Polar Biol (1992) 12: 211 - 218

Polar Biology

Interactions in the microbial community of the marginal ice zone of the northwestern Weddell Sea through size distribution analysis*

Sylvie Becquevort, Sylvie Mathot and Christiane Lancelot

Groupe de Microbiologie des Milieux Aquatiques, Université Libre de Bruxelles, Campus de la Plaine, CP 221, B-1050 Bruxelles, Belgium

Received 31 October 1991; accepted 26 January 1992

Summary. Enumeration and identification of planktonic microorganisms (phytoplankton, bacteria, protozoa) were carried out for 16 stations sampled in the marginal ice zone of the northwestern Weddell Sea during sea-ice retreat in 1988 (EPOS Leg 2). From these data, carbon biomass distribution among various classes, chosen according to size and trophic mode, has been determined. This analysis reveals the general dominance of nano-phytoplankton (74 %), mainly *Cryptomonas* sp.. In two stations only, significant microphytoplanktonic biomass occurred. Bacterioplankton biomass was 16 % of the phytoplanktonic biomass. Protozooplankton appeared as a significant group whose biomass represented an average of 23 % of the total microbial biomass. Maximum phytoplankton and protozooplankton biomass was reached at about 100–150 km north of the receding ice edge whilst bacteria did not show marked spatial variations. From these results, indirect evidence for close relationships between protozoa and bacteria, as well as protozoa and autotrophs, is given. The size range of autotrophic prey and predators overlaps (equivalent spherical diameter range = 6 to 11 μm). This size overlapping increases the complexity of the trophic organization of the microbial community. Our results thus support the idea of a flux of energy not always oriented towards an increasing particle size range. Potential ingestion rate, calculated from a mean clearance rate in the literature, indicated that protozooplankton might ingest as high as 48 % of the daily phytoplankton production in the marginal ice zone.

Introduction

The intensification of research effort in the Southern Ocean and the application of new methods have considerably revised the classical view of the antarctic food web structure dominated by carbon flow from the large diatoms to krill. Recently, Hewes et al. (1985) introduced the concept of an alternate carbon pathway at lower trophic levels in the antarctic food web coexisting in parallel with the classical food chain. In agreement with this, recent studies show that pico- and nano-sized primary (Von Bröckel 1981; Weber and El-Sayed 1987; Hewes et al. 1990) and secondary (Miller et al. 1984; Sullivan et al. 1990) producers are quantitatively important in the Southern Ocean. As a link between these auto- and heterotrophic microorganisms and the grazing zooplankton such as krill, the protozooplankton forms an intermediate group (Nothig 1988; Garrison and Buck 1989; Hewes et al. 1990; Garrison 1991). However, there is still little information about the abundance, distribution and activity of protozoa in the antarctic marine ecosystem or about their seasonal and regional variations (see the review by Garrison and Gowing 1992). Moreover, the information available is often scattered due to interest in specific taxonomic groups rather than in the whole community structure, and in numerical abundance rather than biomass estimate. Assessing the rôle and importance of protozoa in the trophic dynamics of the whole microbial assemblage, however, requires consideration of both biomass and cellular density of various taxonomic groups (Garrison and Gowing 1992).

This paper presents data on the abundance and size distribution of planktonic microorganisms (phytoplankton, bacterioplankton and protozoa) in the marginal ice zone of the northwestern Weddell Sea in spring 1988, and gives additional evidence of the importance of the microbial food web in the Southern Ocean. Owing to the release of active sea-ice microbes in very stable surface waters, marginal ice zones have been reported as regions of enhanced biological activity at all trophic levels (Cota et al. 1991; Smith and Nelson 1985, 1986, 1990; Schalk 1990; Smetacek et al. 1990; Ainley et al. 1986). The physical processes operating within the marginal ice zone greatly stimulate primary production by providing phytoplankton with optimum light conditions through the formation of shallow upper layers due to the addition of meltwater

* Data presented here were collected during the European *Polarstern* Study (EPOS) sponsored by the European Science Foundation

Correspondence to: S. Becquevort

(Smith and Nelson 1985, 1986; Lancelot et al. 1991). Protozoa from the melting sea-ice (Garrison and Buck 1985, 1989, 1991; Garrison et al. 1987; Mathot et al. 1991), due to their high potential growth, are therefore expected to quickly respond to the enhanced primary production associated with the receding pack-ice (Garrison and Buck 1989).

This hypothesis was tested in this study by analysis of trophic relationships between microbial planktonic organisms. These interactions were indirectly determined from the statistical regression analysis relating taxonomic groups selected according to their size (pico-, nano- and micro-) and trophic mode (autotroph versus heterotroph).

Material and methods

Studied area and sampling

Samples were collected during EPOS (European *Polarstern* Study) Leg 2, in the Scotia/Weddell Sea area of the Southern Ocean from 22th November 1988 to 5th January 1989. This paper refers in particular to two transects performed respectively along the meridian 49°W and 47°W between 59°S and 62°S (Fig. 1) as well as to two stations located at 59°S and 61°S which were visited several times during the cruise. During the investigated period, the ice edge moved southwards from 58.5°S in late November to 61°S in early January (Lancelot et al. 1991).

