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The ecology of larger microzooplankton in the Weddell-Scotia Confluence Area: Horizontal and vertical distribution patterns

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ABSTRACT

The distribution of microzooplankton > 15 μm (large dinoflagellates, foraminifers, radiolarians, tintinnids, microcrustaceans and various invertebrate larvae) was studied in samples retrieved from 10 to 400 m in two overlapping transects along 49W, between 57S and 61°30′S (27 Nov.–12 Dec. 1988, and 27 Dec. 1988–4 Jan. 1989). Dinoflagellates and tintinnids concentrated at 50–90 m (10–400 m weighted averages, dinoflagellates: 103 ind./l, 131 mg C/m^2; tintinnids: 9.7 ind./l, 53 mg C/m^2). Copepod nauplii had a more variable vertical pattern with maximum numbers at 100–200 m (10–400 m av.: 2.6 ind./l, 27 mg C/m^2). Foraminifers and radiolarians were most abundant in noticeably deeper waters peaking below 150 m (10–400 m av., foraminifers: 0.2 ind./l, 11 mg C/m^2; radiolarians: 2.7 ind./l, 12 mg C/m^2). Large dinoflagellates accounted, on the average, for 55% of the biomass of the heterotrophs considered in the 10–400 m layer, followed by the tintinnids (23%), copepod nauplii (11%), foraminifers (5%), and radiolarians (5%). The 100–400 m layer hosted up to 87% (mean: 49%) of total 10–400 m integrated microzooplanktonic biomass. The distribution of loricate ciliates was strongly correlated with those of chlorophyll *a*, and especially dinoflagellates (r = 0.832, for log-transformed data), suggesting close trophic relationships between these two groups. The northern sites were generally richer in microzooplankton than the area closer to the ice-edge, and the southernmost ice-covered zone yielded the lowest microplanktonic values. This biological pattern, which was but loosely coupled with the Weddell-Scotia Confluence, with the vertical stability of the water column, and with near-surface concentrations of chlorophyll *a*, can at least partly be explained by differential grazing pressure by crustacean mesozooplankton. The time elapsed between the two transects did not affect the microzooplanktonic assemblages noticeably. Comparisons with previous abundance estimates carried out earlier and later in the growth season suggest that microzooplanktonic abundances increase toward the late summer-fall, probably in response to enhanced availability of nano- and pico-sized producers, characteristic of Antarctic post-bloom conditions.

1. Introduction

Interpretation of the biological processes which characterize the spatial and temporal succession of planktonic systems in the Southern Ocean has changed

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significantly over the last decades. A salient feature is the finding that over 50% of the primary production is based on regenerated nitrogen in the form of ammonium and urea (Glibert *et al.,* 1982; Olson, 1980; Rönner *et al.,* 1983; Sakshaug and Holm-Hansen, 1984; Holm-Hansen, 1985). High ammonium uptake rates, in turn, are associated with nanoplanktonic producers (Probyn and Painting, 1985; Koike *et al.,* 1986), which often dominate the post-bloom successional stages of Antarctic phytoplankton accounting for up to 80%–90% of total autotrophic production (Bröckel, 1981, 1985; Weber and El-Sayed, 1987; Bodungen *et al.,* 1988). The key role attributed to the protozooplankton in these communities stems from its high consumption rates of nano- and picoplanktonic producers (Hewes *et al.,* 1983, 1985; Sakshaug and Holm-Hansen, 1984; Bodungen *et al.,* 1988; Tumantseva, 1989), thus contributing to an active recycling of biogenic materials. Furthermore, it has been suggested that the high standing stocks of Antarctic crustaceans, mainly krill and copepods, which are not efficient consumers of nano- and pico-sized particles, must chiefly rely on microplanktonic heterotrophs which "repackage" the organic matter into a size suitable for consumption at higher levels of the food web (Hewes *et al.,* 1985; Sherr *et al.,* 1986; Garrison and Buck, 1989; Jacques, 1989; Garrison, 1991). Studies of the distributional patterns of the smaller consumers and their spatial and temporal relationships with major hydrological features, chlorophyll *a*, and phytoplankton are of interest since they contribute to our understanding of the functional links between these components of the marine system. In this context, vertical structure is especially important because the role of deep-dwelling (>100 m) microzooplankton in the scavenging and recycling of particulates settling out of the photic layer, and its contribution to the diets of larger zooplankton, can be significant (e.g., Nöthig and Gowing, 1991; Gowing and Garrison, 1992).

The aim of this report is to present an analysis of the horizontal, vertical and temporal distributional pattern of microzooplanktonic abundance and biomass in the ice-edge zone of the Weddell Sea and the Weddell-Scotia Confluence during the austral summer of 1988–1989. Causal settings of the patterns established are discussed taking into account environmental physico-chemical and biological parameters, including phenomena associated with the edge of the ice-pack and frontal processes.

2. Material and methods

Samples for this study were collected aboard R/V *Polarstern* along 2 overlapping transects on 49W, 57S to 61°30'S, during Leg 2 of the European Polarstern Study (EPOS) in the Weddell-Scotia Confluence area (Transect I: 27 November to 12 December 1988, 5 stations; Transect IV: 27 December 1988 to 4 January 1989, 6 stations, see Figure 1 and Hempel *et al.,* 1989). EPOS-LEG 2 (1991) includes a detailed listing of the physical, chemical and biological (chlorophyll *a*) data collected during the cruise.

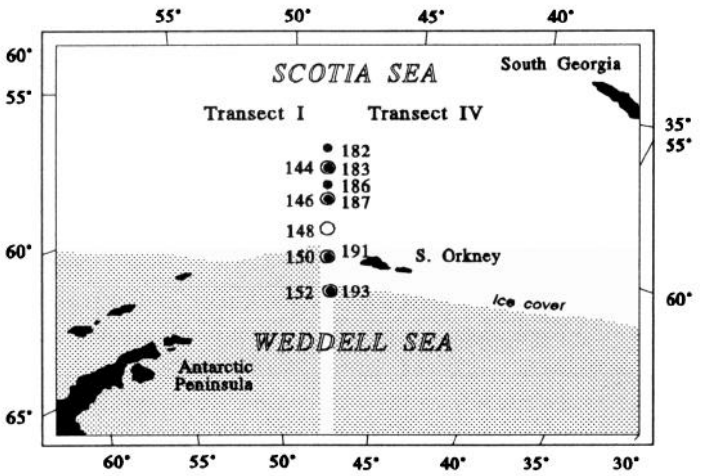

Figure 1. Geographic location of the stations occupied. Large empty circles: first transect (27 Nov. to 12 Dec. 1988); small filled circles: fourth transect (27 Dec. 1988 to 4 Jan. 1989). Arrows indicate approximate positions of the ice-edge in Nov.–Dec. (solid line), and in Dec.–Jan. (broken line).

