Vol. 40: 239–246, 1987 | MARINE ECOLOGY – PROGRESS SERIES
Mar. Ecol. Prog. Ser. | Published October 28

Grazing by microzooplankton in the eastern Canadian arctic in summer 1983

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ABSTRACT: Grazing of microzooplankton on phytoplankton was studied in the eastern Canadian Arctic by the dilution method. In Jones Sound, significantly high growth and grazing coefficients on phytoplankton were observed even though the mixed layer nutrients were low. In Baffin Bay, growth and grazing coefficients could be observed only when excess nutrients (NO_3) were added to the experimental bottles. The microzooplankton community grazed 8 to 15% of initial standing stock and 40 to 114% of potential primary production daily in Jones Sound, and 9 to 15% of initial standing stock and 37 to 88% of potential production daily in Baffin Bay. If nanophytoplankton alone is considered as potential food for microzooplankton, then the grazing impact of this community on the standing stock and production of the total phytoplankton would be on average 5 to 31% d^{-1} in Jones Sound and 10 to 47% d^{-1} in Baffin Bay, respectively. The grazing of the high latitude microzooplankton community studied by the dilution method is comparable to that in the lower latitudes.

INTRODUCTION

Recent studies on the distribution and abundance of microzooplankton (organisms < 200 µm) in temperate and tropical waters have shown that this community contributes a significant proportion to the total zooplankton community in all seasons (Beers & Stewart 1970, 1971, Taguchi 1976, Takahashi & Hoskins 1978, Revelante & Gilmartin 1983, Paranjape et al. 1985). The potential dynamic role of this community as consumers of small phytoplankton and in recycling of nutrients has long been emphasized (Pomeroy 1974, Harrison 1980, Conover 1982, Paasche & Kristiansen 1982, Goldman & Caron 1985). Based on theoretical calculations, microzooplankton were estimated to have consumed 40 to 70% of primary production (Riley 1956, Beers & Stewart 1970) while, based on experimental data, certain components of the microzooplankton community alone would have consumed 20 to 100% of primary production (Heinbokel & Beers 1979, Capriulo & Carpenter 1983, Cosper & Stepien 1984).

Most of these observations on the role of microzooplankton in resource utilization have come from studies done in temperate latitudes. Recently, Taniguchi (1984) showed that absolute abundances of microzooplankton in the boreal Pacific and western Arctic waters were as high as those found in lower latitudes. Similar results have been obtained for Antarctic waters (Garrison et al. 1984). These observations suggest that the grazing impact of microzooplankton on phytoplankton in high latitudes might be similar to that observed in the lower latitudes. However such information is presently not available. We report here experiments conducted to study the grazing impact of the microzooplankton community on phytoplankton by the dilution method described by Landry & Hassett (1982). The experiments were conducted on board CSS *Hudson* (Cruise 83-023) in the summer of 1983 in the eastern Canadian Arctic (Fig. 1).

METHODS

The grazing experiments were performed in Jones Sound and in central Baffin Bay from 19 Aug to 13 Sep 1983. A pumping system described by Herman et al. (1984) was used to collect water for experiments. The instrument package on the system also provided profiles of temperature, conductivity, pressure, *in vivo* fluorescence of chlorophyll *a* and underwater light levels. For each experiment, two 22 l polyethylene carboys were filled with seawater screened through 160 µm mesh. One of the carboys was filtered through Whatman GF/F and stored in a covered water tank cooled with surface water. This filtered seawater was