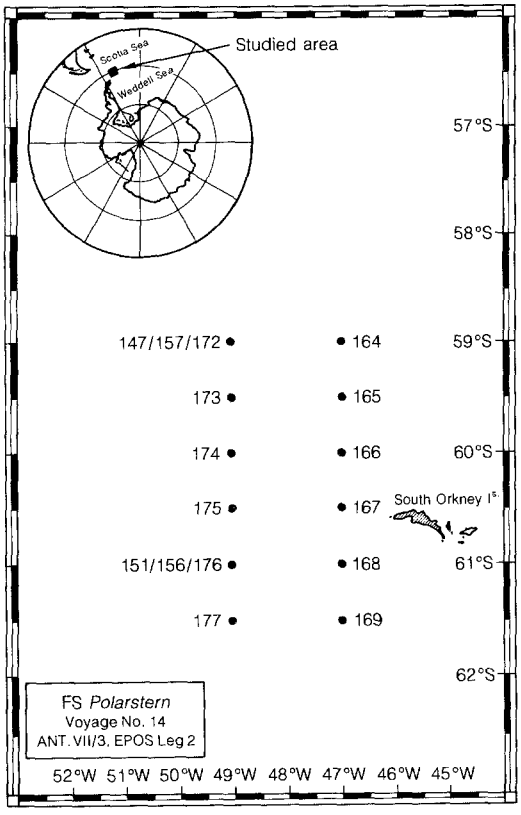

Fig. 1. Partial cruise track of the EPOS Leg 2 (November 1988–January 1989), showing the position of the sampling stations. *Inset* shows location of the study area in the Southern Ocean

Planktonic communities were collected by a Rosette sampler equipped with 12 l Niskin bottles and were preserved with an appropriate fixative immediately after collection. The sampling depth was chosen as deep enough to prevent any strong influence from the ship's hull but always in the upper mixed layer as given by CTD profiles.

Identification and biomass determination

Due to the broad range of sizes covered by microbial assemblages (0.2–200 μm), sampling volume, preservation solution and microscopical technique were chosen according to the average size and the trophic mode of selected taxonomic groups.

Bacteria, heterotrophic and autotrophic flagellates were examinated under an epifluorescence microscope following the method of Porter and Feig (1980). From 2 to 5 ml of water sample were fixed with formaldehyde-40% (final concentration 2%) and 10 to 20 ml with glutaraldehyde-25% (final concentration 0.5%), respectively, for bacteria and flagellates. Both samples were stained with 4'6 diamidino-2-phenylindole (DAPI) and filtered onto Nuclepore black filters (0.2 μm pore size) under a gentle (< 50 mmHg) vacuum (Haas 1982). The filters were rinsed with sterile filtered water, air-dried for 30 s, mounted in paraffin oil and stored in a freezer (−20°C) until examination. The organisms were observed within 6 months of sampling. Bacteria were counted on a minimum of 20 different fields at 1000x magnification. Biovolumes were calculated by treating rods and cocci, respectively, as cylinders and spheres (Watson et al. 1977), and converted to cell carbon by using the biovolume dependent conversion factor established by Simon and Azam (1989). A minimum of 100 flagellates per filter were counted and autotrophs were discriminated from heterotrophs by the red chlorophyll autofluorescence. Cell sizes were measured visually by comparison with an ocular micrometer. Biovolumes were calculated from cells shapes, and converted to cell carbon by multiplying by 0.11 pgC μm^{-3} (Edler 1979).

Diatoms and ciliates were analysed in settling chambers using the inverted microscope technique of Utermöhl (1952). Samples were preserved with glutaraldehyde-lugol (35‰, v/v) solution (final concentration 1%) and stored in the dark at 4°C until examination, (within 9 months of the cruise) with a Fluovert inverted microscope (Leitz). Between 10 and 100 ml of sample were settled for a period varying between 8 and 60 h. Magnification was chosen according to cell size: 400x for cells less than 20 μm, 320x for cells ranging between 20 and 50 μm and 100x or 200x for larger cells. According to Elder's recommendations (1979) and as far as possible, 500 cells per sedimented volume were counted in total, with at least 50 cells of the most abundant species. Cell sizes were measured visually by comparison with an ocular micrometer, and cell volumes were calculated from the stereometric shapes of the cells (Edler 1979). For diatoms, cell volumes were transformed to plasma volumes by assuming the plasma volume to be a homogeneous layer of 1 μm thickness inside the cell wall. Plasma volumes were converted to carbon values by considering a carbon density of 0.11 pgC μm^{-3} (Edler 1979). For ciliates, cell volumes were converted to carbon values using the factor 0.08 pgC μm^{-3} proposed by Beers and Stewart (1970).

Statistical analysis of the results consisted of measuring the Pearson's correlation coefficient(r), i.e. the linear association between the variables which are normally distributed. The significance level of the correlation was tested by the Student test.