At each station, a CTD rosette equipped with Niskin and GoFlo bottles was used to collect water samples from 10, 20, 40, 60, 80, 100, 120, 150, 200 and 400 m (13 out of these 110 data-points—11 stations with 10 sampling depths each—were unavailable). The water (15 liters per sample on average, range: 9 to 22 l) was filtered through a 15 μm-mesh sieve and preserved with acid Lugol's solution. At Sta. 144 samples were also retrieved from depths down to 1150 m, and at Sta. 148 and 183 to 600 m. Large thecate dinoflagellates, foraminifers, radiolarians (including Polycystina and Phaeodaria), tintinnids, microcrustaceans (chiefly copepod nauplii), and various other organisms ("others," comprising of mainly larvae of polychaets, molluscs and echinoderms) were counted in 10 or 25 ml settling chambers under an inverted microscope. Silicoflagellates (*Distephanus speculum* Ehrenberg) were also counted, but analyses of the distribution patterns of these autotrophs are restricted to a few comments. The presence of naked ciliates was recorded whenever they occurred in the samples, but the mesh-size of the sieve used and the filtration method employed only allow using these non-quantitative data in ancillary observations. In most cases whole samples were counted in order to reach at least 100 individuals for each group per sample. Heterotrophic dinoflagellates were assessed on the basis of the examination of live materials under epifluorescent light during the cruise. These observations, a detailed identification guide prepared by J. Larsen (unpublished) during the same expedition, and the work of Balech (1976) were subsequently used in the laboratory for counts of this group. Biomass data were based on size measurements of organisms, and calculation of volumes from appropriate regular geometric shapes. Conversion factors used in order to transform these volumes into

organic carbon values were, dinoflagellates: pg C = $\mu m^3 \times 0.13$ (Edler, 1979); tintinnids: pg C = $\mu m^3 \times 0.053 + 444.5$ (Verity and Langdon, 1984); all other groups pg C = $\mu m^3 \times 0.08$ (Beers and Stewart, 1970).

While the database used for this report has a fairly dense coverage of the 10–200 m vertical interval, farther down only one data point was available (400 m). The inclusion of the 200–400 layer in our analyses, however, was considered pertinent because: (1) Most previous surveys of the abundance of Antarctic microzooplankton were restricted to the upper 150 m and, as our results suggest, populations between 200 and 400 m can represent a significant proportion of total integrated numbers in the water-column; (2) Abundance variations between 200 and 400 m were generally smooth and in agreement with the trend observed in the upper 200 m, thus suggesting that the inclusion of additional data points between 200 and 400 m would not have changed the overall picture significantly; (3) Some groups, like the foraminifers and radiolarians, peak at depths around or below 200 m; eliminating our 400 m samples would clearly have yielded strongly underestimating abundances for these organisms.

While admittedly somewhat arbitrary, the size cutoff value used in this work (15 μm) is dictated by sample collection and processment protocols, which specifically target this component. An altogether different set of techniques, including non-concentrated small-volume samples is used for the size-fraction <15 μm; the latter methods, in turn, do not yield reliable estimates of the abundance of the larger and less numerous microzooplankters. Furthermore, it has been reported that heterotrophs >15–20 μm are chiefly responsible for the transfer of nano-sized particles to larger zooplankton (see below), which makes surveys of this particular group especially interesting for interpretations of food-transfer pathways. Finally, the microzooplankton includes organisms of much relevance to paleoecological studies: analyses of radiolarian and foraminiferal abundance and distribution patterns can significantly enhance our understanding of the environmental signal of their fossil assemblages (Boltovskoy and Alder, 1992).

Naked ciliates, which constitute an important fraction of overall (chiefly nanoheterotrophic) biomass have not been considered in this report. According to Kivi (1991), during the previous leg of the EPOS program (18 October to 13 November 1988), in the 0–80 m layer of the Weddell-Scotia confluence area tintinnids accounted for 7% of total (sheathed + naked) ciliates. However, the average biomass of Antarctic naked ciliates (0.001 μg C/ind., cf. Garrison and Gowing, 1993) is ca. 10 times lower than that of the tintinnids recorded in our survey (0.01 μg C/ind.). Thus, in terms of biomass, tintinnids can represent close to 50% of the organic carbon of total ciliates. Acantharians and heliozoarians were not considered either because the fixation technique used was inadequate for these groups. Gowing (1989) reported maximum concentrations of 2.7 and 4.2 Acantharia and Heliozoa (respectively) per liter in Antarctic waters at 0 to 200 m. Unarmoured dinoflagellates, even when larger

than the mesh-opening used, can be extruded through the gauze during filtration; this circumstance, and the fact that Lugol's solution leads to some shrinkage of the cells (Choi and Stoecker, 1989), accounts for underestimation of dinoflagellate carbon in our work.

3. Results

The two sampling periods (=transects) surveyed were characterized by a microzooplankton-rich northern zone and a microzooplankton-poorer southern part (Figs. 2, 3). In the fertile northern sector, however, noticeably higher values were restricted to one station at each transect (Sta. 146-first transect, and 182-fourth transect; Fig. 3A). Abundances in the 10–400 m layer were higher at these two stations exceeding by 2–3 (foraminifers, radiolarians, nauplii) to 34 times (dinoflagellates) the average at the rest of the sites. In terms of overall microzooplanktonic organic carbon this contrast represents a 10-fold difference. The general composition of the microzooplanktonic assemblage did not show clear trends in association with latitude (Fig. 3B). The two richest stations (146 and 182, Fig. 3A) were largely dominated by dinoflagellates, yet at the remaining sites relative abundances shifted more or less at random between groups (Fig. 3B).

Figures 2 and 4 summarize general data on the vertical distribution and overall abundances of the groups surveyed. Dinoflagellates occupied the uppermost layers, representing ca. 50 to 90% of total microheterotrophic biomass in the top 80 m (Fig. 4A). Copepod nauplii was the only group which showed more or less defined abundance trends, increasing toward the southern stations (Fig. 3B), and especially toward the deeper levels (Fig. 4A). Polycystine radiolarians were about twice as abundant as the Phaeodaria (2.0 and 0.7 ind./l, respectively, at 10–400 m).

