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The microbial food web associated with the ice algal assemblage: biomass and bacterivory of nanoflagellate protozoans in Resolute Passage (High Canadian Arctic)

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ABSTRACT: Biomass and grazing activity of sea ice microorganisms smaller than 20 µm were studied at Resolute Passage in the Canadian Arctic during the algal bloom in spring 1992. The spatial variation in biomass beneath a 225 m^2 area with changing snow cover was almost as great as the temporal change (under a constant snow cover) over the 5 wk sampling period. Cell density in the ice varied from $\leq 7 \times 10^7$ to 2.6×10^9 cells m^{-2}. Total bacterivory of the protozoan community was assessed by measuring the disappearance of fluorescently labelled bacteria over 20 h. Feeding rates by heterotrophic nanoprotozoans (HNAN) were high at the beginning of the sampling period (late April) but decreased to very low values by the end of May; HNAN clearance rates ranged from ≤3 to 86 nl $HNAN^{-1}$ h^{-1} (mean = 12 nl $HNAN^{-1}$ h^{-1}) while ingestion rates ranged from ≤3 to 64 bacteria $HNAN^{-1}$ h^{-1}. The carbon budget analysis indicates that bacteria alone could not provide the required energy for the observed protozoan growth. The results suggest that a shift in the grazing behavior of HNAN occurred during the bloom season, modifying the microbial food web dynamics.

KEY WORDS: Nanoprotozoan · Bacterivory · Arctic

INTRODUCTION

The trophic structure of aquatic food webs affects the flow of energy that reaches top trophic levels. It is generally assumed that a greater number of trophic steps leads to more energy dissipation from respiration and excretion, resulting in less energy being transferred to higher trophic levels (Pomeroy 1984). Numerous studies have demonstrated that the role of bacterioplankton in these flows is important. A significant fraction of the carbon fixed by primary producers is excreted as dissolved organic carbon (DOC; Larsson & Hagström 1982). In assimilating this carbon source, bacterioplankton provide a source of particulate carbon for heterotrophic nanoprotozoans (HNAN) (Williams 1981, Azam et al. 1983). HNAN are currently thought to be major consumers of bacterial production in many aquatic ecosystems (Sherr & Sherr 1984, Porter et al. 1985, Sanders et al. 1989). These organisms play a crucial role in the regulation of microbial pathways of carbon in marine food webs (Sherr et al. 1986, 1988) and can determine the fate of the bacterial production (Pace et al. 1990).

This carbon pathway, known as the microbial loop (Azam et al. 1983), serves to return the energy in DOC to the primary phytoplankton-zooplankton food chain via bacteria and protozoans (Sherr et al. 1986, Carrick et al. 1991). The microbial loop, like nano-planktonic herbivory, can be considered a nutrient link that could become important to phytoplankton dynamics where the allochthonous nutrient supply is limited (Goldman 1984, Caron et al. 1985, Pomeroy & Wiebe 1988). The

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actual contribution of energy through heterotrophic microorganisms to higher trophic levels is a function of the length and efficiency of the food chain (Hagström et al. 1988, Pomeroy & Wiebe 1988). More generally, the microbial food web is thought to increase the overall trophic efficiency of planktonic food webs (Sherr & Sherr 1984, Porter et al. 1985, Gifford 1991).

The microbial food web has been studied in various environments (e.g. Caron et al. 1985, Coffin & Sharp 1987, Weisse 1989, Pace et al. 1990, Pomeroy et al. 1990, Weisse & Scheffel-Möser 1991). However, only a few studies have been completed in the Arctic (e.g. Pomeroy et al. 1990, Smith & Clement 1990, Gradinger et al. 1991). For sea ice microbial communities, most of the work has been done in Antarctica (e.g. Sullivan & Palmisano 1984, Garrison et al. 1986, Stoecker et al. 1992). It is now known that these ecosystems are not barren deserts of ice but support substantial populations of fish, seabirds, and marine mammals. The role of microbial food webs in these trophic transfers is not well established. It has been suggested that in high latitude ecosystems, the microbial loop is not always a dominant part of the marine food web (Nielsen & Richardson 1989, Smith et al. 1989, Pomeroy et al. 1990). Azam et al. (1991) proposed that the role of the microbial loop in Antarctic waters is especially important during the dark winter, when primary production is absent and all secondary production is presumably supported by a detritus-based food web. This role is diminished during spring, when primary production greatly exceeds bacterial production. This kind of variation in the importance of the microbial food web has been observed in other ecosystems as well (see Legendre & Le Fèvre 1991, Selmer et al. 1993 and references therein).

