic relationships of the sea ice meiofauna in Frobisher Bay, Arctic Canada. *Polar Biol* 10:283–292
- Grainger EH, Mohammed AA, Lovrity JE (1985) The sea ice fauna of Frobisher Bay, Arctic Canada. *Arctic* 38:23–30
- Holm-Hansen O, Lorenzen CJ, Holmes RW, Strickland JDH (1965) Fluorometric determination of chlorophyll. *J Cons Perm Int Explor Mer* 30:1–15
- Hoshiai T, Tanimura A, Kudoh S (1996) The significance of autumnal sea ice biota in the ecosystem of ice-covered polar seas. *Proc NIPR Symp Polar Biol* 9:27–34 (National Institute of Polar Research, Tokyo)
- Jassby AD, Platt T (1976) Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. *Limnol Oceanogr* 21:540–547
- Jensen P (1984) Measuring carbon content in nematodes. *Helgol Meeresunters* 38:83–86
- Kern JC, Carey AG (1983) The faunal assemblage inhabiting seasonal sea ice in the nearshore Arctic Ocean with emphasis on copepods. *Mar Ecol Prog Ser* 10:159–167
- Laurion I, Demers S, Vézina AF (1995) The microbial food web associated with the ice algal assemblage: biomass and bacterivory of nanoflagellate protozoans in Resolute Passage (High Canadian Arctic). *Mar Ecol Prog Ser* 120: 77–87
- Lean DRS, Burnison BK (1979) An evaluation of errors in the ¹⁴C method of primary production measurements. *Limnol Oceanogr* 24:917–928
- Lewis EL, Ponton D, Legendre L, LeBlanc B (1996) Springtime sensible heat, nutrients and phytoplankton in the North-water Polynya, Canadian Arctic. *Cont Shelf Res* 16: 1775–1792
- Lorenzen S (1986) *Odontobius* (Nematoda, Monhysteridae) from the baleens plates of whales and its relationship to *Gammarinema* living on crustaceans. *Zool Scr* 15:101–106
- McIntyre AD (1969) Ecology of marine meiobenthos. *Biol Rev* 44:245–290
- McIntyre AD, Warwick RM (1984) Meiofauna technique. In: Holme NA, McIntyre AD (eds) Methods for the study of marine benthos, 2nd edn. Blackwell, Oxford, p 217–244
- Melnikov I (1997) The Arctic sea-ice ecosystem. Gordon & Breach, Amsterdam
- Moens T, Verbeeck L, Vincx M (1999) Feeding biology of a predatory and a facultatively predatory nematode (*Enoploides longispiculosus* and *Adoncholaimus fuscus*). *Mar Biol* 134:585–593
- Moloney CL, Field JG (1989) General allometric equations for rates of nutrient uptake, ingestion and respiration in plankton organisms. *Limnol Oceanogr* 34:1290–1299
- Mysak LA, Huang F (1992) A latent- and sensible-heat polynya model for the North Water, Northern Baffin Bay. *J Phys Oceanogr* 22:596–608
- Nozais C, Duchêne JC (1996) Larval buoyancy and release from terebellid polychaete egg masses. *J Exp Mar Biol Ecol* 203:209–222
- Parkinson CL, Cavalieri DJ, Gloersen P, Zwally HJ, Comiso JC (1999) Arctic sea ice extents, areas, and trends, 1978–1996. *J Geophys Res* 104:20837–20856
- Parsons TR, Maita Y, Lalli CM (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press, Toronto
- Pett RJ, Vickers GP, Acreman JC, Ethier AG (1983) A seasonal study of the epontic and planktonic communities near the Issungnak artificial island and McKinley Bay in the Canadian Beaufort Sea. Arctic Laboratories Ltd, Sydney (Contract ISZ81–00026 for Department of Supply and Services Canada)
- Poltermann M (1998) Abundance, biomass and small-scale distribution of cryopelagic amphipods in the Franz Josef Land area (Arctic). *Polar Biol* 20:134–138
- Riemann F, Sime-Ngando T (1997) Note on sea-ice nematodes (Monhysteroidea) from Resolute Passage, Canadian Arctic. *Polar Biol* 18:70–75
- Riemann F, Ernst W, Ernst R (1990) Acetate uptake from ambient water by the free-living marine nematode *Adoncholaimus thalassophygas*. *Mar Biol* 104:453–457
- Runge JA, Ingram RJ (1988) Underice grazing by planktonic, calanoid copepods in relation to a bloom of ice microalgae in southeastern Hudson Bay. *Limnol Oceanogr* 33: 280–286
- Shuman F, Lorenzen C (1975) Quantitative degradation of chlorophyll by a marine herbivore. *Limnol Oceanogr* 20: 580–586
- Sime-Ngando T, Gosselin M, Juniper SK, Levasseur M (1997) Changes in sea-ice phagotrophic microprotists (20–200 µm) during the spring algal bloom, Canadian Arctic Archipelago. *J Mar Syst* 11:163–172
- Smith REH, Anning J, Clement P, Cota G (1988) Abundance and production of ice algae in Resolute Passage, Canadian Arctic. *Mar Ecol Prog Ser* 48:251–263

