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Dynamics of microplankton communities at the ice-edge zone of the Lazarev Sea during a summer drogue study

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Abstract. Microzooplankton grazing and community structure were investigated in the austral summer of 1995 during a Southern Ocean Drogue and Ocean Flux Study (SODOFS) at the ice-edge zone of the Lazarev Sea. Grazing was estimated at the surface chlorophyll maximum (5–10 m) by employing the sequential dilution technique. Chlorophyll *a* concentrations were dominated by chain-forming microphytoplankton (>20 μm) of the genera *Chaetoceros* and *Nitzschia*. Microzooplankton were numerically dominated by aloricate ciliates and dinoflagellates (*Protoperidinium* sp., *Amphisolenia* sp. and *Gymnodinium* sp.). Instantaneous growth rates of nanophytoplankton (<20 μm) varied between 0.019 and 0.080 day^{-1}, equivalent to between 0.03 and 0.12 chlorophyll doublings day^{-1}. Instantaneous grazing rates of microzooplankton on nanophytoplankton varied from 0.012 to 0.052 day^{-1}. This corresponds to a nanophytoplankton daily loss of between 1.3 and 7.0% (mean = 3.76%) of the initial standing stock, and between 45 and 97% (mean = 70.37%) of the daily potential production. Growth rates of microphytoplankton (>20 μm) were lower, varying between 0.011 and 0.070 day^{-1}, equivalent to 0.015–0.097 chlorophyll doublings day^{-1}. At only three of the 10 stations did grazing by microzooplankton result in a decrease in microphytoplankton concentration. At these stations instantaneous grazing rates of microzooplankton on microphytoplankton ranged between 0.009 and 0.015 day^{-1}, equivalent to a daily loss of <1.56% (mean = 1.11%) of initial standing stock and <40% (mean = 28.55%) of the potential production. Time series grazing experiments conducted at 6 h intervals did not show any diel patterns of grazing by microzooplankton. Our data show that microzooplankton grazing at the ice edge were not sufficient to prevent chlorophyll *a* accumulation in regions dominated by microphytoplankton. Here, the major biological routes for the uptake of carbon therefore appear to be grazing by metazoans or the sedimentation of phytoplankton cells. Under these conditions, the biological pump will be relatively efficient in the drawdown of atmospheric CO_2.

Introduction

The fate of photosynthetically fixed carbon in marine environments can dramatically affect the magnitude of particulate flux, and hence the efficiency of the biological pump in the uptake of atmospheric CO_2 (Longhurst, 1991). Although sinking of dead or senescent phytoplankton cells contributes significantly to the magnitude of carbon flux (Schnack, 1985; von Bodungen *et al.*, 1986; Michaels and Silver, 1988), grazing by zooplankton represents the primary biological route for the transfer of organic carbon from the surface waters to the interior of the ocean. The extent of carbon flux through grazers is strongly determined by the community structure of the consumers and the subsequent partitioning of photosynthetically fixed carbon (Michaels and Silver, 1988; Roman *et al.*, 1993). In regions where macro- and mesozooplankton consume the bulk of the phytoplankton production, the organic flux from the surface waters to the deep ocean, in the form of large, compact and fast-sinking faecal pellets, is generally high (Schnack, 1985; von Bodungen, 1986; Cadee *et al.*, 1992; Gonzalez, 1992a; Fortier *et al.*, 1994). Carbon flux below the zone of regeneration is compounded in that many of the larger herbivores undertake vertical migrations from below the zone of regeneration to the surface waters where they feed (Fortier *et al.*, 1994). Production originating in the surface waters is, therefore, transported below the zone of regeneration.

In contrast, phytoplankton consumed by microzooplankton contribute less to particulate flux for several reasons: (i) microzooplankton produce small faecal pellets (minipellets) which remain in suspension for long periods (Nöthig and von Bodungen, 1989; Elbrächter, 1991; Gonzalez, 1992b); (ii) many protozoans, the dominant component of the microzooplankton (Garrison and Buck, 1989), sequester chloroplasts (Stoecker *et al.*, 1987); (iii) microzooplankton do not undergo vertical migration, thus nutrients contained within the microzooplankton are not transported below the zone of regeneration; (iv) a substantial proportion of the carbon may be retained in the zone of regeneration as a result of coprophagy (Nöthig and von Bodungen, 1989); (v) the close coupling between the microzooplankton and the microbial loop results in the recycling of nutrients in the zone of regeneration (Sherr and Sherr, 1988). Therefore, there appears to be little material available for direct export to the deep ocean.

A major feature of the Southern Ocean is sea ice, which in winter may extend as far north as 56°S (Sullivan *et al.*, 1993). Associated with the retreating ice during summer are phytoplankton blooms which are thought to result from increased *in situ* production associated with increased water column stability imparted by ice melt (Heywood and Whitaker, 1984; Horner, 1985; Smith and Nelson, 1986; Smith and Sakshaug, 1990). The release of epontic cells during ice melt further contributes to increased chlorophyll concentrations in this region (Smith and Nelson, 1986). The species and size composition, and maximum biomass, reached by ice-edge blooms are, however, very variable (Kang and Fryxell, 1993; Lancelot *et al.*, 1993). Although microphytoplankton generally dominate the ice-edge phytoplankton blooms, moderate nanophytoplankton blooms have been recorded in the Weddell Sea (Lancelot *et al.*, 1993).