During the Arctic spring, algal blooms occur at the bottom of the first-year ice as solar radiation increases (Smith et al. 1989, Bergmann et al. 1991). In the surface mixed layer of Resolute Passage, High Canadian Arctic, the quantity of nutrients was 3 to 10 times greater than estimates of the total demand of ice algae during the bloom (Cota et al. 1987). Light, rather than nutrients, was found to be the major environmental factor regulating ice algal growth in Resolute Passage (Gosselin et al. 1993). Heterotrophic microbial communities associated with ice algae develop at the ice-water interface. Bacterial numbers increase exponentially during the bloom, but the net bacterial production was still found to be only a small fraction of the co-occurring algal production (Smith et al. 1989). Gradinger et al. (1991) reported the presence of autotrophic and heterotrophic flagellates as well as ciliates and metazoa at the ice-water interface. Although all these groups have been identified, the trophic links connecting them have still not been elucidated. Nevertheless, evidence drawn from bacterial thymidine assimilation (Smith & Clement 1990) suggests that about half of the bacterial production is either lost from the ice or grazed by the microfauna during the ice algal bloom.

This study constitutes the first attempt to measure grazing activities within the sea ice microbial community. Research focused on the grazing activity of nanoprotozoans on bacteria using fluorescently labelled bacteria (FLB; Marrasé et al. 1992, Sherr & Sherr 1993). Variations in biomass and grazing activity were measured under different snow covers during the ice algal bloom season. The importance of bacteria as a food source for nanoprotozoans and the environmental and ecological controls on bacterivory were evaluated.

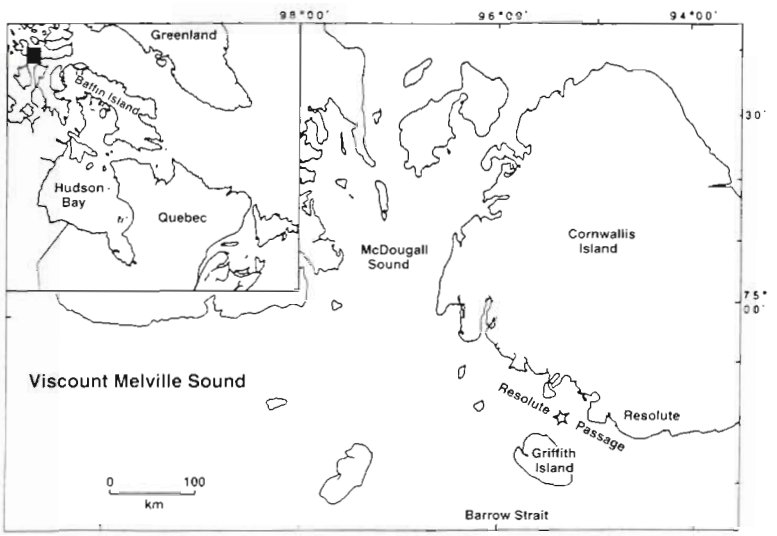

Fig. 1 Location of the sampling site (☆) in Resolute Passage, High Canadian Arctic

MATERIALS AND METHODS

Samples were collected between late April and the end of May 1992 at a field station located on first-year ice in Resolute Passage in the High Canadian Arctic (Fig. 1). The station was located on 2 m of land-fast ice above about 120 m of water. The snow cover varied from 4 to 40 cm during the study period (M. Gosselin & M. Levasseur pers. comm.). Irradiance below the ice-water interface was less than 1% of the incident irradiance (Gosselin et al. 1993). Current speeds just below the ice were generally high (ca 10 cm s^{-1}), extremely variable, and

dominated by semi-diurnal tides (Shirasawa & Ingram 1993). The ice algal bloom occurred from April to June as the sun returned to polar latitudes, and ended when the ice began to melt and algae were released into the water column. Cota et al. (1987) provide additional details on the study site.

Sampling and enumeration of nanoflagellates. Ice cores were collected every 4 d using a SIPRE ice corer. This ice corer has a 7.6 cm internal diameter cylinder and samples the bottom of the ice sheet from the top of the ice (Smith et al. 1987). Three cores were melted and combined to get enough water for the experiments, but no replicates cores were collected. To study the influence of light on the microbial community, 2 sites of different snow cover (thin and thick) were investigated. The thin and the thick snow sites were covered by an average of 8 and 20 cm of snow, respectively. By choosing a constant snow cover thoughout the study, we tried to remove the heterogeneity factor due to the snow cover. Net growth rates of HNAN and autotrophic (or pigmented) nanoflagellates (PNAN) were estimated using an exponential growth model.

$$N_t = N_0 e^{\mu t} \quad (1)$$

where N_0 and N_t are the initial and the final concentrations of cells per m^2 after t days and μ is the net growth rate.

To study the vertical distribution of microorganisms in the ice matrix, 3 profiles were made over the sampling period with an automated arm sampler (Herman et al. 1993) on 7, 16, and 21 May. The automated arm sampler takes the core from under the ice and keeps the interface water in a chamber. Ice layers 0.5 to 2 cm thick were sliced with a small saw and melted in filtered sea water. Enumeration of HNAN, PNAN, and total bacteria, and determination of chlorophyll *a* (chl *a*) concentrations were made for each ice layer. For fluorometric determination of chl *a*, duplicate samples were filtered on Whatman GF/F glassfiber filters and extracted for 24 h in 90% acetone at 0°C (Parsons et al. 1984). In addition, concentrations of nanoflagellates were measured in the water column. Samples were collected with a syringe sampler system (5, 10, 25, and 50 cm from the bottom of the ice sheet), a Niskin bottle (2.5 and 5 m), and also from the chamber water of the automated arm sampler.