It should be stressed that data illustrated in Figures 3 and 4 are based on averaged values, and therefore conceal the conspicuous station-to-station and depth-to-depth variability recorded in the area.

North-south biomass differences (Fig. 3A) were related to the vertical distribution of the microzooplankters, strongest meridional dissimilarities being associated with the surface and subsurface dwellers (dinoflagellates, tintinnids), and much less marked ones with the deeper-living organisms (foraminifers, radiolarians, Fig. 2). As a result of these dissimilar meridional and vertical distributions, in general terms at the northernmost stations (especially numbers 146, 148, 182, 183; see Fig. 1) the 10–50 m stratum hosted higher percentages of the overall (10–400 m) microzooplanktonic biomass (mean: 54%) than farther south (11%). Ice-covered stations 152 and 193 had some of the lowest values in the surface waters (mean: 4%, at 10–50 m).

Data illustrated in Figure 4B, C show that, when evaluated in terms of biomass at isolated levels in the water-column, values for the deeper-dwelling organisms can appear deceivingly small. Integration of low numbers over large depth intervals at 100–200 to 400 m makes these plankters important contributors to total microhetero-

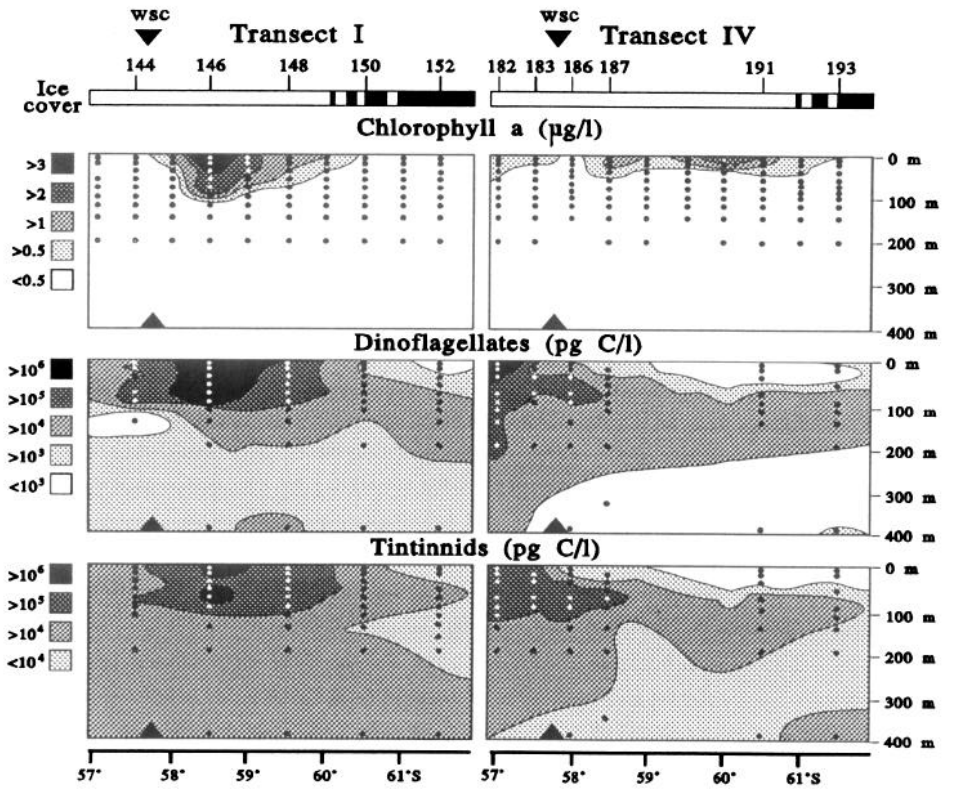

Figure 2. Contours for the biological variables considered. WSC: Weddell-Scotia Confluence (according to Cederlöf *et al.,* 1989).

trophic carbon (Fig. 4C). Moreover, the few data available on microzooplanktonic abundances below 400 m indicate that the deep layers can occasionally further increase integrated biomass significantly. Thus, at Sta. 144, for example, microheterotrophic carbon in the 400–1150 m stratum exceeded that at 0–400 m. At Stas. 148 and 183, however, the 400–600 m layer only added 14% or less to the 0–400 m biomass.

4. Discussion

a. Distribution and structure of microzooplanktonic assemblages. During the first transect the WSC was located just south of Sta. 144; enhanced chlorophyll *a* values at the neighboring Sta. 146 (Fig. 2) could therefore be attributed to upper-layer stabilization associated with WSC frontal processes, and/or to the input of meltwater from the pack-ice (Bennekom *et al.,* 1989). A major microzooplanktonic peak at this site, chiefly due to the dinoflagellates and tintinnids (Figs. 2, 3), probably represents an area of high turnover rates and active grazing. During the fourth transect, on the other hand, the microzooplankton-richest station (Sta. 182, see Figs. 2, 3A) was