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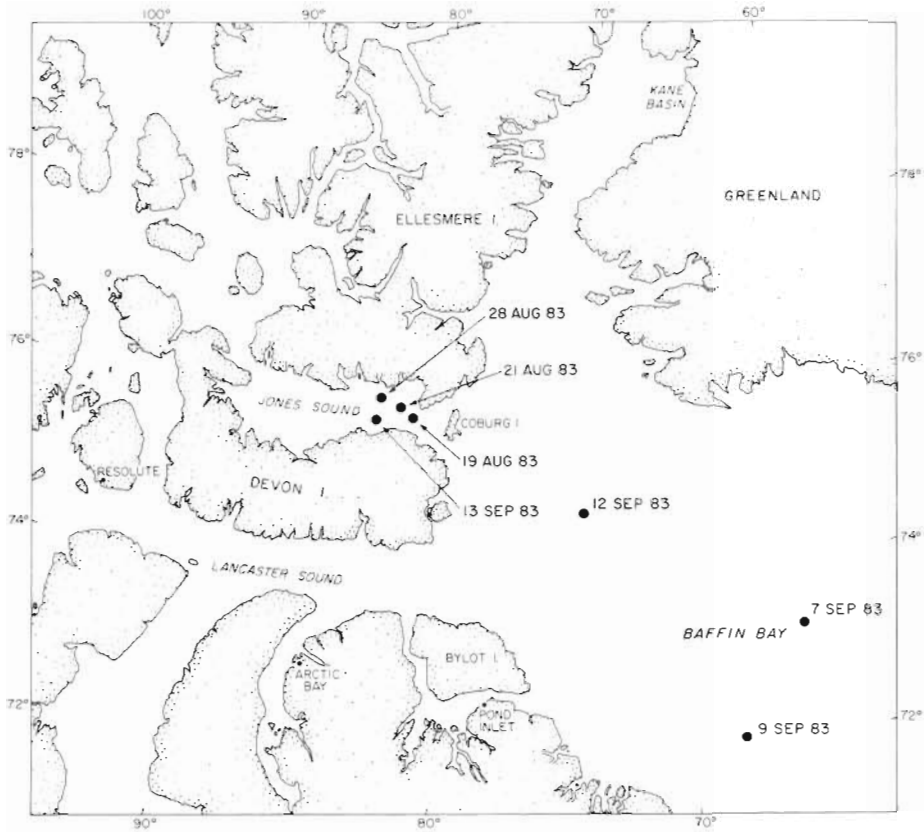

Fig. 1. Station locations in Jones Sound and Baffin Bay where grazing experiments were conducted

used to prepare dilutions of the unfiltered seawater from the second carboy (also kept cool in the water tank). Usually 2 or 3 dilution mixtures were prepared. Three or four 1 l, acid-cleaned, polycarbonate bottles were filled with each dilution mixture. In experiments where nutrient additions were made, excess nitrate (~ 10 µg-at l^{-1}) was added to some bottles and an equal number of additional bottles were prepared without addition of nitrate. All the bottles were incubated on deck in acrylic incubator boxes covered with nickel screens to attenuate incident light to ambient levels. Experiments were run for ~ 24 or 48 h. Incubation temperatures ranged from -1 ° to + 1 °C.

At the beginning of the incubations, samples for nutrients, chlorophyll *a* and microzooplankton abundance were withdrawn from all dilution mixtures. At the end of the incubations, similar samples were withdrawn from all experimental bottles: 100 ml of water was filtered in triplicate through 24 mm Whatman GF/F filters for chlorophyll *a* which were kept frozen until analyses; filtrate was used to measure nutrient concentrations; 500 ml or remaining seawater were preserved in 1% buffered formaldehyde-seawater solution for microzooplankton counts.

Chlorophyll *a* was assayed fluorometrically (Yentsch & Menzel 1963) after extraction in 85% acetone on Turner Designs fluorometer within 36 h after collection. Nutrients were analysed on a Technicon II Autoanalyser on board the ship. Microzooplankton were enumerated after settling 100 ml of sample in chambers using a Zeiss inverted microscope within 1 yr after collection.

In some of the experiments run for 48 h, additional samples of chlorophyll *a* were taken at about 24 h and analysed as described earlier.

The apparent growth rates of chlorophyll *a* in individual bottles were calculated by the exponential growth model given by Landry & Hassett (1982)·

$$P_t = P_o e^{(k-g)t} \quad (1)$$

or

$$\frac{1}{t} \ln \left(\frac{P_t}{P_o}\right) = k - g \quad (2)$$

where P_t = chlorophyll *a* concentration at time t; P_o = initial concentration of chlorophyll *a*; k and g = instantaneous coefficients of population growth and grazing mortality, respectively. The instantaneous coefficients k and g were determined from linear regression analysis between the apparent growth rate of chlorophyll *a* in each bottle and the fraction of raw seawater. A t-test was used to test the hypothesis that $g = 0$ (Snedecor 1956). Both the coefficients were used to calculate the

grazing loss of the potential daily production of chlorophyll while the grazing mortality coefficient was used to calculate the daily loss of the initial standing stock of chlorophyll.