On 17 May, the horizontal heterogeneity of bottom ice biomass and bacterivory of nanoflagellates was studied by making a square grid of 9 cores separated by 5 m. This experiment was not replicated due to logistic constraints.

The bottom 4 cm of all ice cores (the skeletal layer of congelation ice) was cut off and melted in filtered sea water in a proportion of approximately 1:2 to 1:3 to avoid osmotic stress (Garrison & Buck 1986). For ice cores taken with the arm sampler, ice was melted in the chamber water. Salinity of the meltwater was determined using a Solomat MPM 2000 salinometer (Solomat Instrumentation) and ranged from 21 to 27‰. Water temperature was maintained below 1°C during melting and at −1°C afterward with a thermoregulated circulating bath. Subsamples of the meltwater (50 ml) were preserved with 0.5% final volume alkaline Lugol solution followed by 3% final volume borax-buffered formalin for cell enumeration (Sherr et al. 1989).

Subsamples of 1 to 20 ml of preserved samples were stained with DAPI (4,6-diamidino-2-phenylindole) at a final concentration of ~25 µg ml^{-1} and filtered onto 0.8 µm Nuclepore filters for enumeration of nanoflagellate protozoans. Subsamples of 1 to 3 ml were also stained with DAPI and filtered onto 0.2 µm Nuclepore filters for total bacterial counts. Organisms were counted using an epifluorescence microscope (Sherr et al. 1993). The presence of abundant masking diatom chains constrained the filtration volume. Nanoflagellates were classified as autotrophic or heterotrophic based on the presence or absence of chl *a* autofluorescence. Counts were corrected for the dilution of the added seawater.

Measurement of grazing. Grazing activity of protozoa on bacteria was measured for each ice core sampled. Subsamples of 500 ml were taken from the ice meltwater, poured into rinsed glass bottles, and acclimated at *in situ* temperature for 1 h. Bottles were maintained at *in situ* temperature during incubation with a circulating bath pumping water from under the ice. They were exposed to attenuated light conditions inside the tent on the ice camp and were carefully and regularly turned throughout the incubation. Bacterivory was estimated by measuring the long-term disappearance of FLB in the incubation water (Marrasé et al. 1992, Sherr & Sherr 1993). FLB were prepared from a natural assemblage from the St. Lawrence estuary following the procedure of Sherr et al. (1987). Bacteria were concentrated by centrifugation after having grown for 2 d with yeast extract, giving a stock suspension containing approximately 5×10^8 FLB ml^{-1}. FLB were 1 to 2 µm in length, which resembled the size of natural bacterioplankton in this ice system. Incubation bottles were subsampled 2 to 5 times over 20 h. At each sampling time, 10 to 50 ml was removed with an automatic pipette and preserved in the same way as the biomass samples (see above). This preservation method was found to cause less egestion problems (Sherr et al. 1989).

The final FLB concentration added to the incubation bottles ranged between 2.5 and 11.7×10^5 FLB ml^{-1} (mean = 7.7×10^5, standard deviation = 2.1×10^5). This variation was probably due to the fact that the FLB preparation remained clumped even after sonification

and mixing. For long-term disappearance experiments Marrasé et al. (1992) added FLB at concentrations that were 20 to 50% of the abundance of natural bacteria, a compromise between accuracy of measurements and the potential for altering the feeding activity of the community. The natural bacterial concentration in the meltwater averaged approximately 8 and 4×10^5 ml^{-1} for thin and thick snow cover, respectively. The added FLB concentration was then approximately equal to the bacterial concentration in the meltwater. Therefore, although FLB cannot be considered as tracers (McManus & Okubo 1991), these experiments can provide a useful index of the grazing activity of HNAN on bacteria for ice environments.

Clearance rates (*CR*; Fenchel 1984), expressed in nl HNAN^{-1} h^{-1}, were calculated from rates at which fluorescent prey disappeared divided by HNAN concentration ([HNAN]):

$$CR = (\ln N_0 - \ln N_t)\ t^{-1}\ [\mathrm{HNAN}]^{-1} \qquad (2)$$

where N_0 is initial FLB concentration, and N_t is final FLB concentration after t hours. This expression of protozoan feeding rates in long-term disappearance experiments is slightly different from that used by Marrasé et al. (1992). Ingestion rates (*IR*), expressed in terms of bacteria HNAN^{-1} h^{-1}, were calculated from clearance rate values ($IR = CR \times$ bacterial concentration). The bacterial concentration used for the calculation is the sum of FLB and the natural bacteria found in the meltwater, i.e. the concentration to which protozoans were exposed during grazing experiments. Average values for the natural bacterial concentration on both sites were calculated and used to obtain the ingestion rates.