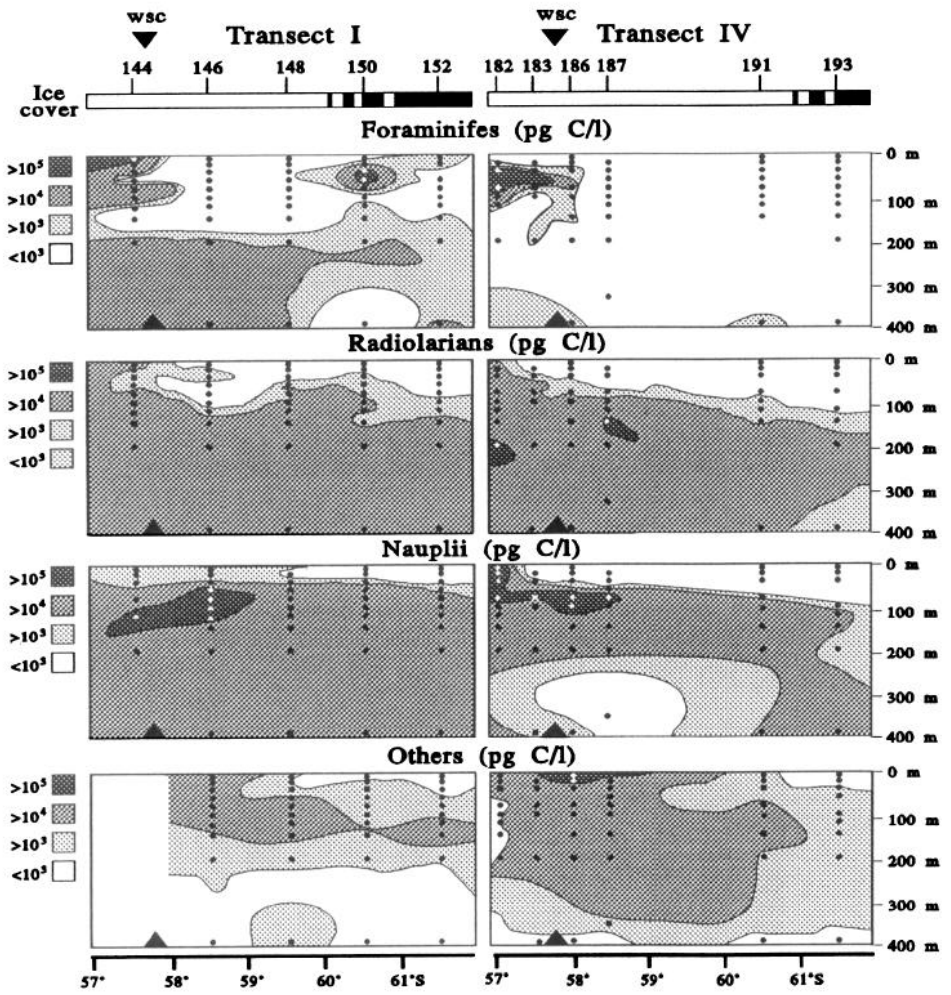

Figure 2. (Continued)

located over 60 miles north of the (less pronounced) front (Cederlöf *et al.,* 1989), rather than to the south of it.

Relationships between microheterotrophic biomass and vertical stability of the upper layer, whose depth ranged from approx. 20 to 40 m throughout the cruise, were also variable. While during the first transect highest 100–10 m sigma-*t* values coincided with the chlorophyll *a* and microzooplankton maxima (Sta. 146), during the fourth transect sigma-*t* differences increased more or less regularly toward the ice-edge (EPOS-LEG 2, 1991), and were thus negatively associated with the meridional distribution of microzooplanktonic biomass (Fig. 3A).

In this respect, our results generally confirm the preliminary conclusions of Smetacek and Veth (1989) and Bennekom *et al.* (1989) for EPOS Leg II, as well as

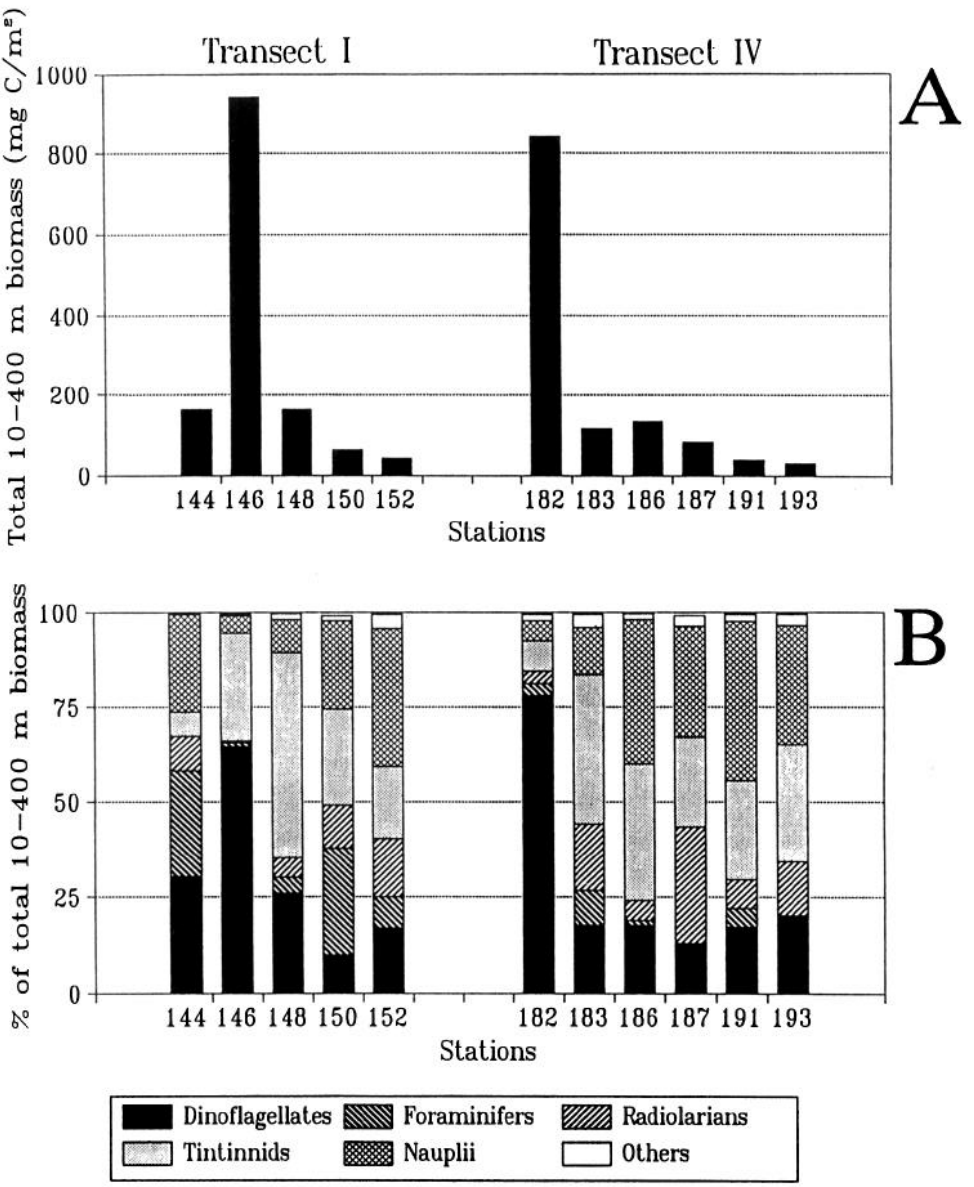

Figure 3. Total 0–400 m integrated biomass (A) and percentage contribution of the groups analyzed (B) at the 11 stations occupied.

previous surveys in the marginal ice-zone of the Weddell Sea (e.g., Nelson *et al.*, 1989), in that factors regulating biological processes in the area include, but are certainly not restricted to, the stratification of the upper layer associated with meltwater from the ice pack, and the Weddell-Scotia Front. Changing spatial