Studies in marine environments have shown that when nano- and picophytoplankton dominate phytoplankton communities, microzooplankton are often the most significant herbivores (Garrison *et al.*, 1993; Kivi and Kuosa, 1994; Lutjeharms *et al.*, 1994). In contrast, where food webs are dominated by microphytoplankton, metazoans often represent the sink for primary production (Huntley *et al.*, 1989). Thus, the pathways of energy flux may vary according to the size composition of phytoplankton at the ice-edge zone.

It has been estimated that production at the Marginal Ice Zone (MIZ) contributes ~40% of the annual primary production south of the Antarctic Divergence (Smith and Sakshaug, 1990). The fate of the photosynthetically fixed carbon in this region is, therefore, of particular importance for the total carbon budget. The aim of this study was to characterize and quantify the grazing impact of microzooplankton at the ice-edge zone of the Lazarev Sea, and to provide data on temporal changes in microzooplankton grazing within the same body of water.

Method

Microzooplankton grazing experiments were conducted at 11 stations during the Southern Ocean Drogue and Ocean Flux Study (SODOFS) in austral summer (December/January) 1995 (Figure 1). The grazing experiments were carried out at

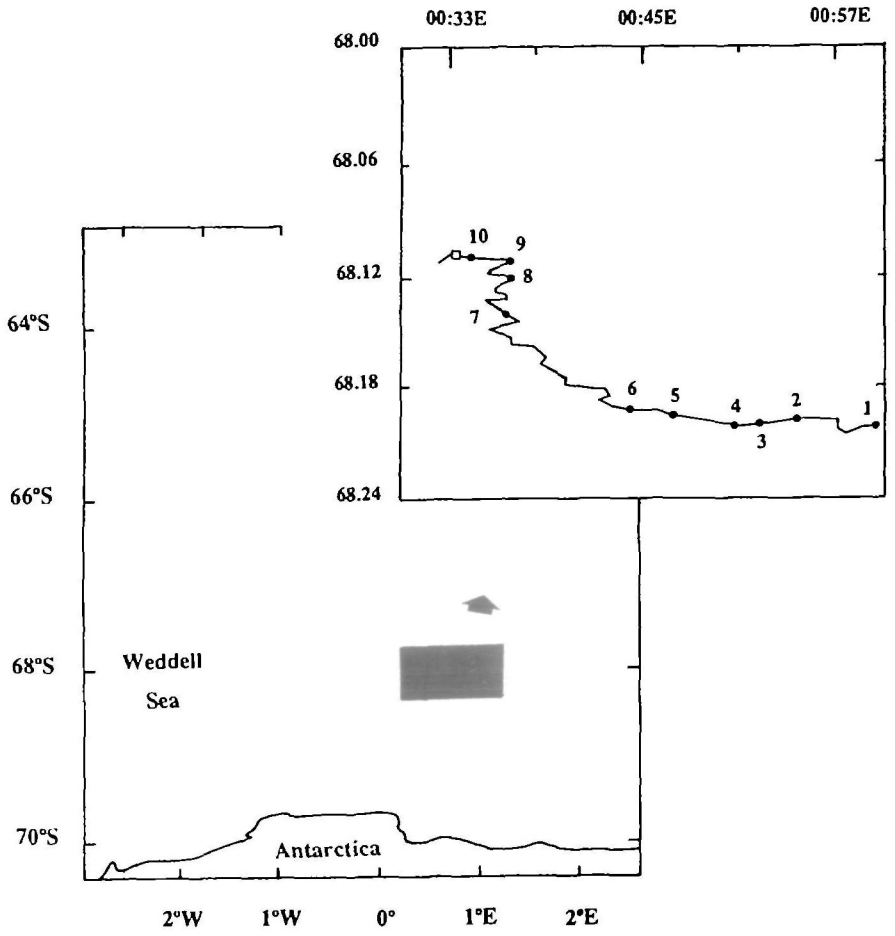

Fig. 1. Drogue drift track and the position of microzooplankton grazing studies conducted during the SODOFS cruise in austral summer (December/January) 1995. □ denotes the position of the time series grazing experiment.

the surface chlorophyll maximum (5–10 m) by employing the seawater dilution technique (Landry and Hassett, 1982).

Water samples for the grazing experiments were collected with 8 l Niskin bottles. For each experiment, 20 l polyethylene carboys were filled with seawater. The water in the carboys was then gently passed through a 200 μm mesh to isolate the microzooplankton community from larger predators. Particle-free water was obtained by passing surface water (obtained using a shipboard Iwaki Magnetic Pump operated at a flow rate of ~5 l min^{-1}) through a 0.2 μm Milli Q (Millipore) filtration system. Dilution series in ratios of 1:0; 3:1; 1:1 and 1:3 in 2 l polyethylene bottles of unfiltered to filtered seawater were then prepared. Three replicates for each dilution series were prepared. The dilution series were incubated on deck for 24 h in perspex incubators cooled with running surface water and screened with shade cloth (neutral spectral transmission) to simulate light intensity at the depth

of collection. To assess diel patterns of grazing by microzooplankton, duplicate time series grazing experiments were conducted at a single station over 24 h with sampling at 6 h intervals, beginning at 06:00 h. During the entire study, wind speed, surface irradiance and cloud cover were monitored.