Carbon conversion factors. To evaluate the carbon content of prey and predators, lengths and widths of protozoans and bacteria were measured and volumes were calculated by assuming that cells were spherical or ellipsoidal. Individual protozoans were measured under epifluorescence microscopy using an ocular micrometer (n = 30 to 35 cells). Bacteria were measured with an image analysis system coupled with an epifluorescence microscope (n = 250 to 300 cells). We assumed that there were no significant changes in the size distribution of HNAN or the bacteria population during the season or under different light conditions. The conversion factor used to calculate carbon content was 220 fg C µm^{-3} for nanoprotozoans (Børsheim & Bratbak 1987) and bacteria (Bratbak & Dundas 1984, Kottmeier et al. 1987, Smith et al. 1989).

RESULTS

Bacteria, HNAN, PNAN, and chl *a* were most abundant in the lowest 2 cm of the ice matrix (Fig. 2). For example, 78% of the total bacterial biomass, 82% of HNAN, 81% of PNAN, and 94% of chl *a* were found in the lower 2 cm of a 4 cm core on 21 May 1992. The other profiles showed similar biomass distributions. Values were low in the water just under the ice-water interface (e.g. less than 1% of the total biomass for HNAN, PNAN, and chl *a* and less than 5% for bacteria; 21 May 1992) and lower than the detection limit deeper in the water column.

Spearman rank correlations were calculated to investigate the effect of snow thickness on microbial biomass and activity (Sokal & Rohlf 1981). Significant inverse correlations ($p < 0.05$) were found between the snow thickness and the abundance of HNAN, PNAN, and bacteria (Fig. 3a, b). At low values of snow depth, HNAN were more abundant than PNAN; this trend was reversed at greater snow depths. Furthermore, a positive correlation ($p < 0.01$) between snow thickness and bacterivory was observed (Fig. 3c). When there was little snow, higher light intensities, and higher biomasses, the clearance rate of bacteria was very low. However, it increased (from 5 to 25 nl HNAN^{-1} h^{-1}) when snow depth exceeded 25 cm where algae was scarce.

The number of nanoflagellates (HNAN + PNAN) in the lower 4 cm of the ice increased from 2.4 to 25.9 × 10^8 cells m^{-2} under the thin snow cover and from 0.3 to 14.8 × 10^8 cells m^{-2} under the thick snow cover during

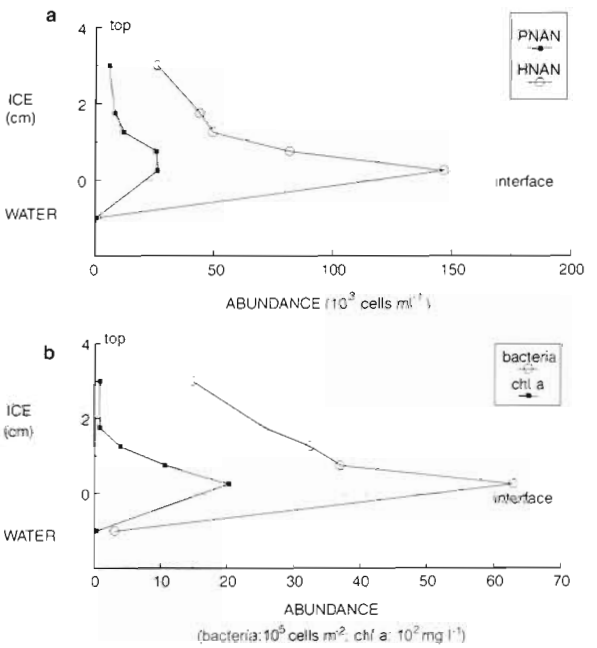

Fig. 2. Vertical distribution of (a) pigmented (PNAN) and heterotrophic (HNAN) nanoflagellates, and (b) bacterial biomass and chlorophyll *a* concentration, in the lower 4 cm of the ice on 21 May 1992

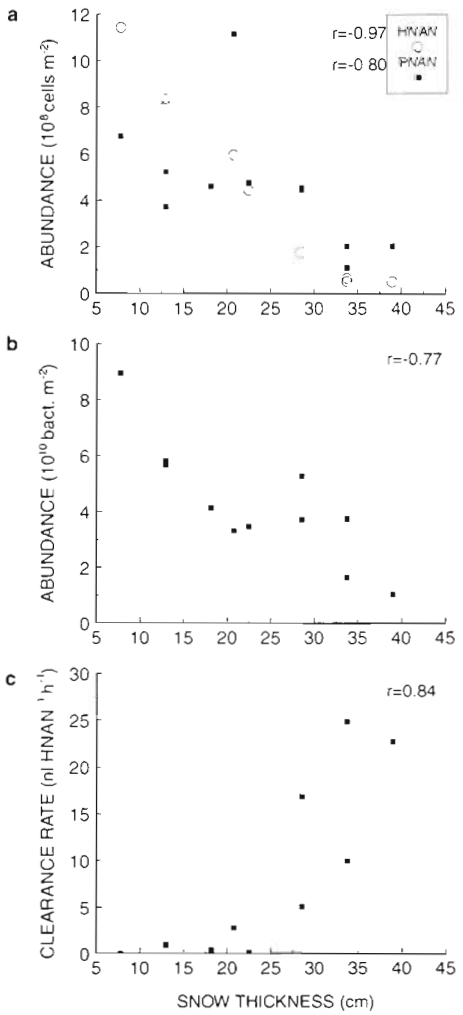

Fig. 3. (a) Nanoflagellate concentration, (b) bacterial concentration, and (c) clearance rate in the bottom 4 cm of sea ice beneath variable snow cover Spearman's rank coefficient (r) is indicated for each graph. Significance levels are all $p < 0.05$