RESULTS

Jones Sound

On the first 2 visits to Jones Sound (18, 20 and 28 Aug 1983), the water column was characterized by a shallow mixed layer, low nutrients and conspicuous subsurface maxima of chlorophyll and primary production. On the third visit (13 Sep 1983), the water column had become mixed, nutrients were high and maximum chlorophyll values were found at the surface (Fig. 2).

The grazing experiments on 19 and 21 Aug 1983 were conducted for 24 h. Although the mixed-layer nutrient concentrations were low, the instantaneous growth rates (and 95% confidence interval) for phytoplankton were 0.211 (± 0.036) and 0.187 (± 0.026) d^{-1}. The instantaneous mortality of phytoplankton or the grazing coefficients for these 2 d were 0.157 (± 0.052) and 0.166 (0.036) d^{-1}. On 28 Aug the experiment was run for 48 h with additional chlorophyll samples taken at 24 h. Growth rate and grazing coefficient were not significantly different from zero ($p < 0.05$) for the first 24 h. For the total incubation period (48 h), however, statistically significant growth, 0.111 (± 0.02) d^{-1} and the grazing coefficient, 0.128 (± 0.034) d^{-1} were observed (Table 1, Fig. 3), even in the absence of measurable nitrate.

On the third visit to Jones Sound (13 Sep 1983), nitrate levels in the surface mixed layer had reached 2 to 3 μg-at l^{-1} (Fig. 2). The grazing experiment performed on this visit was with nutrient addition for a duration of 48 h. Significant growth rates were observed in control and treatment bottles, in both 24 and 48 h time intervals. In the first 24 h, growth rates in control and treatment bottles were 0.244 (± 0.026) and 0.341 (± 0.048) d^{-1}, and over the total incubation period (48 h), were 0.224 (± 0.036) and 0.286 (± 0.012) d^{-1}. The instantaneous grazing mortality coefficients were 0.102 (± 0.034) and 0.163 (± 0.064) d^{-1} for the total incubation period (Table 1, Fig. 3).

Central Baffin Bay

The profiles of biological properties for 6 Sep 1983 (Fig. 2) were typical for other stations in the central Baffin Bay where grazing experiments were conducted (7, 9 and 12 Sep 1983). The physical and biological observations suggested post-spring bloom conditions, somewhat similar to those on the second visit to Jones Sound (28 Aug). A nutrient-poor surface mixed layer, and prominent subsurface chlorophyll and primary production maxima, were observed (Fig. 2).