Before the incubations were begun, water samples (250 ml) from each bottle were taken for the initial chlorophyll *a* concentration. The corresponding bottles were sampled again at the end of the incubation to determine the final chlorophyll *a* concentrations. Chlorophyll *a* was fractionated into nano- (<20.0 μm) and microplankton (>20.0 μm) size classes. The picophytoplankton size class (0.2–2.0 μm) was not sampled during this study as it constituted ≤5% of the total stock throughout the period of the investigation (P.W.Froneman unpublished data). Chlorophyll *a* concentrations were determined fluorometrically (Turner 111 fluorometer) after extraction in 100% methanol for 6–12 h (Holm-Hansen and Riemann, 1978).

To identify and enumerate the various components of the microzooplankton communities at each grazing station, a 250 ml sample of natural seawater obtained from the 1:0 dilution series (pre-screened) was fixed with 10% Lugol's solution (Leakey *et al.*, 1994a; Stoecker *et al.*, 1994). The water samples were then examined using the Utermöhl settling technique and employing a Nikon-TMS inverted microscope operated at ×400 magnification (Reid, 1983). A minimum of 500 cells or 100 fields were counted for each sample. The microzooplankton species were identified using the works of Wood (1954) and Boltovskoy (1981).

The apparent growth rate of chlorophyll *a* in each bottle was calculated using the exponential model of Landry and Hassett (1982):

$$P_t = P_0 e^{(k-g)t}$$

where P_t is the chlorophyll *a* concentration at time t, P_0 is the initial chlorophyll *a* concentration, and k and g are the instantaneous algal growth and microzooplankton grazing coefficients, respectively. The coefficients were determined from linear regression analysis (95% confidence limits) between the dilution factor and apparant growth rate of chlorophyll *a* in each bottle using the computer program Statgraphics, Version 5.0 (Statistical Graphics Corporation, 1992). Both g and k were used to calculate the grazing loss of potential production, while only the grazing mortality coefficient (g) was employed to calculate the daily loss of initial standing stock.

Correlation analysis was performed to identify possible relationships between grazing rate, temperature, microzooplankton abundance and chlorophyll. Grazing rate data, expressed as a percentage, were transformed using the arcsin transformation (Sokal and Rolhf, 1969), while chlorophyll concentration values were transformed using the factor log $(x + 1)$ (Legendre and Legendre, 1983). The computer package, Statgraphics, Version 5.0, was again used for this analysis.

Results

Chlorophyll a and phytoplankton

The contribution of the nano- (<20 μm) and microphytoplankton (20–200 μm)

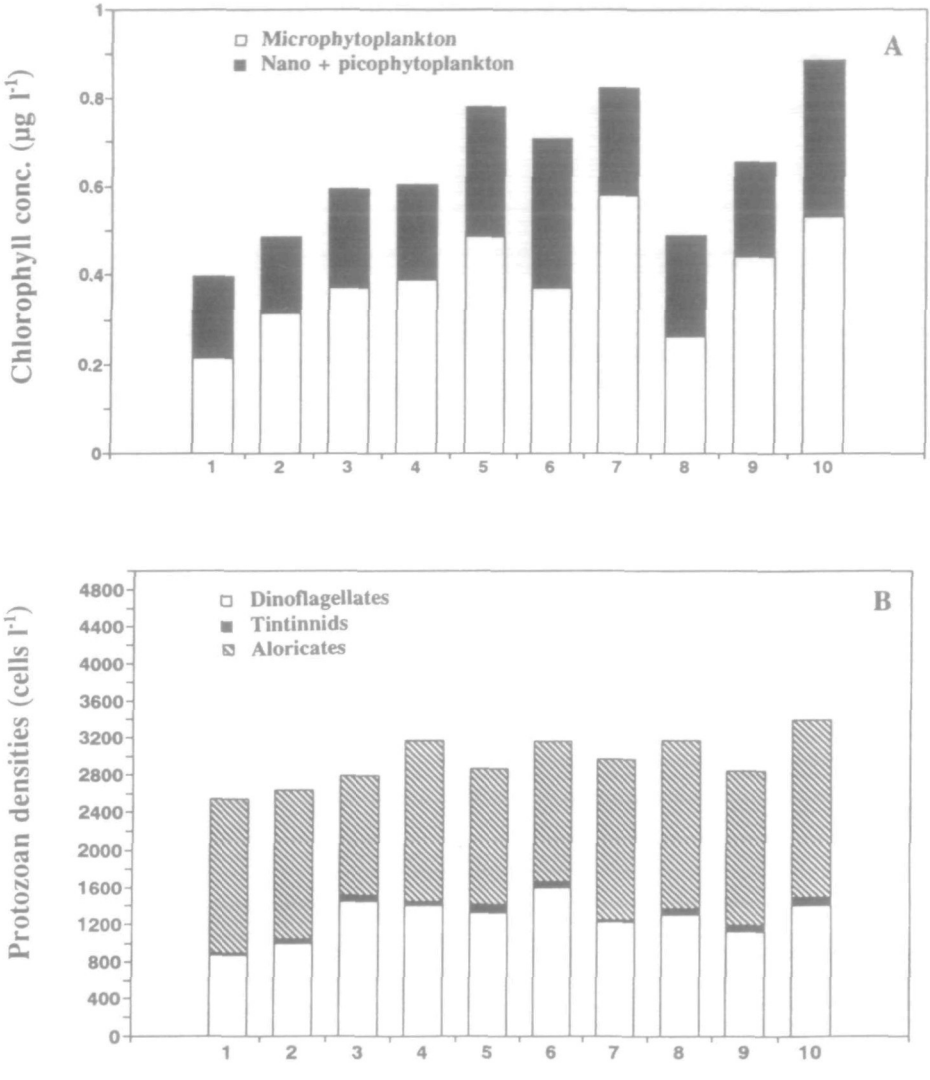

Fig. 2. Size-fractionated surface chlorophyll *a* concentrations (**A**) and protozoan community structure (**B**) during the SODOFS cruise conducted in late austral summer (December/January) 1995.