- Smith REH, Cavaletto JF, Eadie BJ, Gardner WS (1993) Growth and lipid composition of high Arctic ice algae during the spring bloom at Resolute, Northwest Territories, Canada. *Mar Ecol Prog Ser* 97:19–29
- Smith REH, Gosselin M, Kudoh S, Robineau B, Taguchi S (1997) DOC and its relationship to algae in bottom ice communities. *J Mar Syst* 11:71–80
- Smith SD, Muench RD, Pease CH (1990) Polynyas and leads: an overview of physical processes and environment. *J Geophys Res* 95:9461–9479
- Steiner G (1958) *Monhystera cameroni* n. sp.—a nematode commensal of various crustaceans of the Magdalen Islands and Bay of Chaleur (Gulf of St. Lawrence). *Can J Zool* 36:269–278
- Stirling I (1980) The biological importance of polynyas in the Canadian Arctic. *Arctic* 33:303–315
- Stirling I (1997) The importance of polynyas, ice edges, and leads to marine mammals and birds. *J Mar Syst* 10:9–21
- Tchesunov AV (1986) A new free-living nematode connected with sea Arctic ice. *Zool Zh* 65:1782–1787 (in Russian)
- Tchesunov AV, Riemann F (1995) Arctic sea ice nematodes (Monhysteroidea), with descriptions of *Cryonema crassum* gen. n., sp. n. and *C. tenue* sp. n. *Nematologica* 41:35–50
- Tremblay C, Runge JA, Legendre L (1989) Grazing and sedimentation of ice algae during and immediately after a bloom at the ice-water interface. *Mar Ecol Prog Ser* 56:291–300
- Vézina AF, Demers S, Laurion I, Sime-Ngando T, Juniper SK, Devine L (1997) Carbon flows through the microbial food web of first-year ice in Resolute Passage (Canadian High Arctic). *J Mar Syst* 11:173–189
- Warwick RM, Gee JM (1984) Community structure of estuarine meiobenthos. *Mar Ecol Prog Ser* 18:97–111
- Warwick RM, Price R (1979) Ecological and metabolic studies on free-living nematodes from an estuarine mud-flat. *Estuar Coast Shelf Sci* 9:257–271
- Werner I (1997) Grazing of Arctic under-ice amphipods on sea-ice algae. *Mar Ecol Prog Ser* 160:93–99
- Wieser W (1960) Benthic studies in Buzzards Bay. II. The meiofauna. *Limnol Oceanogr* 5:121–137
- Zar JH (1984) *Biostatistical analysis*, 2nd edn. Prentice-Hall International, Englewood Cliffs, NJ

Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

*Submitted: March 14, 2000; Accepted: August 24, 2000
Proofs received from author(s): July 10, 2001*