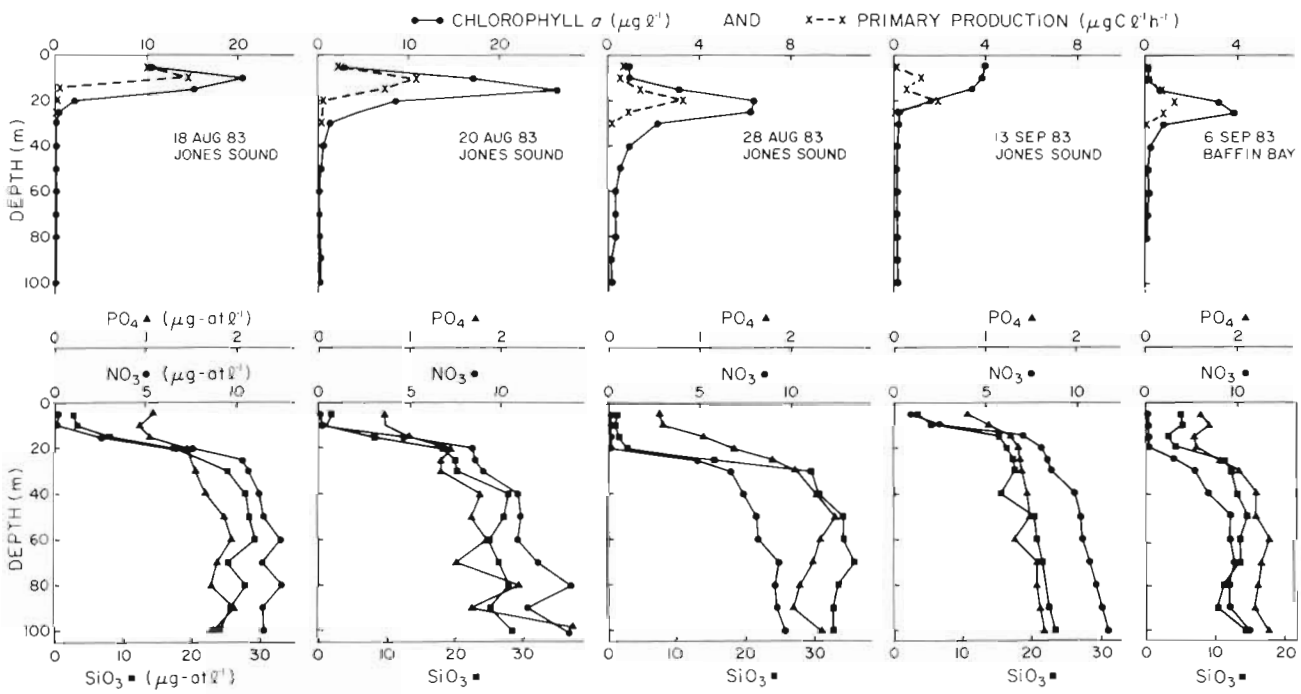

Fig. 2. Vertical profiles of chlorophyll *a*, primary production and nutrients in Jones Sound and Baffin Bay

Table 1. Summary of microzooplankton grazing experiments in the eastern Canadian Arctic. Location, initial chlorophyll *a*, growth and grazing coefficients and effects on the initial standing stock and potential primary production

Location	Date (1983)	Depth (m)	Chloro-phyll *a* ($\mu g\ l^{-1}$)	Treat-ment	Duration (h)	Growth coefficient *k* (d^{-1}) ± 95 % CI	Grazing coefficient *g* (d^{-1}) ± 95 % CI	Initial standing stock removed % (range)	Potential primary production removed % (range)
Jones Sound	19 Aug	10	7.902	–	24	0.211 ± 0.036	0.157 ± 0.052	14.5 (10.0–18.9)	76.6 (66.4–90.6)
Jones Sound	21 Aug	5	2.605	–	24	0.187 ± 0.026	0.166 ± 0.036	15.2 (12.1–18.2)	89.3 (79.3–102.3)
Jones Sound	28 Aug	10	0.898	–	24	−0.005 ± 0.044 ns	0.015 ± 0.072 ns	–	–
					48	0.097 ± 0.02	0.111 ± 0.032	10.5 (7.6–13.3)	113.7 (95.2–141.8)
Jones Sound	13 Sep	10	2.361	–	24	0.244 ± 0.026	0.102 ± 0.034	9.7 (6.6–12.7)	46.4 (39.0–51.6)
				–	48	0.224 ± 0.036	0.084 ± 0.048	8.1 (3.5–12.4)	40.2 (35.4–46.9)
				NO_3	24	0.341 ± 0.048	0.163 ± 0.064	15.0 (9.4–20.3)	51.2 (41.3–57.4)
				NO_3	48	0.286 ± 0.012	0.120 ± 0.016	11.3 (9.9–12.7)	45.3 (43.8–47.6)
Baffin Bay	7 Sep	20	0.736	NO_3	48	0.295 ± 0.028	0.165 ± 0.040	15.1 (11.8–18.5)	59.2 (55.1–65.0)
Baffin Bay	9 Sep	20	0.290	NO_3	24	0.064 ± 0.074 ns	0.095 ± 0.108 ns	–	–
				NO_3	48	0.283 ± 0.030	0.095 ± 0.046	9.1 (4.8–13.1)	36.7 (33.7–40.6)
Baffin Bay	12 Sep	20	0.505	NO_3	48	0.193 ± 0.030	0.167 ± 0.042	15.4 (11.8–18.9)	87.8 (76.8–102.3)

ns: not significant at $p < 0.05$

In Baffin Bay, 3 experiments were conducted for a duration of 48 h; nitrate was added to all with appropriate controls. On 9 Sep only, additional chlorophyll samples were taken at 24 h. The experimental bottles with added nutrients gave instantaneous growth rates of chlorophyll ranging from 0.193 (± 0.030) to 0.295 (± 0.028) d^{-1} (Fig. 4). Grazing coefficients from these experiments were 0.165 (± 0.040), 0.095 (± 0.046) and 0.167 (± 0.042) d^{-1}, respectively (Table 1, Fig. 4). None of the control bottles showed positive growth of chlorophyll ($p < 0.05$). For the experiment on 9 Sep, where additional chlorophyll samples were taken at 24 h, no positive growth was observed even in bottles with added nutrients ($p < 0.05$), but significant growth occurred after 48 h, suggesting that the phytoplankton populations had been severely nutrient starved at this time.