fractions to total chlorophyll *a* concentrations varied considerably during the drogue study. However, the contribution of the microphytoplankton, contributing 54–70% to total chlorophyll, was always greater than that of the nanophytoplankton fraction (Figure 2A). Microphytoplankton chlorophyll concentrations ranged between 0.215 and 0.581 µg l^{-1}, and were dominated by chain-forming *Chaetoceros* spp. and *Nitzschia* spp., and large cells such as *Corethron criophilum* and *Rhizosolenia* spp. (Table I). Concentrations of nanophytoplankton chlorophyll ranged from 0.172 to 0.356 µg l^{-1} and were dominated by unidentified flagellates.

Table I. Composition of plankton communities during the Southern Ocean Drogue and Ocean Flux Study (SODOFS) experiment conducted in austral summer (December/January) 1994/1995. Results are expressed as cells per litre

Species	Day									
	1	2	3	4	5	6	7	8	9	10
Diatoms										
Astermophalus sp.	25	75	–	100	–	200	–	50	–	25
Biddulphia sp.	–	50	50	75	–	200	75	–	25	75
Cylindrotheca closterium	125	225	75	325	150	250	125	50	225	125
Dactyliosolen antarcticus	75	–	25	125	50	–	75	50	50	50
Chaetoceros sp.	375	575	800	575	625	525	475	1225	1050	900
C.atlanticus	175	125	300	125	50	275	225	225	100	175
C.dichaeta	525	1200	925	850	1425	925	875	1350	1550	1600
Coscinodiscus sp.	25	–	25	50	25	–	–	–	–	–
Corethron criophilum	250	275	475	450	675	425	650	300	600	575
Eucampia antarctica	–	–	50	25	–	–	25	25	–	50
Navicula sp.	150	125	25	–	175	–	25	75	175	25
Nitzschia sp. (cells)	625	450	525	175	575	225	100	475	400	375
Nitzschia sp. (chains)	425	380	500	375	175	250	225	175	725	125
N.pelagica	75	75	75	125	150	200	175	50	50	75
Pseudonitzschia group	75	175	100	100	25	100	25	–	175	–
Rhizosolenia sp.	150	75	150	175	125	250	175	150	200	125
R.alata	200	175	100	125	225	150	125	150	225	175
R.hebetata var. *semispina*	50	75	50	100	25	75	50	50	75	25
Thalassiosira sp.	25	100	150	25	75	150	75	50	50	50
Total	3450	4155	4425	3900	4550	4250	3675	4475	5700	5000
Silicoflagellates										
Distephanus speculum	200	550	175	50	100	150	675	525	200	50
Dinoflagellates										
Amphisolenia sp.	125	175	275	225	325	325	350	175	400	350
Amphidinium sp.	25	25	75	150	175	275	125	50	25	100
Ceratium sp.	25	50	25	–	–	50	25	25	25	75
Dinophysis sp.	75	25	–	25	25	50	–	25	25	50
Gymnodinium sp.	275	300	350	250	275	300	275	325	325	325
Gonyaulax sp.	–	–	–	–	25	25	–	–	–	–
Protoperidinium sp.	375	475	750	725	700	650	475	725	375	575
Total	875	1000	1450	1400	1325	1600	1225	1300	1125	1400
Ciliates										
Aloricate ciliates	1650	1600	1275	1725	1450	1500	1725	1800	1650	1900
Tintinnids	25	50	75	50	100	75	25	75	75	100
Total	1675	1650	1350	1775	1550	1575	1750	1875	1925	2000
Foraminiferans										
Acanthochiasma sp.	–	–	–	25	–	–	25	–	–	–
Globigerina sp.	–	–	–	25	25	–	25	–	25	–
Nanoplankton	2225	2450	2475	1950	2325	2650	1975	2000	2475	2600

Microzooplankton community and species composition

During the entire drogue study, protozoan densities ranged between 2550 and 3400 ind. l^{-1} (Table I; Figure 2B). The ciliates, comprising aloricate ciliates and tintinnids, dominated numerically the protozooplankton stock, accounting for

Table II. Estimates of phytoplankton production and grazing by microzooplankton measured with the dilution technique during a SODOFS experiment conducted in austral summer (December/January) 1994–1995. Values in parentheses are standard errors. r^2 is the coefficient of determination obtained from regression analysis between the apparent growth rate of phytoplankton and dilution