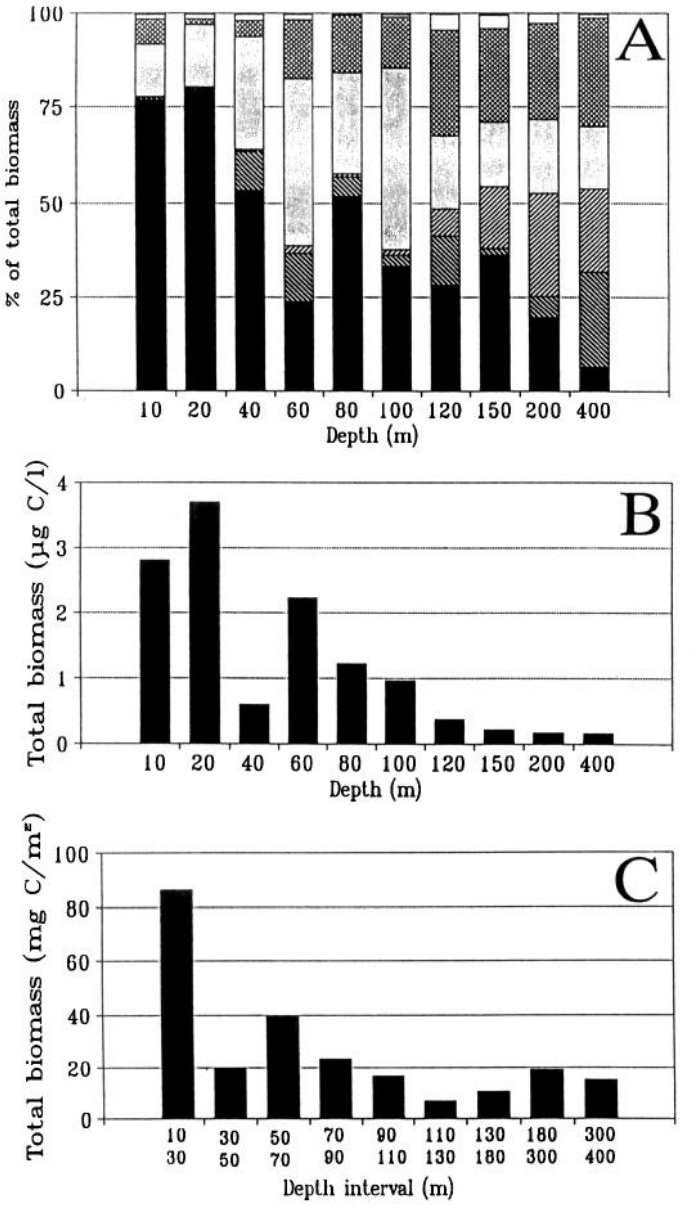

Figure 4. Vertical distribution of microzooplankton, as shown by averaged values for all stations. For biomass data illustrated in the bottom panel (C) discrete values (B) were extrapolated to depth intervals indicated.

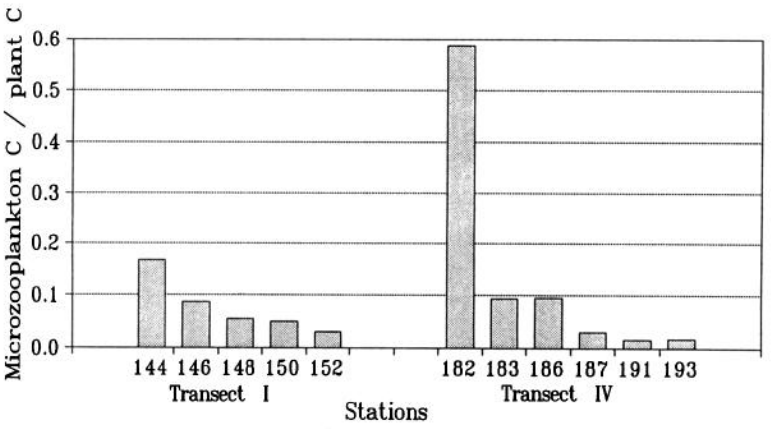

Figure 5. Ratio between microzooplankton and plant carbon (the latter estimated on the basis of chlorophyll a values, cf. El-Sayed and Taguchi, 1981).

relationships between the distribution of phytoplanktonic and microzooplanktonic maxima, on the other hand, disagree with the conclusions of Lancelot *et al.* (1991a,b), who suggested tight and highly predictable coupling between the producers and microzooplankton.

The north-south gradients showed differences in microzooplanktonic biomass and vertical structure, the southern area being characterized by sparser communities located deeper in the water-column than the Scotia Sea (Figs. 2, 3). As discussed above, measured hydrographic properties and distribution of chlorophyll *a* were unable to fully explain these dissimilarities. We therefore turned our attention to various aspects of food supply for, and grazing pressure on microzooplanktonic organisms, which can also exert a strong selective pressure on the distribution of their populations.

At the sites surveyed, in the 0–200 m layer microzooplankton carbon averaged approx. 10% of plant carbon (the latter calculated on the basis of chlorophyll *a* values, cf. El-Sayed and Taguchi, 1981; see Fig. 5). Considering that only organisms above 15 μm are included, this figure is comparable to previous estimates for the Antarctic (e.g., southern Weddell Sea: 25%, for the large protozooplankton, cf. Bodungen *et al.,* 1988; Weddell Sea marginal ice-zone: 9–23%, cf. Garrison and Buck, 1989). An interesting feature, however, is that the range of variation between stations for these phytoplankton/microzooplankton ratios was extremely high, spanning from 0.016 to 0.586, with a conspicuous north-south gradient (Fig. 5). These dissimilarities were paralleled by the makeup of the autotrophic assemblages, the richer northern areas being dominated by large (>10 μm) cells, while in the poorer southern ones most of the phytoplanktonic biomass was represented by cells <10 μm (Eckernkemper *et al.,* 1989; Jacques and Panouse, 1991; Schloss and Estrada, 1993). Thus, the southern locales were generally poorer in primary producers (Fig. 2), and

especially in large phytoplanktonic cells, and also hosted the lowest microzooplanktonic biomass and lowest microzooplankton vs. plant carbon ratios (Fig. 5). This trend was somewhat surprising because enhanced availability of small-sized food particles should in principle have favored protozooplanktonic growth, and the shorter generation times of the smaller autotrophic nanoplankters would be expected to yield higher (rather than lower) microzooplankton:chlorophyll ratios. While short-term variations in phyto and zooplanktonic numbers might be partly responsible for this pattern, the occurrence of krill and copepod fecal pellets in our samples suggests that this drop in microzooplankton numbers towards the ice-edge (Figs. 2, 3A) may be largely due to zooplanktonic grazing. Very abundant fecal material was recorded in our samples at Stas. 148–152 (transect I), and 186–193 (transect IV), at depths ranging between 40 and 200 m, which agrees with data on krill and "oval" pellets reported by González (1992), and with the distribution of peak net zooplankton and micronekton biomass within the marginal ice-zone (Schalk, 1990). The spatial coincidence between larger zooplankton, abundant fecal material and phytoplanktonic communities strongly dominated by nanoplankton supports this assumption insofar as crustacean grazing exerts a strong selective pressure on the food-particles shifting their size-range toward the smaller fraction (Boyd, 1982; Quetin and Ross, 1985). Concordantly, the conspicuous drop in large diatom cells in the water-column adjacent to the ice-edge (as compared with the ice assemblages) recorded by Mathot *et al.* (1991) during the same cruise was also tentatively attributed to enhanced grazing pressure.