Results

Biomass distribution of main taxonomic groups

Average carbon biomass distribution among the principal components of the microbial assemblages of the marginal

ice zone of the northwestern Weddell Sea is shown in Table 1. These components were chosen according to size (nano-, micro-) and trophic mode (phyto-, protozoo-, bacterioplankton). Within each trophic mode, the most abundant groups of organisms were considered. Phytoplankton biomass, ranging between 7.7 and 79.8 $\mu gC\,l^{-1}$ with a mean value of 25.7 $\mu gC \cdot l^{-1}$, constituted by far the bulk of the microbial biomass, contributing an average of 66% of the total microbial carbon (Table 1). Among the autotrophs, the nanophytoplankton were the most important, representing 74% of the total phytoplankton biomass with an average of 18.9 $\mu gC \cdot l^{-1}$. As a general trend, flagellates dominated this community (87%), whilst diatoms constituted the bulk of microphytoplankton (99%). In one case however (station 147), when a small *Chaetoceros* was abundant, diatoms significantly contributed to the nanophytoplankton. Naked flagellates identified as Prasinophyceae, Cryptophyceae and Prymnesiophyceae were the dominant autotrophic nanoplankton. Among these, *Cryptomonas* was the most important genus, contributing most to the bulk of the nanophytoplankton. Centric diatoms constituted the bulk of the microphytoplankton, with *Corethron*, *Thalassiosira* and *Rhizosolenia* being the principal genera.

The protozooplankton accounted for 9.1 $\mu gC \cdot l^{-1}$, contributing 23% of the total microbial biomass. On average, it represented 35% of the phytoplankton biomass. Like the phytoplankton, the protozooplankton was dominated by nano-sized taxa, in which heterotrophic dinoflagellates and other flagellates contributed, respectively, to 29 and 37% of the total nanoprotozooplankton biomass. The microzooplankton was composed of dinoflagellates and ciliates, the latter constituting 55% of the biomass of this component.

The bacterioplankton biomass generally varied around 4.3 $\mu gC \cdot l^{-1}$. On one occasion however (station 157), a particularly high bacterial biomass of 10 $\mu gC \cdot l^{-1}$ was observed; this was 1.3 times greater than the phytoplanktonic standing stock. This elevated bacterial biomass followed the passage of a krill swarm.

Size spectrum of phyto- and protozooplankton C biomass

Size distributions of microbial carbon biomass were expressed, according to Sheldon and Parsons (1967), on a logarithmic scale of particle diameter, i.e. the calculated equivalent spherical diameter (ESD). Essentially three patterns of phytoplankton size distribution were observed in the investigated area (Fig. 2). At most stations (11 stations out of 16, Table 2), phytoplankton was dominated by organisms for which the ESD ranged between 6 and 10 μm (Fig. 2a). Two stations (stations 147 and 176) clearly displayed a different phytoplanktonic size spectrum characterized by three peaks: one located in the nano-size range, identical to that reported for most of the stations, and two others situated in the micro-size range (Fig. 2b). Unlike all other stations, three stations (151, 156 and 157) had very low total phytoplanktonic biomass (7.7–14.4 $\mu gC \cdot l^{-1}$, mean = 11 $\mu gC \cdot l^{-1}$) and did not show any distinct peak in the phytoplankton size spectrum (Fig. 2c).

The size distribution of protozoa carbon biomass appeared less regular than for the phytoplankton. As a general trend, however, at stations of nano-autotrophic dominance, protozooplankton was also dominated by nano-sized organisms. For those stations, the highest protozooplanktonic biomasses were recorded together with highest nano-sized phytoplanktonic biomasses (Fig. 2a). On the other hand, stations characterized by high biomass of both nano- and micro-sized phytoplankton (stations 147 and 176) were dominated by a peak of protozooplankton in the micro-sized range whilst nano-sized protozooplankton were insignificant (Fig. 2b). All

Table 1. Mean and extreme values of biomass for main microbial groups. Units are $\mu gC \cdot l^{-1}$. * = % of the total microbial biomass

Organisms	Nano-size, (< 20 μm) Mean (min. – max.)	Micro-size, (> 20 μm) Mean (min. – max.)	Total Mean (min. – max.)
Phytoplankton			
Diatoms	2.0 (0.1–18.6)	6.7 (0.0–50.3)	8.7 (0.1–68.9)
Dinoflagellates	0.5 (0.0–2.1)	0.0 (0.0–0.5)	0.5 (0.0–2.1)
Other flagellates	16.4 (4.4–79.1)	0.1 (0.0–2.0)	16.5 (0.2–79.1)
Total	18.9 (3.4–79.3)	6.8 (0.0–52.8)	25.7 (7.7–79.8)
%*	49	17	66
Protozooplankton			
Choanoflagellates	0.1 (0.0–0.4)	–	0.1 (0.0–0.7)
Dinoflagellates	1.3 (0.3–3.4)	1.3 (0.0–7.4)	2.6 (0.7–7.7)
Other flagellates	3.4 (0.3–20.3)	–	3.4 (0.3–20.3)
Ciliates	0.2 (0.0–1.0)	1.6 (0.5–6.5)	1.8 (0.5–6.7)
Amoebae	1.2 (0.0–5.6)	–	1.2 (0.0–5.6)
Total	6.2 (0.7–27.6)	2.9 (0.5–11.2)	9.1 (1.8–29.2)
%*	16	7	23
Bacterioplankton			4.2 (1.4–10.00)
%*			11

Table 2. Classification of stations according to C biomass distribution of phytoplankton plotted against equivalent spherical diameter. A: see Fig. 2A, B: see Fig. 2B, C: see Fig. 2C

Stations	A	B	C
Transect 49°W			
147		*	
151			*
156			*
157/6			*
172	*		
173	*		
174	*		
175	*		
176		*	
177	*		
Transect 47°W			
164	*		
165	*		
166	*		
167	*		
168	*		
169	*		

the other stations analysed presented low biomasses of protozooplankton equally distributed up to 64 μm ESD (Fig. 2c).