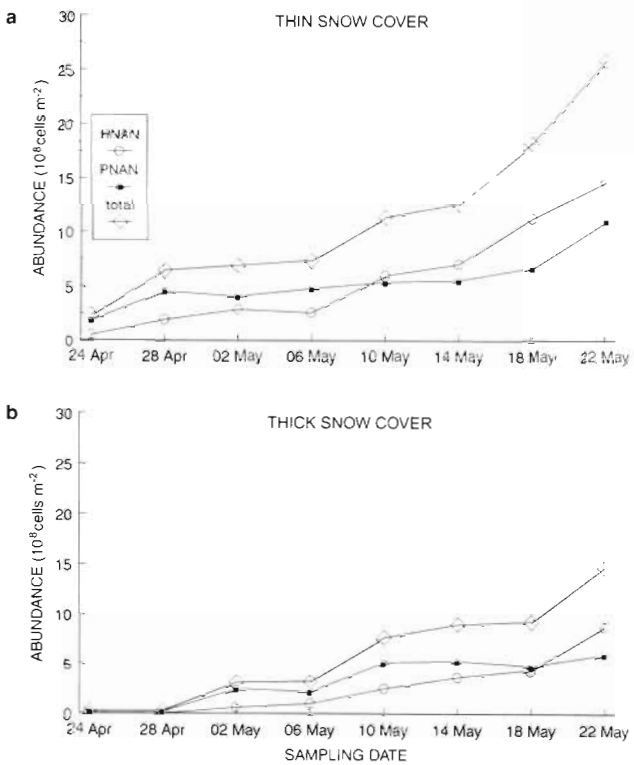

Fig. 4. Seasonal variation of heterotrophic (HNAN) and pigmented (PNAN) nanoflagellates for (a) thin and (b) thick snow cover

the sampling period (Fig. 4a, b). Net growth rates are given in Table 1. The significance level of the exponential regression analysis was always <0.01. Unexpectedly, net growth rates were faster under thick snow cover than under thin. As the season progressed, heterotrophs always increased in relative abundance to autotrophs (see Fig. 4).

The ice meltwater also contained rod-shaped or ellipsoidal bacteria 1 to 5 µm in length at concentrations ranging from 10^{10} to 10^{11} cells m^{-2}. They were counted separately from the ordinary spherical bacteria because they were larger and were stained differently by DAPI. They were almost absent in the water below the interface in contrast to ordinary small bacteria, which were still found in concentrations near 4×10^5 ml^{-1}. A net growth rate of 0.12 d^{-1} was estimated for these large bacteria from their accumulation in sea ice.

Clearance rates, calculated from the FLB disappearance rate, gave values ranging from ≤3 to 86 nl HNAN^{-1} h^{-1}, with mean values over the time series of 5 and 23 nl HNAN^{-1} h^{-1}, for thin and thick snow cover, respectively. Using the total bacterial concentration (FLB + natural bacteria) in the meltwater, ingestion rates ranged from 3 to 64 bacteria HNAN^{-1} h^{-1}. The clearance rate of bacteria for thin and thick snow cover decreased to near zero as the season progressed (Fig. 5). However, the clearance rate under the thick snow had a higher initial value (86 nl HNAN^{-1} h^{-1}) than for the thin snow (12 nl HNAN^{-1} h^{-1}).

We can estimate whether the observed consumption of bacteria was sufficient to satisfy the carbon requirement (in fg C cell^{-1} h^{-1}) for the net HNAN population

Table 1. Net growth rates for heterotrophic (HNAN) and autotrophic (PNAN) nanoflagellates calculated with an exponential growth model for 2 different snow covers. Significance level of the regression analysis is $p < 0.01$

Snow depth	Net growth rate (d^{-1})	
	HNAN	PNAN
Thin	0.108	0.046
Thick	0.182	0.126