The microplankton community

On the first visit to Jones Sound, phytoplankton were dominated by chain-forming diatoms *Thalassiosira* spp. and *Fragillaria* spp; on subsequent visits small *Chaetoceros* spp. and 'spherical cells' (3 to 10 µm) were predominant. In Baffin Bay, coccolithophorids, 'spherical cells' and *Nitzschia* spp. were abundant (Trotte 1985). In all the grazing experiments in Jones Sound and Baffin Bay, the microzooplankton assemblage was dominated by oligotrich ciliates of the genera *Lohmanniella, Strombidium* and *Laboea*. Tintinnines were represented by *Leprotintinnus pellucidus, Parafavella denticulata* and *Tintinnopsis* sp. and generally were < 20 % of the total. Copepod nauplii and bivalve larvae were the only metazoans, present in small numbers. A mean numerical abundance of 2700 (range 2100 to 3200) ind l^{-1} of total microzooplankton was recorded.

DISCUSSION

The dilution method to estimate the grazing impact of the total microzooplankton community on phytoplankton was first used by Landry & Hassett (1982), and was later used specifically for bacteria-bacterio-

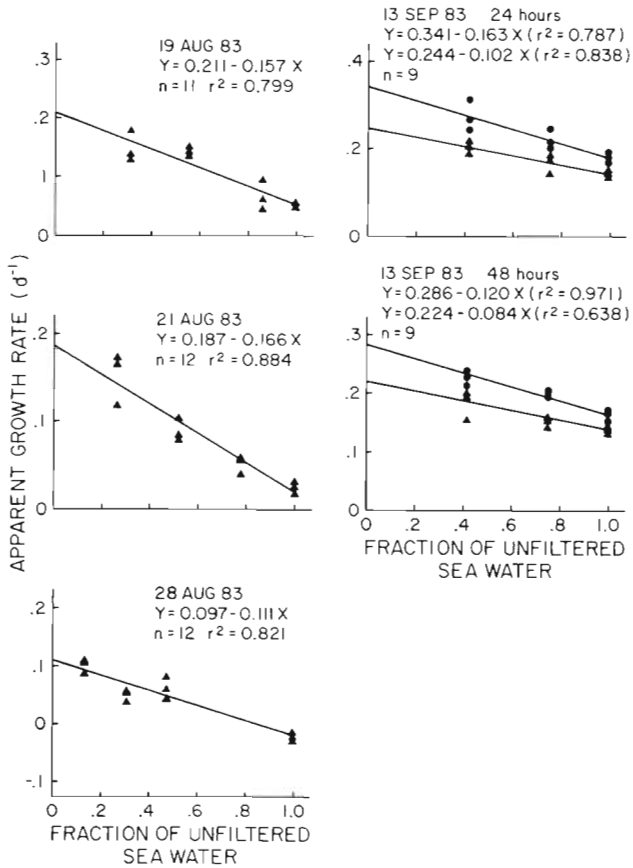

Fig. 3. Relation between apparent growth rate and fraction of unfiltered water in Jones Sound. Lines fitted by least-square regression. (▲) No treatment; (●) with excess NO_3