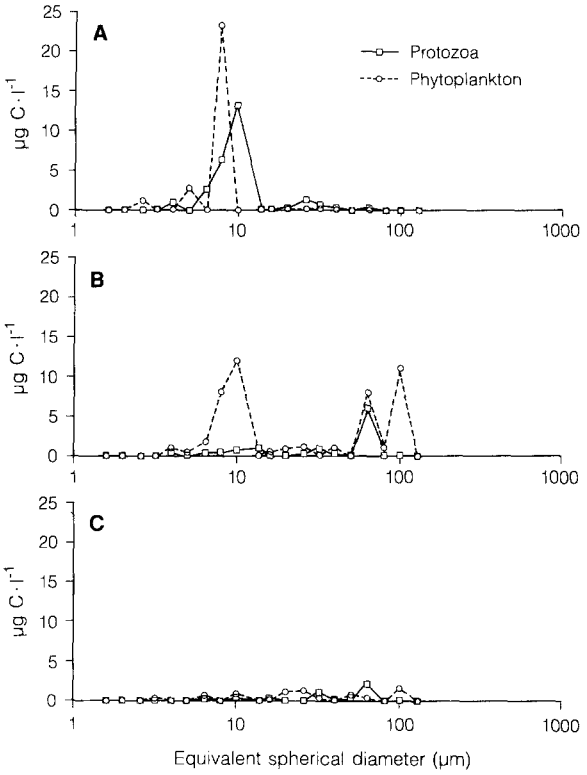

Fig. 2A–C. Typical C biomass (expressed as μg carbon per litre) distribution of phytoplankton and protozooplankton plotted against equivalent spherical diameter. **A** station 172, **B** station 176, **C** station 157

Biomass distribution of auto- and heterotrophic microorganisms and ice retreat

Figure 3 shows carbon biomasses of phytoplankton, bacterioplankton and protozooplankton measured during a 2 day cross-section conducted along meridian 49°W, perpendicular to the ice retreat.

A high phytoplanktonic biomass of 80 $\mu gC \cdot l^{-1}$ was recorded in the area recently free of ice, about 100–150 km north of the receding ice edge (Fig. 3a, b). North as well as south of this maximum phytoplankton position, biomass was very low, particularly in the heavy ice covered areas (more than 80% ice cover) where phytoplankton was about one order of magnitude lower than the observed maximum.

Protozooplankton biomass closely followed phytoplankton biomass by increasing at the time of phytoplankton bloom and maintaining levels during the decline of the autotrophs (Fig. 3b, c). At phytoplankton maxima, protozoan biomass reached 30 $\mu gC \cdot l^{-1}$, i.e. 26% of the total microbial carbon. At the northern station, however, protozoan biomass was identical to phytoplankton biomass suggesting than these grazers do control phytoplankton development in this area.

Bacterioplankton biomass varied between 2.5 and 5.5 $\mu gC \cdot l^{-1}$ representing, on average, 7% of the total microbial carbon (Fig. 3d). No clear relationship between spatial variation of bacterioplankton and those of phytoplankton and protozooplankton is evidenced by Fig. 3.

Discussion

Biomass distributions and interactions in the microbial community

Quantitative analysis of the phytoplankton community of the marginal ice zone of the northwestern Weddell Sea indicates that phytoplankton biomass was maintained at a low level during the period of ice retreat, with values ranging between 7.7 and 79.8 $\mu gC \cdot l^{-1}$. Maximum values were observed in the marginal ice zone, at about 100–150 km north of the receding ice edge, as is often observed in this area (Smith and Nelson 1986). Accordingly, corresponding chlorophyll *a* concentrations were generally less than 1 μgl^{-1} (Jacques and Panouse 1989, 1991). Taxonomic analysis revealed that low phytoplankton biomass was accompanied by the dominance of nanoplanktonic flagellates (mainly *Cryptomonas* sp., see also Buma et al. 1989), in agreement with observations by Hewes et al. (1990) in the same area. According to these authors, nanophytoplanktonic forms dominate in regions with low chlorophyll *a* values (<1 $\mu g \cdot l^{-1}$) and the increase in phytoplankton biomass results from an increase of the microphytoplanktonic forms, mainly diatoms. On two occasions (stations 147 and 173), high chlorophyll *a* concentrations of 2.2 and 2.4 $\mu g \cdot l^{-1}$ were measured (Jacques and Panouse 1989, 1991). However, even though