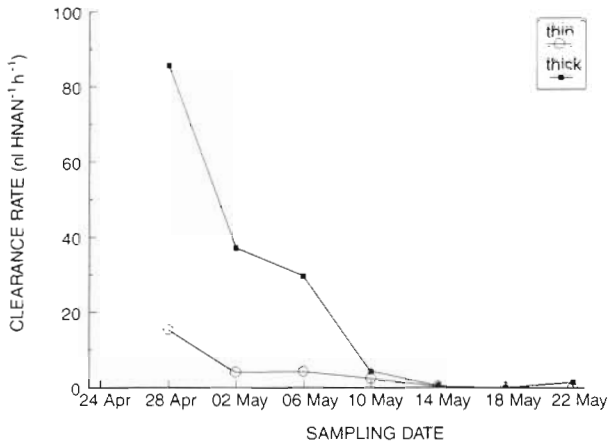

Fig. 5. Seasonal variation of protozoan clearance rates for thin and thick snow cover

growth. For these calculations, HNAN cell size (V), carbon content (f), growth rate (μ, in h^{-1}), and growth efficiency (E) are needed:

$$\text{Carbon requirement} = E^{-1} \mu V f \quad (3)$$

Measurements of HNAN <20 µm gave an average volume of 118 μm^3. The net growth rate of HNAN obtained was 0.108 and 0.182 d^{-1} for the thin and the thick snow cover sites, respectively. Carbon demands based on net growth rates have to be considered as minimal because the HNAN mortality due to grazing was not considered. We assume a growth efficiency of 40% (Sanders et al. 1992), which falls within the range of values reviewed by Caron & Goldman (1990). Based on cell volumes and the carbon conversion factor, minimal carbon demand for HNAN was 292 and 492 fg C $HNAN^{-1}$ h^{-1} for thin and thick snow sites respectively.

The average bacterial cell volume was 0.472 μm^3, giving a carbon content of 104 fg C $cell^{-1}$. This result is similar to that of Smith et al. (1989) for the lower 4 cm of the ice near Resolute Passage in 1985. The consumer demand in carbon units can be converted to the number of bacteria that need to be ingested for comparison with measured ingestion rates. Carbon requirements are compared to grazing activity for the 2 sites and for different sampling dates in Table 2. We assumed a constant growth rate throughout the sampling period. The bacterial ingestion rate seemed sufficient to meet the protozoan carbon demand at the beginning of the sampling period but became inadequate for both sites after 10 May.

DISCUSSION

Abundance, distribution and growth

The occurrence of a biomass maximum in the lower decimeters of the ice is well documented. Kottmeier et al. (1987) concluded that the bottom 5 cm of Antarctic land-fast ice contained most of the actively growing bacteria even though bacterial biomass extended throughout the bottom 20 cm (Sullivan & Palmisano 1984). In Arctic land-fast ice, Gradinger et al. (1991) reported that autotrophic cells were located mostly in the lowest 10 cm while bacteria and HNAN were distributed more homogeneously in the lower 30 cm of the ice matrix. We found that most of the biomass occurred in the first 2 or 3 cm (Fig. 2). Those differences may be due to differences in methodology (thickness of ice slices) or may indicate that the vertical distribution of sea ice microbial communities can be spatially and temporally (from year to year) different depending on temperature and on ice formation history, which determine the volume fraction and physicochemical properties of brine pockets (Gow et al. 1990). Palmisano et al. (1987) concluded that high salinity brine may be one factor that limits the vertical distribution of microalgae within the ice. Salinity in ice brine channels can be higher than 50‰ (Gradinger et al. 1991).

Snow cover, modifying under-ice irradiance, seems to be a major factor influencing the heterogeneity of biomass, growth rates, and grazing rates of the sea ice microbial community, especially in a context of light limitation. Gosselin et al. (1986) concluded from their research in the southeastern Hudson Bay that the horizontal heterogeneity of the snow-ice cover provided diversified bottom-ice habitats where irradiance did or did not meet the physiological requirements of the ice microalgal cells, resulting in strong patchiness in the distribution of those cells. In the High Arctic, Welch & Bergmann (1989) found that snow cover indirectly con-

Table 2. Protozoan carbon requirements corresponding to the observed net growth rate and seasonal evolution of ingestion rates for the 2 different snow covers. Carbon requirements and ingestion rates are in bacteria $HNAN^{-1}$ h^{-1}

Snow depth	Carbon requirement	Ingestion rate 28 Apr	2 May	6 May	10 May	14 May	18 May	22 May
Thin	3	30.6	5.5	5.6	4.2	≤3	≤3	≤3
Thick	5	63.7	34.5	25.2	4.9	≤3	≤3	≤3

trolled algal growth by its effect on light. Our results show that abundances and grazing activity of protozoans were also related to the snow cover (Fig. 3). Over an area of 225 m^2 with snow cover ranging from 8 to 40 cm, the nanoflagellate biomass and the ingestion rates varied over 1 order of magnitude. From these results, it is clear that the thickness of snow cover must be taken into account when sampling the bottom ice.

The number of heterotrophic nanoprotozoa (0.2 to 35×10^3 ml^{-1} melted sea ice) we found at the ice-water interface is in the upper part of the range commonly found in marine waters. Abundances of HNAN in open ocean waters, continental shelf waters, and estuaries range from 10^2 to 10^4 ml^{-1} (reviewed in Sherr & Sherr 1984). Garrison & Buck (1989) reported values lower than 10^3 HNAN ml^{-1} for the ice edge zone water in the Weddell Sea, Antarctica. Gradinger et al. (1991) found concentrations of heterotrophic flagellates lower than 1.1×10^3 ml^{-1} in the lowest 20 cm of melted Arctic sea ice. Nonetheless, these comparisons must be made with caution as the thickness of the ice cores and the vertical distribution of the cells in the ice were different.