It is probable that the southernmost deeper concentration of microzooplankton (which reportedly constitutes an important food-item for the Euphausiacea: Hopkins and Torres, 1989; but see also Marchant and Nash, 1986; Tanoue and Hara, 1986) illustrated in Figure 2, was also due to enhanced euphausiid grazing pressure closer to the surface: highest metabolic rates (as measured by respiratory ETS activity) and shallowest concentrations of these crustaceans were recorded in the ice-edge zone (Cuzin-Roudy and Schalk, 1989; Schalk, 1990).

While our survey focused on the heterotrophic plankton >20 μm, it should be noticed that the naked ciliates and the smaller heterotrophic flagellates, which can make up a substantial part of the overall heterotrophic fraction below 200 μm (Hewes *et al.,* 1985; Buck and Garrison, 1988; Garrison and Buck, 1989) have not been accounted for in our calculations. Data for EPOS Leg II support the assumption that the north-south shift in the size of the autotrophs was accompanied by an increase in the numbers of nanoplanktonic consumers (Buma *et al.,* 1989; Schloss and Estrada, 1993). If, as suggested by Quetin and Ross (1985), this size-class is not efficiently grazed upon by the dominant zooplankton, then the role of microzooplankton for sustaining the animal biomass at higher trophic levels of the food-web would be further enhanced in this southern sector. Analyses of the gut-contents of the dominant meso- and macrozooplanktonic consumers in the marginal ice-zone of the

Weddell Sea, showing a shift from predominantly phytoplankton-based diets in ice-free waters to carnivory in ice-covered areas (Hopkins and Torres, 1989), reinforce the above conclusion.

b. Deep-dwelling microzooplankton. Because many previous attempts at quantifying the magnitude of the microzooplanktonic trophic loop were based on casts to 100–150 m or less (e.g., Hewes *et al.,* 1985; Garrison and Buck, 1989), it is suggested that they might have underestimated the overall abundance of these organisms in Antarctic waters. Our data indicate that, although on the average the 10–100 m interval hosted ca. 80% of the overall microzooplanktonic biomass down to 400 m, values as low as 17–20% were recorded at the ice-covered sites (Stas. 152, 191). Populations below 400 m can further increase the 10–400 m biomass over twofold: at Station 144 the 400–1150 m layer contained >200 μg microzooplanktonic C/m^2, over 70% of which was represented by foraminifers and nauplii.

Admittedly, some of our tintinnids, foraminifers and radiolarians retrieved at the lower levels could have been represented by empty shells in the process of sedimentation, rather than by physiologically active organisms. However, species of both these sarcodines are known to live at depths in excess of several thousand meters (Petrushevskaya, 1967, 1971; Boltovskoy and Wright, 1976; Kling, 1979; Morley and Stepien, 1985), and reported mean percentages of empty polycystine skeletons at depths of 200–500 m in the Weddell Sea are only 20% (Nöthig and Gowing, 1991). Tintinnids, on the other hand, possess organic loricae which account for up to 79% of the overall organic carbon of the ciliate (i.e., protoplast + lorica; Gilron and Lynn, 1989), thus making empty loricae a very significant contributor to total organic material.

While sizable when integrated over large depth-intervals, the significance of this biomass as a food-source for larger filter-feeding zooplankton is probably limited by its low concentration which can render its acquisition energetically disadvantageous. On the other hand, deep-dwelling microzooplankton are probably important to remineralization of material flux from the upper layers.

An interesting outcome of our results is the relationship between depth of distribution of the microzooplankters and their association with phytoplankton-rich areas. Figure 6 shows that the horizontal (10–400 m integrated) distribution of dinoflagellates and tintinnids, which were most abundant in the upper 100 m, was positively correlated with integrated chlorophyll *a* in the 0–200 m layer (Table 1). Foraminifers and radiolarians, on the other hand, which occupied noticeably deeper waters, did not concentrate under areas of high phytoplankton biomass. In other words, the deeper a group dwells, the less affected its distribution seems to be by near-surface primary production. At the scale of our geographic coverage, also ice-cover had the smallest influence on radiolarian and foraminiferal densities: ice-free vs. ice-covered (10–400 m integrated) abundance ratios were approx. 30 to

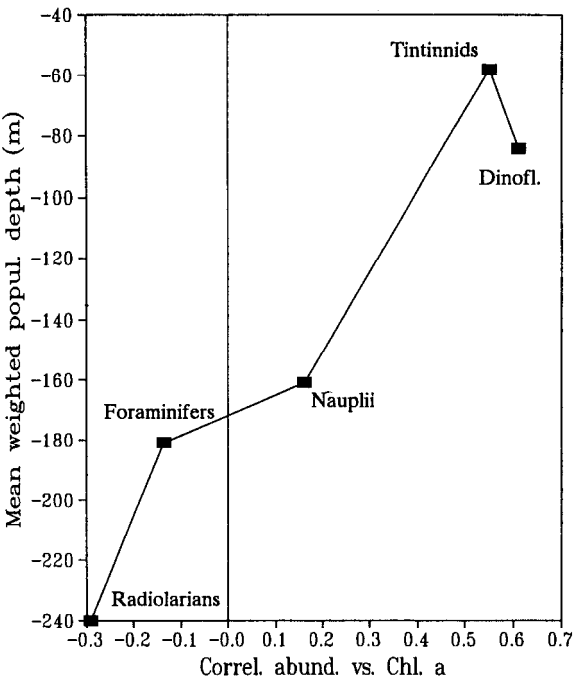

Figure 6. Relationships between average population depth and spatial correlation of abundance (0–400 m integrated values) with the concentration of chlorophyll *a* (in the 0–200 m layer).