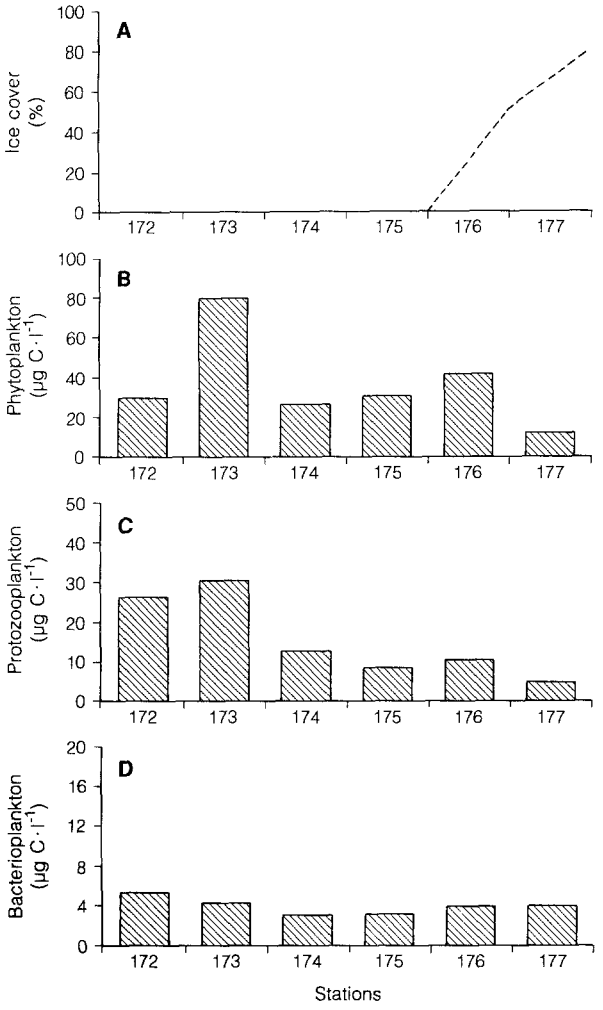

Fig. 3A–D. Distribution of (**A**) sea ice cover, (**B**) phytoplankton, (**C**) protozooplankton and (**D**) bacterioplankton biomasses along the transect 49°W

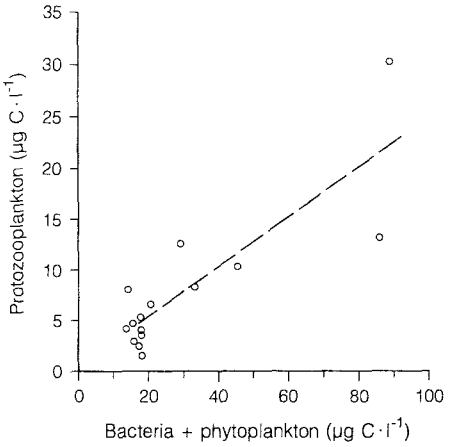

Fig. 4. Relationship between total protozooplankton biomass and combined biomass of bacterio- and phytoplankton. Units are µg carbon per litre. Equation: $y = 0.54 + 0.24x$, $R = 0.85$

microphytoplankton was an important component of station 147, station 173 was largely dominated by nanoplanktonic forms. Thus, obviously, the ice edge phytoplanktonic blooms can be dominated by either micro- or nanophytoplanktonic forms. According to Jacques and Panouse (1991), the dominance of a nanoplanktonic community results from a heavy grazing pressure on the diatoms and a little appetence of the herbivorous zooplankton for cryptophyceans.

The occurrence of nanophytoplankton in the studied area was accompanied by the simultaneous development of protozoa (Fig. 3). Accordingly, a significant positive correlation between protozoa biomass and the combined biomass of phytoplankton and bacteria was found (Fig. 4). The protozoa contributed 26% of the total microbial carbon (phyto and protozooplankton), and hence must be considered as a key component of the planktonic food web.

The co-occurrence of nanophytoplankton and protozoa seems to be a general feature of the marginal ice zone of the Weddell Sea, with protozoa accounting for 10–58% of the total carbon biomass (Table 3). Table 3 suggests a general dominance of flagellates, including naked flagellates, dinoflagellates and choanoflagellates, contributing 33–88% of total protozoan biomass.

The trophic rôle of protozoa was indirectly estimated from the correlation analysis of the data presented here. According to Fenchel (1987) and Longhurst (1989), the size of ingested food depends on the feeding mechanisms of protozoa. To further investigate trophic relationships between consumers and their food, multiregression analysis of each dominant taxonomic group of either nano- or micro-sized protozooplankton on each different potential food resource (bacterioplankton and both nano- and micro-sized phytoplankton) was carried out. Correlation coefficients specific to each food-consumer analysis are given in Table 4. In this table, bacteria are considered both as potential consumers of organic matter of phytoplankton origin either produced by excretion or by lysis, and as food for protozoa (Table 4). The lack of correlation between bacterial and phytoplanktonic biomasses indicates either heavy grazing on bacteria as well as on phytoplankton or that the bulk of dissolved organic matter utilizable by bacteria is not provided by direct phytoplankton exudation but rather by phytoplankton lysis (autolysis or diffusion from uncompletely digested fecal material of macro-or micrograzers). According to Billen and Becquevort (1991), a strong coupling between phytoplankton and bacteria is expected when organic matter of phytoplankton origin is produced as a monomeric substance, directly utilizable by bacteria. These monomers are produced mainly by exudation whilst lysis releases macromolecular substances. Utilization of the latter by bacteria thus requires prior extracellular enzymatic hydrolysis of the material, which considerably delays the response of bacteria to the supply of organic matter of phytoplankton origin. An alternative hypothesis is that the bulk of dissolved organic matter does not originate from local phytoplankton lysis but from release, at the time of ice melting, of dissolved organic matter from sea-ice assemblages. Among protozoa, only the filter-feeding ones, i.e.