The presence of a significant fraction of large bacteria in our ice samples suggests that heterotrophic activity was taking place (Kottmeier et al. 1987). Large bacteria were not found in the sea water under the ice, suggesting that special conditions for their growth, such as higher substrate abundance and nutrients, are found in brine channels (Grossi & Sullivan 1985). Pomeroy et al. (1990) reported dense aggregations of rod-shaped bacteria measuring from 1 to 5 µm associated with detritus and diatom frustules in floating clumps of ice algae that had melted out of the ice sheet. The observations of Pomeroy et al. (1990) were made at the same site as our study (Resolute Passage), but later in the season (June 1988), when algae are released from the melting ice. Sullivan & Palmisano (1984) and Kottmeier et al. (1987) reported the presence of large, abundant, morphologically distinct sea ice bacteria in Antarctica. These larger bacteria may represent a potential food resource for larger protozoans, such as ciliates, in an abbreviated food chain (Sherr & Sherr 1987).

Dynamics of grazing and carbon flows

Clearance rates measured in this study (from ≤3 to 86 nl HNAN^{-1} h^{-1}; mean = 12 nl HNAN^{-1} h^{-1}) fall in the range of values reported from various coastal or freshwater environments. Clearance rates assessed with different methods and on different communities vary from 0.1 to 100 nl HNAN^{-1} h^{-1} (reviewed by Berninger et al. 1991). Our ingestion rates calculated from clearance rates ranged from ≤3 to 64 bacteria HNAN^{-1} h^{-1} (averaging 13 bacteria HNAN^{-1} h^{-1}). This agrees well with previous studies that reported values from near 0 to >100 bacteria HNAN^{-1} h^{-1} (Berninger et al. 1991, Weisse & Scheffel-Möser 1991).

A maximal ingestion rate G_m (µg C consumed µg^{-1} C of grazer body mass h^{-1}) can be estimated from the body weight of the grazer and the temperature of the water (Moloney & Field 1989, Connolly & Coffin in press):

$$G_m = 0.0045 W^{-0.25} e^{0.06T} \quad (4)$$

where W is the weight in mg and T the temperature in °C. The allometric approach has also been used by Garrison & Buck (1991) to estimate herbivory in Antarctic sea ice. This value, multiplied by the carbon content of grazers and divided by the carbon content of prey for Resolute Passage samples, gives 54 bacteria HNAN^{-1} h^{-1}, assuming an average protozoan weight of 1.18×10^{-7} mg and a water temperature of −1.7°C. Our ingestion rates seem reasonable compared to this maximal value.

Because the brine was diluted by melting ice when samples were collected and processed, determining the true bacterial concentration that protozoa were exposed to is difficult. It is well known that prey density can significantly influence the grazing behavior of predators (Parslow et al. 1986, Sanders et al. 1990). In some cases, a threshold concentration of bacterial prey exists below which grazers change their feeding behavior and growth rate. This limit is near 10^6 bacteria ml^{-1} for some environments (e.g. Fenchel 1982, Sanders et al. 1990, Weisse 1990). The final bacterial concentration that protozoans were exposed to in our grazing experiments was near this feeding threshold. Organisms may experience higher prey concentrations in brine channels. The brine volume fraction of an ice core is a function of temperature and ice structure (Cox & Weeks 1982, Gow et al. 1990). Golden & Ackley (1981) estimated this fraction to be 5 to 12% by volume of land-fast ice. Thus, to estimate the effect of dilution we assumed that bacteria and protozoans were concentrated in a 12% brine volume fraction and that the prey concentration experienced by protozoa in the ice was then an order of magnitude higher. Assuming that the mean clearance rate was still 12 nl HNAN^{-1} h^{-1}, the ingestion rate ($IR = CR \times$ bacterial concentration) would reach 72 bacteria HNAN^{-1} h^{-1} in brine channels compared to 8 bacteria HNAN^{-1} h^{-1} in the meltwater. However, the clearance rate is often reduced at higher prey concentration and the estimates of ingestion here are approximate. Nevertheless, this exercise provides an upper limit to the grazing estimates and is similar to values calculated from HNAN biomass (above). To avoid this kind of interpretational problem, it may be

useful to perform short-term uptake assays (Sherr et al. 1989) for different prey concentrations.

Many factors exist that may introduce artifacts into the calculation of clearance rates and ingestion rates. As previously mentioned, feeding rates are closely related to bacterial concentration. The bacterial concentration to which the protozoans were exposed in the incubation meltwater was enhanced by the addition of FLB, but was probably lowered by melting processes. Density relationships between HNAN and bacteria in the brine channels may be quite different from those in our experiments since we were unable to reproduce natural conditions. On the other hand, the clearance rates may have been overestimated since HNAN <20 µm were considered the sole bacterial predators (see Eq. 2). Other organisms that were present in the samples, such as ciliates or pigmented nanoflagellates (mixotrophic algae), may have grazed on bacteria as well (Sherr & Sherr 1987, Sanders 1991). Moreover, changes in the ambient bacterial population were not followed through the season, and we used the same batch of FLBs for the entire study. Protozoans are known to have a preference for larger prey (Andersson et al. 1986, Pace et al. 1990). Consequently, there is a possibility that the decrease in clearance rate we observed over the duration of the study was partly due to greater discrimination against FLB with time, assuming an augmentation of the mean bacterial cell size.