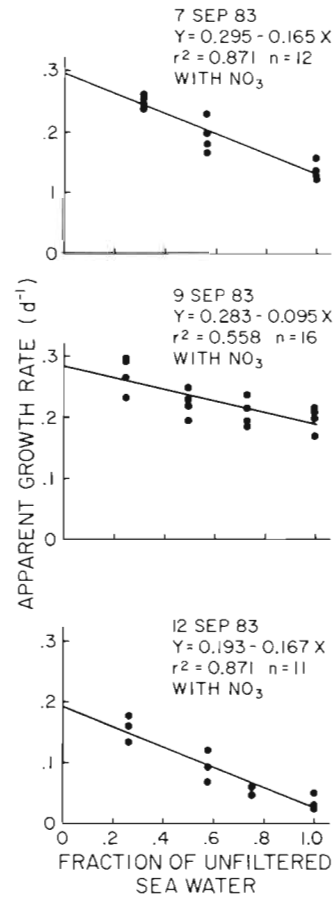

Fig. 4. As in Fig. 3 in central Baffin Bay

vore interactions (Landry et al. 1984, Campbell & Carpenter 1986). Recently, Burkill et al. (1987) used the method to show taxon-specific grazing of microzooplankton by discriminating algal pigments with high performance liquid chromatography. The method is simple as it avoids excessive manipulations of the microzooplankton community. The method assumes that the phytoplankton growth is exponential and is unaffected by dilution, and that the grazers do not respond to decreased food levels (i.e. dilutions) by reducing their feeding effort (see Landry & Hassett 1982 for further discussion).

Another assumption implicit in the method is that the grazer population is not adversely affected by manipulations in preparation of dilution mixtures. Gifford (1985a) has reported losses of oligotrich grazers due to collection and handling. In the present experiments, samples for microzooplankton grazers were not collected during the course of the experiments but similar experiments conducted on the Grand Banks showed that the small decrease (10 %) in the number of grazers (usually oligotrichs) mostly occurred in the first 4 h of incubation and the grazer population remained stable (or increased) until the end of incubation (Paranjape unpubl. data).

Li & Dickie (1985) pointed out another potential complication in preparation of dilution mixtures if 0.2 µm Nuclepore filters are used to prepare filtered seawater. These filters allow passage of some components of photosynthetic picoplankton which in the absence of grazers grow in numbers and size at a high rate, thereby confounding the interpretation of dilution experiments. However, Li (1986) has pointed out in a separate series of experiments that Whatman GF/F filters could effectively retain cultures of cyanobacteria and therefore can provide reasonably 'clean' chlorophyll-free filtered seawater to prepare dilution mixtures. In the present experiments, Whatman GF/F filters were used to prepare filtered seawater as well as to collect chlorophyll samples. However, true controls (filtered seawater only) were not run in these experiments.

The question of nutrient addition in dilution experiments has been alluded to by Landry & Hassett (1982). In fact, the method assumes that the phytoplankton growth coefficient k remains constant in long incubations because of non-limiting supply of nutrients;

otherwise the estimated grazing coefficient would be exaggerated leading to overestimate of grazing mortality of phytoplankton. In one experiment in Jones Sound (13 Sep), where statistically significant growth and grazing coefficients in experiments with and without nutrient addition were obtained, the negative slopes were not different statistically ($p < 0.05$) in both 24 and 48 h incubations, suggesting that the grazing activity of microzooplankton did not change due to nutrient addition. In Baffin Bay, phytoplankton did not respond to increased nutrient supply for the first 24 h period but showed significant growth after 48 h. This lag in growth of chlorophyll *a* is not unexpected in severely nutrient-starved phytoplankton (Collos 1986). In none of the experiments, however, were qualitative changes in species composition of phytoplankton and microzooplankton in bottles with or without nutrient addition after incubation observed.

The dilution experiments gave statistically significant estimates of instantaneous coefficients of growth and grazing mortality of chlorophyll (Table 1). In Jones Sound, growth coefficients were similar to grazing coefficients even when nutrients were low, suggesting balance between production and consumption. In central Baffin Bay, excess nutrients were added to the experimental bottles; therefore the observed growth coefficients would not be expected to reflect natural growth rates. However, they are not excessively higher than those in Jones Sound (also see below).

Data from *in situ* ^{14}C productivity measurements were available for the same depths in the same locations where the grazing experiments were conducted (Irwin et al. 1985). With the relation between the phytoplankton carbon and daily photosynthetic rate developed by Harrison et al. (1982), the growth rate of phytoplankton (μ in doublings d^{-1}) can be calculated to compare with the growth coefficients obtained from the dilution experiments (Table 2). The growth coefficients (k d^{-1}) from the grazing experiments (Table 1) were converted to μ by dividing k by ln 2.

The growth rates (μ) of phytoplankton calculated by the 2 methods were comparable (Table 2). In experiments where nutrients were added to the experimental bottles, the values of μ were higher but were within the range of values reported by Harrison et al. (1982) for mixed-layer, Arctic phytoplankton community.