Table 3. Relative abundance of protozoa and particularly heterotrophic flagellates in the Scotia and Weddell Seas

% of combined phyto- and protozoo-plankton biomass	Heterotrophic flagellate fraction (%)	Period	Site	Source
42±15	33	January 1985	Southeastern Weddell Sea	Nöthig 1988
16±11	50	February 1985	Southeastern Weddell Sea	Nöthig 1988
10±2	50	Nov.–Dec. 1983	Scotia-Weddell Sea area	Garrison and Buck 1989
10±2	71	March 1986	Western Weddell Sea area	Garrison and Buck 1989
33	52	January 1981	Scotia Sea	Hewes et al. 1990
58±10	88	June–Aug. 1988	Scotia-Weddell Sea area	Garrison et al. 1992
26±10	67	Nov.–Dec. 1988	Northwestern Weddell Sea	This study

Table 4. Correlation analysis between microbial organisms calculated according to the method of Pearson followed by the Student test. Coefficients r and (P) are reported for the significant correlations $*P<0.05$, $**P<0.005$, $***P<0.0005$; n.s. = not significant ($P>0.05$)

Food resource Consumer	Bacterio-plankton	Nanophyto-plankton	Microphyto-plankton	Total phyto-plankton
Bacterioplankton	–	–	–	n.s.
Nanoprotozooplankton				
Choanoflagellates	0.86***	n.s.	n.s.	n.s.
Other flagellates	n.s.	0.85***	n.s.	n.s.
Ciliates	0.44*	n.s.	n.s.	n.s.
Total	n.s.	0.80**	n.s.	n.s.
Microprotozooplankton				
Dinoflagellates	n.s.	n.s.	0.84***	n.s.
Ciliates	n.s.	n.s.	0.67**	n.s.
Total	n.s.	n.s.	0.95***	0.63**
Total protozooplankton	n.s.	0.83**	n.s.	0.68**

choanoflagellates (0.86, $P<0.0005$) and to a lesser extent nano-sized ciliates (0.44, $P<0.05$), should be active bacteria consumers as suggested by the significant correlations relating these taxonomic groups to bacteria (Table 4).

However, the significant positive correlation between total protozooplankton and total phytoplankton (0.68, $P<0.005$) suggests that these microheterotrophs quickly respond to phytoplankton, thus maintaining the low phytoplankton biomass. Moreover, the highly significant correlations existing between distinct taxonomic groups indicate a strong trophodynamic relationship between protozoa and phytoplankton within the same size range, especially between heterotrophic nanoflagellates and nanophytoplankton (0.85, $P<0.0005$) and between heterotrophic dinoflagellates and microphytoplankton (0.84, $P<0.0005$). This is particularly evident from the superposition of Fig. 2a, b in which peaks of both protozoan biomass and phytoplankton biomass clearly overlap. In this case, the size of predator of about 10 times that of their prey as suggested by Azam et al. (1983) does not hold, mostly due to the abundance of heterotrophic dinoflagellates. In microcosm experiments carried out with samples taken in the same area during the same period, Björnsen and Kuparinen (1991) indeed found an average linear size ratio less than 1 : 2 between nanophytoplankton prey and the heterotrophic dinoflagellates which were by far the dominant predators. Moreover, these microorganisms have been shown to feed on particles that approach or exceed their own sizes (Gaines and Elbrächter 1987;

Hansen 1991). No significant relationship between the various selected taxonomic groups of protozoa could be deduced from our data (Table 4).

Rôle of protozoa in controlling phytoplankton and bacteria development: an assumption

The rôle of protozoan grazing in controlling bacteria and phytoplankton development at the receding ice edge has been assessed by comparing the potential ingestion rate of protozoa with the net primary (Mathot et al. this volume) and bacterioplankton (Billen and Becquevort 1992) productions measured simultaneously. Potential ingestion rate of protozoa on bacteria and phytoplankton was calculated from protozoan biovolume measurements, abundance and food (bacteria and phytoplankton) concentrations using a maximum volume-specific clearance rate. According to Fenchel (1987), a maximum hourly clearance rate of 10^5 body volume per protozoa is characteristic of protozoa feeding on particle suspension. This values agrees very well with that experimentally determined by Björnsen and Kuparinen (1991) during the same cruise but for one protozoan taxon in particular. Indeed, these authors evaluated the range of maximum hourly clearance rate per heterotrophic dinoflagellate to be 0.8–1.2 10^5 body volume.

Results of this calculation, a typical example of which is illustrated by Fig. 5, clearly indicate that protozoan food requirements are primarily met by primary production, which contributes more than 95% of the total food production (combined phyto- and bacterioplankton production). Results shown in Fig. 5 suggests, in addition, that protozoa do actively control phytoplankton development at the receding ice edge, particularly in the recently free-of-ice area where calculated protozoan ingestion rates are higher than primary production. Within the marginal ice zone, potential ingestion rate by protozoa represents on average 48% of the net primary production.