(A) <20 μm size fraction

Station number	Chl-a (μg l^{-1})	r^2	Growth coefficient (k) day^{-1} ($\times 10^{-2}$)	Grazing coefficient g (day^{-1}) ($\times 10^{-2}$)	% Initial stock removed (day^{-1})	% Potential production grazed (day^{-1})	Chlorophyll doublings day^{-1}
1	0.183	40.04*	1.85 (0.005)	−1.24 (0.002)	1.26	67.31	0.027
2	0.172	49.55*	7.96 (0.004)	−4.78 (0.002)	4.71	60.83	0.115
3	0.224	49.56*	7.58 (0.003)	−3.58 (0.001)	3.57	48.30	0.109
4	0.215	43.18*	6.21 (0.005)	−4.68 (0.002)	4.65	76.09	0.082
5	0.296	52.18**	4.52 (0.002)	−2.01 (–)	3.71	44.62	0.065
6	0.338	66.87**	7.16 (0.003)	−4.22 (–)	4.37	59.76	0.103
7	0.245	57.71**	3.36 (0.004)	−3.16 (0.001)	3.26	94.37	0.048
8	0.226	69.31*	4.68 (0.002)	−3.98 (–)	0.42	85.03	0.067
9	0.215	56.31*	4.68 (0.001)	−4.56 (0.002)	4.65	97.09	0.015
10	0.356	51.53*	7.41 (0.008)	−5.16 (0.003)	6.99	70.33	0.107
(B) >20 μm size fraction							
1	0.215	46.81*	6.14 (0.003)	−1.49 (0.001)	1.49	25.00	0.088
2	0.315	59.73*	2.31 (0.01)	−0.93 (0.004)	0.94	40.76	0.033
3	0.371	48.55**	2.04 (0.004)	3.14 (0.002)	–	–	0.029
4	0.389	47.60*	1.06 (0.002)	0.14 (–)	–	–	0.015
5	0.488	75.36**	1.09 (0.003)	0.55 (–)	–	–	0.016
6	0.371	39.63**	1.67 (0.002)	0.21 (–)	–	–	0.024
7	0.581	53.37*	2.32 (0.002)	0.28 (–)	–	–	0.032
8	0.264	59.43*	6.76 (0.005)	0.38 (–)	–	–	0.097
9	0.441	50.01*	4.73 (0.001)	−0.87 (0.001)	0.91	19.19	0.068
10	0.532	76.23**	1.19 (0.003)	0.67 (0.001)	–	–	0.017

* $P < 0.05$; ** $P < 0.01$.

48–62% of the total. Aloricate forms constituted the main component of the ciliate group, with densities ranging between 1275 and 1900 ind. l^{-1} (Table I; Figure 2B). Tintinnid densities were always <100 ind. l^{-1} (Table I).

Densities of dinoflagellates ranged from 875 to 1600 cells l^{-1} (Table I; Figure 2B). Among the flagellates, members of the genus *Protoperidinium* were the most abundant species with densities ranging from 375 to 725 ind. l^{-1} (Table I). The second most abundant dinoflagellates during the study were *Gymnodinium* spp. with densities ranging between 250 and 450 ind. l^{-1}. Also well represented were unidentified species of the genus *Amphisolenia* (densities of between 125 and 400 ind. l^{-1}) and *Amphidinium* spp. (densities range from 25 to 275 ind. l^{-1}). Amongst the dinoflagellates, the least well-represented group recorded during the study was the genus *Gonyaulax*. Densities of this group were always <25 ind. l^{-1}.

Abundances of larger protozooplankton, e.g. foraminiferans, were low (<25 ind. l^{-1}) throughout the drogue study. Two species of foraminiferans, *Acanthochiasma* sp. and *Globigerina* sp., were recorded (Table I).

Grazing rates

Instantaneous growth and grazing coefficients with the confidence limits derived from the grazing experiments are shown in Tables II and III. In all dilution experiments, the relationship between apparent growth rate and dilution was significantly linear ($P < 0.05$ in all cases).

No temporal patterns in growth or grazing on nanophytoplankton community were identified (Table IIA). Instantaneous growth rates (k) of the nanophytoplankton ranged between 0.02 and 0.08 day^{-1}. This level of growth is equivalent to between 0.03 and 0.12 chlorophyll doublings day^{-1}. Instantaneous grazing rates

Table III. Diel estimates of phytoplankton production and grazing during a SODOFS experiment conducted in austral summer (December/January) 1994–1995. Values in parentheses are standard errors. r^2 is the coefficient of determination obtained from regression analysis between the apparent growth rate of phytoplankton and dilution

(A) <20 μm phytoplankton production and grazing by microzooplankton on nanophytoplankton

Time (h)	Chl-a (μg l^{-1})	r^2	Growth coefficient (k) day^{-1} ($\times 10^{-2}$)	Grazing coefficient g (day^{-1}) ($\times 10^{-2}$)	% Initial stock removed (day^{-1})	% Potential production grazed (day^{-1})	Chlorophyll doublings day^{-1}
06:00							
1	0.387	58.13*	2.98 (0.005)	−2.56 (0.003)	2.53	86.32	0.043
2	0.401	47.69*	3.01 (0.008)	−1.79 (0.004)	1.97	60.41	0.043
12:00							
1	0.356	48.90*	3.41 (0.001)	−3.16 (0.005)	3.12	92.68	0.049
2	0.403	53.19**	2.01 (0.003)	−1.11 (0.004)	1.09	56.22	0.029
18:00							
1	0.304	49.57*	4.31 (0.007)	−2.78 (0.003)	2.73	64.93	0.062
2	0.289	68.33**	3.63 (0.003)	−2.01 (0.009)	1.76	56.60	0.052
0:00							
1	0.424	41.89*	4.56 (0.009)	−3.89 (0.007)	3.82	85.53	0.066
2	0.427	67.97*	4.03 (0.005)	−2.96 (0.003)	2.92	73.86	0.058