Therefore, if experimentally determined growth rates are assumed to represent those of the field population, the microzooplankton grazing impact on the initial standing stock and potential production of phytoplankton can be calculated. In Jones Sound, the microzooplankton community could remove 8 to 15 % of the initial standing stock per day and 40 to 114 % of the potential production daily. In central Baffin Bay, losses due to grazing would amount to 9 to 15 % and 37 to 88 % of the standing stock and production, respectively (Table 1). In coastal waters off Washington, USA, 6 to 24 % of phytoplankton standing stock and 17 to 52 % of production was consumed daily by microzooplankton (Landry & Hassett 1982), while in the neritic, inshore waters of Halifax Harbor, Canada, the microzooplankton community of < 102 µm was able to consume daily up to 124 % of the standing stock and 56 % of the primary production (Gifford 1985b). In the Celtic Sea, the impact of microzooplankton grazing varied seasonally, ranging from 13 to 42 % within the thermocline in summer and 30 to 65 % of the standing stock of phytoplankton in autumn (Burkill et al. 1987). These estimates were derived from experiments using a similar dilution method. Other estimates of microzooplankton community grazing or that of a dominant component of it, based on theoretical considerations (Riley 1956, Beers & Stewart 1971), or laboratory experiments (Capriulo & Carpenter 1980, 1983) are in the same range of values as those found in this study.

The use of chlorophyll as an index of phytoplankton biomass and its production and consumption exclude other potential food sources for microzooplankton, such as non-photosynthetic bacteria, flagellates and detritus, most of which cannot be distinguished without the use of fluorescence microscopic techniques (e.g. Haas 1982, Landry et al. 1984). It also assumes that all or most chlorophyll containing plankters can be utilized as a food source. Food selectivity by microzooplankton on the basis of size and qualitative composition in a natural assemblage of phytoplankton is becoming apparent (Rassoulzadegan & Etiènne 1981, Burkill et al. 1987). Certain components of microzooplankton community, such as tintinnines, can only ingest maximum food particle size 40 to 50 % of their

Table 2. Growth rate (μ in doublings d^{-1}) of phytoplankton estimated by 2 methods. k from Table 1; PC: phytoplankton carbon; ΔPC: daily photosynthetic rate. Phytoplankton carbon calculated from regression of particulate organic carbon and chlorophyll *a* form the mixed layer; PC = 41 × chlorophyll *a*

Location	Date (1983)	$\mu = k/\ln 2$ (d^{-1})	$\mu = \log 2$ (PC + ΔPC/PC) (d^{-1})
Jones Sound	19 Aug	0.304	0.306
Jones Sound	21 Aug	0.270	0.307
Jones Sound	29 Aug	0.160	0.303
Jones Sound	13 Sep	0.323	0.303
		0.413*	
Baffin Bay	7 Sep	0.426*	0.304
Baffin Bay	9 Sep	0.408*	–
Baffin Bay	12 Sep	0.278*	–

* With excess NO_3

oral lorical diameter (Blackbourn 1974, Heinbokel 1978) while oligotrichs are able to ingest food items as large as themselves (Gifford 1985a). It is generally agreed however that nanoplankton (< 20 μm size) would be most suitable or preferable food for most microzooplankton (Taniguchi 1977, Capriulo & Carpenter 1980, Cosper & Stepien 1984). In Jones Sound, an average of 42 % of chlorophyll passed through a 20 μm screen, while in Baffin Bay, the average was 77 % (Trotte 1985). If nanoplankton alone is considered as a potential food source for microzooplankton, then the grazing impact of this community on the initial standing stock and the potential primary production of the total phytoplankton (Table 1) would be reduced to 5 and 31 % in Jones Sound and 10 and 47 % in Baffin Bay, respectively.

Recent quantitative abundance estimates of microzooplankton in polar waters (Bröckel 1981, Tumantseva 1982, Taniguchi 1984) suggest that the absolute abundances of this community in the productive season are comparable to the values in temperate and tropical waters. The results of the experiments reported here provide further evidence (Hewes et al. 1985, Harrison 1986) that the potential dynamic role in transfer of energy and recycling of nutrients assigned to this community in the lower latitudes (Pomeroy 1974, Conover 1982) also holds for the colder regions.

Acknowledgements. I thank Dr T. Platt for helpful advice on many aspects of this work. Drs T Platt, R. J. Conover and W G. Harrison improved the manuscript with their helpful comments.

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This article was presented by Dr R. J. Conover; it was accepted for printing on August 2, 1987