While keeping these uncertainties in mind, we can still elaborate some interesting hypotheses. The comparison of calculated carbon requirements and measured ingestion rates for the thin and thick snow cover sites suggests that bacterial feeding rates were insufficient to support the observed net growth of protozoa after 10 May. However, bacteria were certainly an important part of the protozoan diet early in the sampling season. Nanoflagellate protozoa can graze on small algae not much smaller than themselves (Goldman & Caron 1985), or may use dissolved organic carbon (DOC) and nitrogen (DOM) in an abbreviated food chain (Sherr 1988, Marchant & Scott 1993, Tranvik et al. 1993). Small algae and small pigmented nanoflagellates were relatively abundant in the Resolute Passage samples (see PNAN abundances in Fig. 4). Assuming the same carbon conversion factor for PNAN as for HNAN, the average carbon content of the PNAN pool was 134 to 196% of the bacterial pool after 10 May, thus representing a significant source of food for HNAN. These autotrophs could be the 'missing' food that supported the observed HNAN growth, especially at the end of the sampling period. Protozoa may have a preference for larger prey (Andersson et al. 1986) or may consume algae as well as bacteria (Goldman & Caron 1985). As autotrophs become more abundant with increasing light, they may become a more significant fraction of the protozoan diet. Similarly, DOM from diatom exudates and PNAN excretion that increases as the bloom season advances could also have met the additional energy requirement of the nanoflagellates.

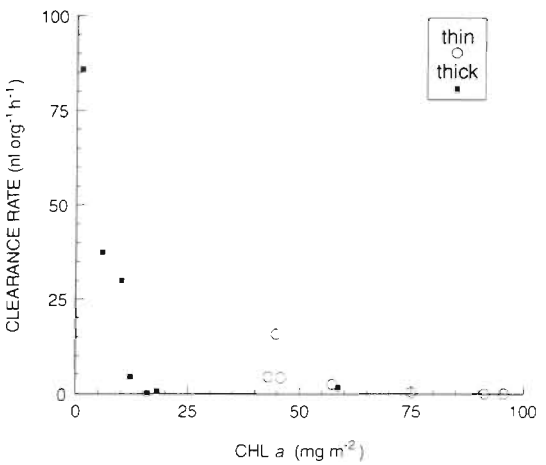

Fig. 6. Relation between clearance rate and chl *a* concentration for thin and thick snow cover. Significance level of the logarithmic regression is $p < 0.01$ with $r = 0.75$

Either hypothesis could explain why grazing on bacteria decreased over the season and was lower under a thinner snow cover. For these 2 situations, grazing on bacteria was lower when autotrophic cells (PNAN or chl *a* values) were found in higher concentration. A significant inverse correlation ($p < 0.01$, $r = 0.75$) was found between the chl *a* concentration in the ice and the clearance rates of bacteria for time series of thin and thick snow covers (Fig. 6). The relationship is logarithmic and there seems to be a threshold chl *a* concentration (near 60 mg m^{-2}) below which feeding on bacteria becomes relatively important. It is possible that protozoans feed on bacteria when algae are scarce (Sherr et al. 1991). Moreover, as the ice algal bloom, consisting mainly of diatoms, was taking place, the PNAN growth seemed to be suppressed (Fig. 4a, b). This suppression may be due to photoinhibition (Barber & Andersson 1992) or to the grazing pressure of protozoans on this size fraction.

An important question is what happened to the bacterial population when they were under reduced grazing pressure (Fuhrman & Azam 1980, Weisse & Scheffel-Möser 1991). Maranger et al. (1994) found an increase in bacterial abundance from 0.6 to 42 $\times$ 10^{10} cells m^{-2} accompanied by a decrease in individual cell production in the lower 4 cm of the ice in Resolute Passage in spring 1992. The accumulation of less active bacterial cells in the ice could be related to the reduction in grazing pressure (see the nurturing effect in Sieburth & Davis 1982).

Our study suggests that the structure of the microbial food web changed during the ice algal bloom. There was important bacterivory early in the study that decreased to almost zero after 10 May, just as the algal bloom was reaching its maximum. All of our data lead to the hypothesis that the consumption of small algae or direct ingestion of DOM by HNAN may have become more important at this time of the year. Bacterivory may be an important carbon pathway at the beginning of the bloom or in the winter season, when autotrophic cells are scarce (Azam et al. 1991). For future studies, we propose the use of fluorescently labelled algae (Sherr et al. 1991) and FLB to measure direct protozoan feeding rates during the formation of the ice algal bloom. In addition, the measurements of DOM uptake rates by protozoans would also be essential for determining their importance in meeting the energy requirements.

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