(B) >20 μm phytoplankton production and grazing by microzooplankton on microphytoplankton

06:00							
1	0.378	59.31**	4.56 (0.004)	−0.03 (–)	0.31	6.25	0.066
2	0.398	65.23*	4.07 (0.001)	−0.01 (–)	0.50	8.31	0.059
12:00							
1	0.477	78.56*	6.75 (0.003)	−0.04 (0.001)	0.42	1.50	0.097
2	0.394	43.67*	1.72 (0.001)	0.40 (0.003)	–	–	0.025
18:00							
1	0.389	43.92*	3.45 (0.001)	0.03 (–)	–	–	0.050
2	0.401	55.32*	3.67 (0.002)	0.05 (–)	–	–	0.053
0:00							
1	0.400	63.21**	1.31 (0.004)	0.10 (–)	–	–	0.019
2	0.406	59.02*	1.23 (0.001)	0.09 (–)	–	–	0.018

* $P < 0.05$; ** $P < 0.01$.

(g) of microzooplankton on nanophytoplankton ranged from 0.01 to 0.05 day^{-1}. These correspond to daily losses of between 1.3 and 7.0% (mean = 3.8%) of the initial standing stock, and 45–97% (mean = 70.4%) of the potential primary production of the nanophytoplankton fraction. During these experiments, the relationship between algal growth and grazing mortality was always significant ($r^2 = 0.58$; $P < 0.05$).

Instantaneous growth rates in the microphytoplankton fraction were lower and ranged between 0.02 and 0.07 day^{-1} (Table IIB). These rates correspond to chlorophyll doubling rates ranging between 0.02 and 0.10 day^{-1}. Microzooplankton grazing resulted in a decrease in the microphytoplankton concentration in only three experiments (Table IIB). Here, the instantaneous grazing rates of microzooplankton on microphytoplankton ranged between 0.001 and 0.01 day^{-1}. This level of grazing corresponds to a daily loss of initial standing stock of <1.5% (range 0.9–1.5%) or <40% of the potential production (range 19–41%). Pearson and fifth order partial correlation analysis between microzooplankton abundance, herbivory, chlorophyll concentration and temperature showed no significant relationships during the entire investigation ($P < 0.05$ in all cases).

During the time series grazing experiments, both the growth coefficients of the nano- and microphytoplankton fractions, and microzooplankton grazing impact on the two fractions, were in the same range as that obtained in the previous grazing experiments (Table IIIA and B). Grazing by microzooplankton resulted in a decrease in nanophytoplankton concentration during all experiments (Table IIIA), while decreases in the microphytoplankton concentration were observed during three experiments (Table IIIB). No diel patterns in the grazing impact of microzooplankton on nano- or microphytoplankton were evident during the time series experiments (Table IIIA and B). Indeed, analysis of variance indicated that the grazing impact of microzooplankton on the nanophytoplankton and microphytoplankton did not differ significantly between different times of the day ($F = 0.897$ and $F = 0.352$, respectively; $P < 0.05$ in all cases).

Discussion

In the course of this study, the drogue drifted <25 nm in a westerly direction in ~12 days (Figure 1), suggesting that it had drifted in the Eastwind Drift flowing adjacent to the Antarctic continent (Gow and Tucker, 1990). Oceanographic data show that the entire study was carried out in the same water mass (G. Rigg, personal communication). Conditions during the experiment were characterized by low wind speeds (between 1.4 and 19.8 knots), and high surface light intensities ranging between 564 and 2797 $\mu E\ m^{-2}\ s^{-1}$. The phytoplankton community was dominated by microphytoplankton, which comprised 54–70% of total chlorophyll a measured (Figure 2A).

During the entire study, the microzooplankton assemblages were numerically dominated by protozooplankton with densities ranging between 2550 and 3400 cells l^{-1} (Table I; Figure 2B). The densities and species composition of the protozooplankton assemblages were in the same range as previously observed in similar studies conducted at the ice-edge zone of the Weddell Sea (Garrison and

Table IV. Microzooplankton grazing and phytoplankton growth rates derived from grazing studies conducted in various oceanic environments employing the dilution technique

Author	Region	Grazing coefficient (day^{-1})	Growth coefficient (day^{-1})	Temperature (°C)
Burkill *et al.*, 1987	Celtic Sea	0.14–1.04	–0.07–1.04	ND
Paranjape, 1987	Canadian Arctic	0.08–0.17	–0.01–0.30	ND
Gifford, 1988	Halifax Harbour	0.02–1.44	0.24–1.92	2–20
Verity and Vernet, 1992	Norwegian Sea	0.08–0.34	–0.13–0.21	ND
Burkill *et al.*, 1993	Northeastern Atlantic	0.02–0.57	ND	9–16
Verity *et al.*, 1993	North Atlantic	0.21–1.09	–0.05–0.97	ND
Burkill *et al.*, 1995	Bellingshausen Sea	0.03–0.52	ND	–2–0
Landry *et al.*, 1995	Equatorial Pacific	0.39–1.08	–0.04–1.10	ND

ND, no data presented.