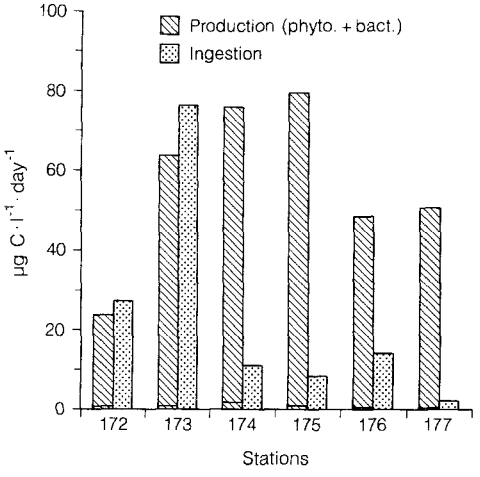

Fig. 5. Potential carbon utilization by protozoa (estimated from ingestion rates) of the combined net primary and bacterioplankton production, along the transect 49° W. *Horizontal bars* show the contribution of the bacterioplankton production to the combined bacterio-and phytoplanktonic production

The contribution of protozoa to food resources available to krill and other zooplankton can be grossly evaluated from the above calculations using the protozoa growth efficiency value of 0.38 experimentally determined by Björnsen and Kuparinen (1991) for local populations of heterotrophic dinoflagellates. Budget calculations indicate that protozoa in the marginal ice zone of the northwestern Weddell Sea provide 18% of food resources available to mesoplankton during spring.

Conclusion

The determination of size distribution and abundance of auto-and heterotrophic microorganisms in the marginal ice zone of the Weddell Sea during spring 1988 gives additional evidence for the dominance of nano-sized autotrophic communities and the quantitative importance of protozooplankton in this sector of the Southern Ocean.

However, the specific analysis of the trophic relationships between the various dominant taxonomic groups revealed a microbial network of high complexity, mainly due to a size overlapping of the various consumers and their respective food. This gives rise to a network of microbial pathways in which the energy flow is not only directed towards larger particles.

Under these circumstances, grazing measurements of each dominant taxonomic group are needed to accurately assess the carbon utilization by protozoa, but results of calculations already suggest that protozoa are potentially able to utilize significant portions of the daily production of bacterioplankton and phytoplankton.

Acknowledgements. This work is part of the Belgian Scientific Research Programme on Antarctica, funded by the Science Policy Office (Brussels, Belgium), under contract No. ANTAR/05. Data presented here were collected during the European *Polarstern* Study (EPOS) sponsored by the European Science Foundation and the Alfred-Wegener-Institute for Polar and Marine Research. We thank C.D. Hewes and two anonymous reviewers for suggestions.

References

Ainley DG, Fraser WR, Sullivan CW, Torres JJ, Hopkins TL, Smith WO Jr (1986) Antarctic mesopelagic micronekton: evidence from seabirds that pack ice affects community structure. Science 232:847–849

Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. Mar Ecol Prog Ser 10:257–263

Beers JR, Stewart GL (1970) Numerical abundance and estimated biomass of microzooplankton. In: Strickland JDH (ed) The ecology of the plankton of La Jolla California in the period April through September 1967. Bull Scripps Inst Oceanogr 17:67–87

Billen G, Becquevort S (1991) Phytoplankton-bacteria relationship in the Antarctic marine ecosystem. Polar Res (in press)

Bjørnsen PK, Kuparinen J (1991) Growth and herbivory by heterotrophic dinoflagellates in the Southern Ocean, studied by microcosm experiments. Mar Biol 109:397–405

Buma A, Estrada M, Larsen J, Riebesell U, Schloss I, Thomsen HA (1989) Unicellular organisms studied alive using photographic and video techniques. In: Hempel I, Schalk PH and Smetacek V (eds) Reports on Polar Research – The Expedition ANTARKTIS VII/3 (EPOS LEG 2) of the RV "Polarstern" in 1988/89, pp 102–110

Cota GF, Kottmeier ST, Robinson DH, Smith WO Jr, Sullivan CW (1991) Bacterioplankton in the marginal ice zone of the Weddell Sea: biomass, production and metabolic activities during austral autumn. Deep-Sea Res 37:1145–1167

Edler L (1979) Recommendations for marine biological studies in the Baltic Sea. Phytoplankton and Chlorophyll. Baltic Mar Biol 5:1–38

Fenchel T (1987) Ecological physiology: Feeding. In: Brock TD (eds) Ecology of protozoa: The biology of free-living phagotrophic protists. Springer, Berlin, pp 32–52

Gaines G, Elbrächter M (1987) Heterotrophic nutrition. In: Taylor FJR (ed) The biology of dinoflagellates. Blackwell, Oxford, pp 224–268

Garrison DL (1991) An overview of the abundance and role of protozooplankton in Antarctic waters. J Mar Syst 2:317–331

Garrison DL, Buck KR (1985) Sea-ice algal communities in the Weddell Sea: species composition in ice and planktonic assemblages. In: Gray JS, Christiansen ME (eds) Marine biology of polar regions and effects of stress on marine organisms. John Wiley, New York, pp 103 122

Garrison DL, Buck KR (1989) Protozooplankton in the Weddell Sea, Antarctica: abundance and distribution in the ice edge zone. Polar Biol 9:341–351

Garrison DL, Buck KR (1991) Surface-layer sea ice assemblages in Antarctic pack ice during the austral spring: environmental conditions, primary production and community structure. Mar Ecol Prog Ser 75:161–172