10 for dinoflagellates and tintinnids, respectively, while for nauplii, radiolarians and foraminifers the figure dropped to below 3. For the diatoms (Schloss and Estrada, 1993; 0–100 m) and silicoflagellates the same ratio was approx. 17.

In addition to the dissipation of the near-surface productivity signal at depths exceeding 150–200 m that can contribute to generate the pattern described, a complementary explanation to account for these contrasts might reside in the dissimilar life-spans of the groups involved. While dinoflagellates and tintinnids have generation times of 1 to 3 days (Bjørnsen and Kuparinen, 1991; Heinbokel, 1978, 1988), for sarcodines and crustaceans these are between one month (Caron and Swanberg, 1990) and over a year. Thus, abundance changes in response to short-term variations in near-surface productivity and ice-cover would necessarily be restricted to the organisms with faster reproduction rates (Gowing and Garrison, 1991).

Polycystine peak concentrations in the deep waters are probably a response to the higher temperatures (Fig. 7), which in this area characterize strata >200 m of the Warm Deep Water (Gordon, 1967; Carmack and Foster, 1977). This relationship, which was also reported by Gowing and Garrison (1991) for the winter, can have important implications for paleoecological studies insofar as the signal of polycystine

Table 1. Correlation indices between variables based on all the data-points available (log-transformed data; $90 < n < 100$; values above 0.6 are highlited in bold).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Depth	1.000													
2 Temp.	0.351	1.000												
3 Sal.	0.572	−0.017	1.000											
4 Sig.-*t*	**0.734**	−0.185	**0.817**	1.000										
5 NO_3	**0.691**	0.189	**0.615**	**0.682**	1.000									
6 PO_4	**0.643**	0.186	0.585	**0.645**	**0.979**	1.000								
7 NH_4	−0.228	0.125	−0.330	−0.418	−0.428	−0.283	1.000							
8 Chl. *a*	−0.516	−0.217	−0.431	−0.457	**−0.859**	**−0.855**	0.425	1.000						
9 Silic.	−0.213	0.202	−0.415	−0.490	−0.388	−0.417	0.326	0.413	1.000					
10 Din.	−0.255	0.063	−0.496	−0.524	−0.513	−0.557	0.240	0.550	**0.762**	1.000				
11 For.	−0.016	0.088	−0.154	−0.196	0.027	0.035	0.099	−0.137	0.311	0.181	1.000			
12 Rad.	0.417	0.564	0.124	0.079	0.411	0.353	−0.179	−0.290	0.261	0.169	0.282	1.000		
13 Tint.	−0.370	−0.008	−0.546	−0.577	−0.594	−0.587	0.493	**0.613**	**0.706**	**0.832**	0.138	0.029	1.000	
14 Naup.	0.095	0.117	−0.120	−0.108	−0.049	−0.088	−0.016	0.165	0.428	**0.634**	0.237	0.259	0.470	1.000
15 Oth.	−0.236	0.281	−0.269	−0.371	−0.216	−0.232	0.047	0.109	0.252	0.427	−0.075	0.075	0.335	0.302

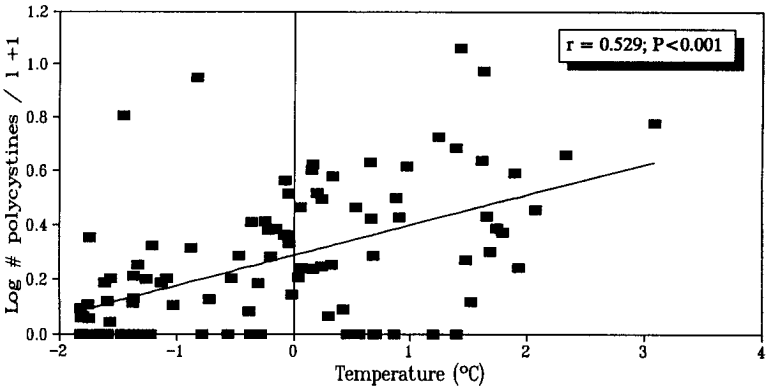

Figure 7. Linear regression and actual data points for polycystine abundances vs. water temperature (data from discrete depths between 0 and 400 m).

thanatocoenoses generated in this layer would be warmer than the corresponding conditions in the upper mixed layer (Boltovskoy and Alder, 1992).

c. Temporal succession. As opposed to the above discussed contrasts between northern and southern stations, the time elapsed between the two transects investigated did not affect the structure or the abundance of the microheterotrophic community substantially (Figs. 2, 3). Also net zooplankton and micronekton biomass did not vary in the period concerned (Schalk, 1990). This is especially interesting in view of the fact that the producers' spectrum changed dramatically from an assemblage dominated by >10 μm diatoms (70% of overall phytoplanktonic biomass) during transect I, to one where they dropped to $<20\%$, during transect IV (Jacques and Panouse, 1991). The contribution of smaller naked ciliates and other nanoplanktonic heterotrophs also seems to have increased noticeably between the two transects; Schloss and Estrada (1993), for example, found that choanoflagellate densities in the 0–80 m layer soared from approx. 10^8 to 3×10^9 ind./m^2. Naked ciliates were abundant in some of our materials from the fourth transect (Sta. 191 and, especially, 182 and 183), where they reached peak abundances at approx. 40 m. Absolute abundances and relative composition of the groups enumerated, however, did not vary significantly (Fig. 3), which suggests that during the time elapsed an additional size-class of consumers developed, but the original microzooplanktonic assemblage was not replaced.

While life-spans of the sarcodines (Caron and Swanberg, 1990) and of the copepods are too long for their numbers to grow on such short time scales in response to enhanced availability of adequately-sized food, dinoflagellate and tintinnid reproduction rates are fast enough for their populations to increase noticeably between the two sampling periods. As discussed above, the fact that they did not

show any sizable abundance variations could be due to higher macrozooplanktonic grazing pressure in this new environment with scarce net phytoplankton.

d. Correlations between variables. Table 1 summarizes the results of correlation analyses between the variables considered using all the available data-points. Due to the high number of degrees of freedom (up to 98), most correlations are highly significant, yet the percentage of associated variance they account for is usually below 50%. Negative correlations between nutrients vs. chlorophyll *a* and silicoflagellates point to depletion by biological activity and to contrasting depth-distributions (i.e., nutrient concentrations increase with depth).