Buck, 1989; Garrison, 1991). Assuming that total phytoplankton carbon can be calculated using the equation $C_a = 80chl^{0.6}$ (Hewes *et al.*, 1990), and the carbon content of microzooplankton calculated using the formula of Garrison and Buck (1989), $\log_{10}(pg) = 0.94\log_{10}[\text{cell volume}] - 0.6$, microzooplankton carbon contributed ≤7% of total carbon in the 2–200 μm fraction during this study. This result is similar to the <12% cited by Garrison and Buck (1989) in a study conducted at the ice-edge zone of the Weddell Sea. Our estimate is, however, conservative since cell shrinkage of up to 44% in samples fixed with Lugol's solution has been documented (Leakey *et al.*, 1994a). It should also be noted that we were unable on this occasion to differentiate between the auto- and heterotrophic components of the protozoan assemblages in the Lugol's solution. In a previous study, using epifluorescent techniques, we have shown that the autotrophic component of the protozoan assemblage comprised <25% of the total cell counts (Froneman and Perissinotto, 1996b).

Growth rate estimates of phytoplankton during the drogue study ranged between 0.01 and 0.08 day^{-1}, equivalent to 0.02–0.12 chlorophyll doublings day^{-1} (Table IIA and B). These results compare well with phytoplankton growth rate estimates obtained in various marine environments employing the dilution technique (Table IV). These estimates are, however, lower than those obtained during one of our previous studies conducted in the same region (Froneman and Perissinotto, 1996b). Bacterial growth rate estimates and size-fractionated primary production studies were also low during the entire study (B. Tibbles, personal communication; R.K.Laubscher, personal communication), suggesting that the activity of the entire biological system was low during this period. Although the elevated production of ice algae is well documented (Smith, 1987; Lizotte and Sullivan, 1991), the degree to which ice algae released during ice melt remain active in the water column is unclear (Smith and Sakshaug, 1990). It is widely accepted that nutrient limitation plays no role in Antarctic phytoplankton, except for some silicate (Si) limitation of the most demanding diatoms (Jacques, 1989). During this investigation, Si concentrations were >61 μmol l^{-1} (R.K.Laubscher, personal communication), far above the threshold required for Antarctic diatoms with thin frustules, such as *Chaetoceros* and *Nitzschia* sp. (Jacques, 1989). These

facts suggest that algal growth was not limited by nutrients. Ecophysiological studies of ice flora have shown that they exhibit photoinhibition at high light intensities (Smith and Sakshaug, 1990; Lizotte and Sullivan, 1991). For example, the optimum light intensity (I_k) at which maximum production occurs for *Chaetoceros* sp. lies between 3 and 10 W m^{-2} (~3.59 μE m^{-2} s^{-1}) (Jacques, 1983). Thus, high light intensities in the surface waters would inhibit growth of phytoplankton communities dominated by ice flora (e.g. *Chaetoceros* spp.). Indeed, photoinhibition is likely to be of significance in water bodies of high solar irradiance and low wind speeds (Kirk, 1994). This, however, does not preclude high production rates of ice flora at reduced light intensities. Also, the presence of *Rhizosolenia* spp. and *Corethron criophilum*, which are regarded as the second stage in the succession of diatom species (Samyshev, 1991), suggests some degree of overlap between the ice-associated and open-water communities, possibly reflecting the effects of mesoscale hydrography or diatom succession patterns.

Microzooplankton grazing removed <10% of the initial standing stock of the nanophytoplankton during the grazing experiments (Tables IIA and IIIA). Despite the low impact on the initial standing stock, the grazing impact on the potential production ranged from 45 to 97% (Table IIA). This reflects the low growth rates of phytoplankton during the study (Table IIA and B). The relationship between grazing and growth rate of nanophytoplankton was significant ($P < 0.05$), suggesting a close coupling between phytoplankton and microzooplankton. Although the grazing rates reported in this study (0.03–0.05 day^{-1}) are among the lowest reported in the literature (Table IV), data suggest that microzooplankton grazing alone was sufficient to control the growth of the nanophytoplankton fraction. This result is consistent with similar studies conducted in the MIZ of the Weddell Sea during spring which demonstrated that protozoan grazing rates were higher than primary production in areas dominated by nanoplankton (Garrison *et al.*, 1993; Lancelot *et al.*, 1993; Kivi and Kuosa, 1994). Therefore, protistan grazing at the ice-edge appears only to control phytoplankton in regions dominated by nanoflagellates (Kivi and Kuosa, 1994; Scharek *et al.*, 1994). Similar grazing patterns have also been reported from studies conducted in the northern hemisphere (Paranjape, 1990; Verity and Vernet, 1992). It must be pointed out, however, that the use of chlorophyll *a* as an indicator of grazing excludes other potential food sources such as heterotrophic components. The absence of significant correlations between microzooplankton abundance, grazing impact and nanophytoplankton concentrations may be explained by the wide range of trophic responses reported in the literature.