Garrison DL, Gowing MM (1992) Protozooplankton. In: Friedmann EI (ed) Antarct Microbiol (in press)

Garrison DL, Buck KR, Fryxell GA (1987) Algal assemblages in Antarctic pack ice and in ice-edge plankton. J Phycol 23:564–572

Garrison DL, Buck KR, Gowing MM (1992) Plankton assemblage in the ice edge zone of the Weddell Sea during the austral winter. Mar Chem (in press)

Haas LW (1982) Improved epifluorescence microscopy for observing planktonic microorganisms. Ann Inst Oceanogr 58:261–266

Hansen PJ (1991) Dinophys – a planktonic dinoflagellate genus which can act both a prey and a predator of a ciliate. Mar Ecol Prog Ser 69:201–204

Hewes CD, Holm-Hansen O, Sakshaug E (1985) Alternate carbon pathways at lower trophic levels in the Antarctic food web. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food.webs. Springer, Berlin, pp 277–283

Hewes CD, Sakshaug E, Reid FMH, Holm-Hansen O (1990) Microbial autotrophic and heterotrophic eucaryotes in Antarctic waters: relationships between biomass and chlorophyll, adenosine triphosphate and particulate organic carbon. Mar Ecol Prog Ser 63:27–35

Jacques G, Panouse M (1989) Phytoplankton biomass distribution. In: Hempel I, Schalk PH and Smetacek V (eds) Reports on Polar Research – The Expedition ANTARKTIS VII/3 (EPOS LEG 2) of the RV "Polarstern" in 1988/89, pp 61–67

Jacques G, Panouse M (1991) Biomass and composition of size fractionated phytoplankton in the Weddell-Scotia Confluence area. Polar Biol 11:315–328

Lancelot C, Veth C, Mathot S (1991) Modelling ice edge phytoplankton bloom in the Scotia-Weddell sea sector of the Southern Ocean during spring 1988. J Mar Syst 2:333–346

Lancelot C, Billen G, Veth C, Becquevort S, Mathot S (1991) Modelling carbon cycling through phytoplankton and microbes in the Scotia-Weddell Sea area during sea ice retreat. Mar Chem 35:305–324

Longhurst AR (1989) Pelagic ecology: Definition of pathways for material and energy flux. In: Denis MM (ed) Océanologie: Actualité et prospective. Centre d'Océanologie de Marseille, pp 263–288

Mathot S, Becquevort S, Lancelot C (1991) Microbial communities from sea ice and adjacent water column at the time of ice melting in the northwestern part of the Weddell sea. Polar Res (in press)

Mathot S, Lancelot C, Dandois JM (1992) Gross and net primary production in the Scotia-Weddell sea during spring 1988: magnitude and extension to the whole Southern Ocean. Polar Biol (in press)

Miller MA, Krempin DW, Manahan DT, Sullivan CW (1984) Growth rates, distribution and abundance of bacteria in the ice-edge zone of the Weddell and Scotia Seas, Antarctica. Antarct J Rev 19:103–105

Nöthig EM (1988) On the ecology of the phytoplankton in the southeastern Weddell Sea (Antarctica) in January/February 1985. Ber Polarforsch 53:1–118

Porter KG, Feig YS (1980) The use of DAPI for identifying and counting aquatic microflora. Limnol Oceanogr 25:943–948

Schalk PH (1990) Biological activity in the Antarctic zooplankton community. Polar Biol 10:405–411

Sheldon RW, Parsons TR (1967) A continuous size spectrum for particulate matter in the sea. J Fish Res Board Can 24:909–915

Simon M, Azam F (1989) Protein content and protein synthesis rates of planktonic marine bacteria. Mar Ecol Prog Ser 51:201–213

Smetacek V, Scharek R, Nöthig E-M (1990) Seasonal and regional variation in the pelagial and its relationship to the life history cycle of krill. In: Kerry KR, Hempel G (eds) Antarctic ecosystems. Ecological change and conservation. Springer, Berlin Heidelberg, pp 103–114

Smith WO Jr, Nelson DM (1985) Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. Science 227:163–166

Smith WO Jr, Nelson DM (1986) Importance of ice edge phytoplankton blooms in the Southern Ocean. BioScience 36:251–257

Smith WO Jr, Nelson DM (1990) Phytoplankton growth and new production in the Weddell Sea marginal ice zone in the austral spring and autumn. Limnol Oceanogr 35:809–821

Sullivan CW, Cota GF, Krempin DW, Smith WO Jr (1990) Distribution and activity of bacterioplankton in the marginal ice zone of the Weddell-Scotia Sea during austral spring. Mar Ecol Prog Ser 63:239–252

Utermöhl H (1958) Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. Mitt Int Verein Theor Angew Limnol 9:1–38

Van Bröckel K (1981) The importance of nanoplankton within the pelagic Antarctic ecosystem. Kieler Meeresforsch, Sonderh 5:61–61

Watson SW, Novitsky TJ, Quinby HL, Valois FW (1977) Determination of bacterial number and biomass in the marine environment. Appl Environ Microbiol 33:940–946

Weber LH, El-Sayed SZ (1987) Contributions of the net, nano- and picoplankton to the phytoplankton standing crop and primary productivity in the Southern Ocean. J Plankton Res 9:973–994