Tintinnids were strongly correlated with chlorophyll *a*, silicoflagellates, and especially with dinoflagellates ($r = 0.832$). The latter association is especially noteworthy because it is consistent with previous results in the Weddell Sea ($r = 0.891$: Boltovskoy *et al.,* 1989), and in the Bransfield-Bellingshausen area ($r = 0.970$: Alder and Boltovskoy, 1991). The fact that tintinnids feed chiefly on dinoflagellates has been reported for some low-latitude species (Stoecker *et al.,* 1984; Kopylov and Tumantseva, 1987), but these results may not apply to all loricate ciliates (Verity, 1991). Complementary information on the potential availability of dinoflagellates as a food-source for tintinnids can be derived from size-distribution patterns in the two groups. Spittler (1973), Heinbokel (1978), and Kopylov and Tumantseva (1987) concluded that the ciliates ingest particles up to approx. 40% of their lorica oral diameter. According to our measurements, approx. half of the tintinnids retrieved in the Weddell-Scotia confluence area had oral diameters >40% of the average dinoflagellate size (30.9 μm). However, our 15 μm-mesh sieve must have missed the lower end of the dinoflagellate size-range, which can host sizable proportions of all dinoflagellate specimens (Kopczynska *et al.,* 1986; Estrada and Delgado, 1990). Thus, although high correlations and the ancillary data reviewed suggest that tintinnids feed chiefly on dinoflagellates, the information available is insufficient for drawing a firm conclusion. An alternative explanation to the coupling between heterotrophic dinoflagellates and tintinnids could also reside in shared food resources (Alder and Boltovskoy, 1991).

e. Regional comparisons and inferred seasonal trends. Given the lack of seasonal time-series surveys on the microzooplankton of the Weddell Sea, comparison of our data with the results of studies carried out in the same and neighboring areas at different times of the year can offer hints as to the temporal evolution of this component of the planktonic system. Of special interest are comparisons with works encompassed by the AMERIEZ program (Antarctic Marine Ecosystem Research at the Ice Edge Zone: Buck *et al.,* 1992; Gowing *et al.,* 1987; Buck and Garrison, 1988; Garrison and Buck, 1989; Gowing, 1989; Smith and Garrison, 1990) because of similarities in the area and the groups covered, and because AMERIEZ 86 surveyed

Table 2. Comparative data for microzooplanktonic abundances in the vicinity of the ice-edge zone of the Weddell Sea: averages and ranges (in parentheses). AMERIEZ 86 data for Phaeodaria are: mean "small Phaeodaria" (which comprise >99% of total phaeodarians, cf. Gowing, 1989), and range: total Phaeodaria. Values in square brackets are for AMERIEZ 83 (Nov.–Dec. 1983). AMERIEZ data are from Buck *et al.* (1992); Garrison and Buck (1989), and Gowing (1989).

	AMERIEZ 86 March	EPOS Leg II Nov.–Jan.
Total sta. (ice covered)	7 (43%)	11 (36%)
Protozooplankton biomass (mg C/m^2; 0/10–100 m)	386 (102–652) [229 (55–596)]	178 (7–862)
Tintinnids (0/10–100 m)		
Under ice ind./l	110	2
mg C/m^3	0.35	0.04
Open water ind./l	140	43
mg C/m^3	0.62	0.55
Phaeodarians (ind./m^3)		
0/10 m	53 (<112–167)	42 (0–250)
50 m	273 (<105–1304)	127 (0–765)
100 m	976 (<175–3132)	278 (0–560)
150 m	1009 (182–2466)	826 (0–2280)
200 m	1911 (1176–3000)	1105 (150–3150)
0/10–200 m approx. mean	700	534
Polycystines (ind./m^3)		
0/10 m	(<112–435)	805 (0–5000)
50 m	(<86–392)	623 (0–2700)
100 m	(<111–1325)	845 (0–3190)
150 m	(182–2181)	2205 (280–8340)
200 m	(940–1566)	2726 (340–10530)
Foraminifers (ind./m^3)		
0/10 m	(<88–286)	148 (0–1500)
50 m	(<70–144)	572 (0–2606)
100 m	(<111–612)	185 (0–1318)
150 m	(<88–625)	37 (0–149)
200 m	(<120–147)	75 (0–299)

the marginal ice-zone closer to the end of the growth season (March), while EPOS Leg II was centered on the Southern Ocean spring-summer (Nov.–Jan.; see Table 2).

Our 0–100 m tintinnid abundances were lower than those reported by Buck *et al.*, 1992. (Table 2) for March, and by Boltovskoy *et al.* (1989) for Feb.–March in the ice-free central and northern parts of the Weddell Sea (100 to 130 ind./l at 9 m, cf. Boltovskoy *et al.*, 1989; vs. 47 ind./l at 10 m in open-water stations during EPOS Leg II). Gowing (1989) reported approx. 700 phaeodarians/m^3 in the upper 200 m of the

Weddell Sea marginal ice-zone (March); our mean value was 534 ind./m^3 (Table 2). The maxima listed in Table 2 seem to suggest that our collection yielded higher numbers of polycystines and foraminifers, yet comparisons based on peak values are deceiving, especially when such high fluctuations are involved. On the other hand, radiolarian abundances in Nov.–Jan. 1989 (this work) were considerably higher than those found by Morley and Stepien (1985) in Weddell Sea ice-covered areas in Oct.–Nov. (1981): in 0–100 m vertical tows they found, on the average, 56 polycystines and 30 phaeodarians per m^3; while our mean numbers for the 10–100 m depth-interval were 753 and 170, respectively.

While admittedly spotty and fragmentary, the data reviewed seem to show some congruency insofar as protozooplanktonic abundances generally increase from early spring to late summer-early fall. Increasing abundances toward the autumn are also suggested by comparing the results of AMERIEZ 83 (Nov.–Dec.) and AMERIEZ 86 (March; cf. Garrison and Buck, 1989; see Table 2). This trend is in good agreement with the sharp February–April peak in radiolarian fluxes in the Weddell Sea (Abelmann, 1992; Abelmann and Gersonde, 1991). In Antarctic waters the late summer–early fall period is generally characterized by post bloom conditions, when small phytoplankters are often the dominant producers (Weber and El-Sayed, 1987; Bodungen *et al.,* 1988); more abundant protozooplanktonic populations might therefore constitute a response to the enhanced availability of small-sized food particles. Concomitantly, their significance as a trophic link between these nanoplankters and larger metazooplankton is also probably higher than earlier in the growth season. Nöthig and Gowing (1991) further concluded that this trend extends into the winter, when heterotrophic processes in general and the role of large protozooplankton in particular are highest.

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