Throughout the SODOFS study, grazing by microzooplankton generally did not result in a decrease in the microphytoplankton concentration (Tables IIB and IIIB). Consequently, grazing by microzooplankton is not sufficient to control biomass accumulation in communities dominated by microphytoplankton. These facts suggest that pre-screening the water samples through a 200 μm mesh did not have any dramatic effects on the microzooplankton grazing experiments. However, screening may have removed some large diatoms which may have been prey for dinoflagellates. The inability of protozoans to graze on microphytoplankton reflects morphological constraints associated with feeding (see Hansen

et al., 1994; Peters, 1994). Meso/macrozooplankton grazing studies conducted during the same period showed that grazing by the tunicate, *Salpa thompsoni*, was sufficient to control phytoplankton growth during the pre-bloom period (Perissinotto and Pakhomov, in preparation). Under bloom conditions, however, sedimentation of phytoplankton cells was probably the main contributor to carbon flux. Recent studies suggest that ice algae released into the water column have a tendency to form aggregates with high sinking rates (Riebesell *et al.*, 1991; cited by Scharek *et al.*, 1994). Indeed, sediment trap studies conducted at the ice-edge zone have shown the important contribution of sinking phytoplankton cells to carbon flux (von Bodungen *et al.*, 1986, 1988; Matsuda *et al.*, 1987; Fischer *et al.*, 1988).

Microzooplankton grazing did not display any diel patterns throughout the period of investigation (Table IIIA and B). Diel feeding patterns by larger metazoan grazers are primarily the result of vertical migrations from below the zone of regeneration to the surface waters as a predator avoidance strategy (Gliwicz, 1986; Perissinotto, 1989; Longhurst, 1991). Depth profile studies of the Southern Ocean have demonstrated that the protozooplankton biomass is most concentrated in the upper water column, suggesting a close relationship with the sources of primary production (Garrison and Buck, 1989; Pierce and Turner, 1992; Garrison *et al.*, 1993). Microzooplankton, therefore, do not appear to migrate vertically. Recent studies on the feeding dynamics of ciliates showed no clear-cut diurnal grazing patterns (Kivi and Setälä, 1995). On the basis of their results, Kivi and Setälä (1995) suggest that natural ciliate populations are always, within the framework of their temperature-limited metabolism, exercising clearance activity at their maximum possible rates. Grazing by ciliates, the dominant component of the microzooplankton during this study, is independent of time in the presence of an adequate food supply. Similar grazing patterns for flagellates have also been documented (Peters, 1994).

The results of the grazing experiments conducted during this study largely indicate that microphytoplankton are not grazed by microzooplankton (Table IIB). This result implies that the sedimentation of phytoplankton cells, or grazing by macro- and mesozooplankton at the ice edge, represent the primary trophic route for summer production in regions of the ice edge where microphytoplankton dominate. Indeed, a previous study on microzooplankton grazing in the Southern Ocean showed that microzooplankton removed <25% of summer production when microphytoplankton dominated chlorophyll biomass (Froneman and Perissinotto, 1996b). This provides partial support for the model proposed by Huntley *et al.* (1991) which suggests that up to 80% of the net primary production is channelled into macrozooplankton.

Dramatic seasonal differences in the physical conditions in the MIZ, and associated changes in phytoplankton abundance and distributional patterns, have been observed (Kang and Fryxell, 1993). Recent studies in the Weddell Sea and Atlantic sector of the Southern Ocean have demonstrated a shift in the size composition of phytoplankton from a community dominated by microphytoplankton in summer, to one dominated by nanophytoplankton in winter (Garrison *et al.*, 1991, 1993; Leakey *et al.*, 1994b). In winter, therefore, grazing by microzooplankton is

sufficient to control the growth of phytoplankton (Garrison *et al.*, 1993; Lutjeharms *et al.*, 1994; Froneman and Perissinotto, 1996a), and particulate organic carbon (POC) flux to the deep ocean is reduced due to the close coupling between the microzooplankton and the microbial loop, with consequent recycling of nutrients in the zone of regeneration (Longhurst, 1991). Evidence of this is presented in a number of sediment trap studies conducted in Antarctic waters (Matsuda *et al.*, 1987). These show that minimum POC flux rates (<10 mg C m^{-2} day^{-1}) coincide with the winter months, while the highest rates (120–135 mg C m^{-2} day^{-1}) are recorded in the summer, when microphytoplankton dominate the chlorophyll biomass. This result reflects a decrease in phytoplankton standing stock and lower grazing impact of the meso- and macrozooplankton during winter.

A potentially important source of POC flux in winter may, however, result from carnivory by meso- and macrozooplankton eating microzooplankton in the absence of microphytoplankton. In the Southern Ocean, carnivory on microzooplankton by larger metazoan grazers has been documented for the summer period (Hopkins and Torres, 1989; Hopkins *et al.*, 1993; Perissinotto and Pakhomov, in preparation). A general shift to zooplankton prey when phytoplankton become scarce has also been shown in a variety of other oceanic areas (Landry, 1981; cited in Hopkins and Torres, 1989). Recent studies conducted in the Weddell Sea in winter have shown that copepods feeding exclusively on phytoplankton cannot meet their metabolic costs (Bathmann *et al.*, 1993). Alternative food sources which could potentially meet these energy demands include detritus and protozooplankton. Also, recent studies conducted in coastal waters west of the Antarctic Peninsula have concluded that carnivory is the dominant trophic mode during winter (Huntley and Nordhausen, 1995). These results point to the importance of protozoans as trophic links, coupling production in the nano- and picoplankton to the higher trophic levels during winter. However, their contribution to the increase in the number of trophic steps would result in a less efficient biological pump.

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