Distribution and role of microprotozoa in the Southern Ocean

Verteilung und Einfluß von herbivoren Protozoen auf Phytoplanktonbestände und Vertikalflüsse im Südpolarmeer

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SUMMARY

Distribution and composition of microprotistplankton (phytoplankton and protozoa between 20 and 200 µm) and mesoprotozooplankton (protozoa > 200 µm) were studied during the Southern Ocean-Joint Global Ocean Flux Study (SO-JGOFS) cruise ANT X/6 of *R/V Polarstern,* during austral spring 1992. The growth and feeding response of an Antarctic heterotrophic dinoflagellate (*Protoperidinium cf. pellucidum*) as a function of food concentration was also studied under controlled conditions. These experimental results combined with the field data on microphytoplankton and microprotozoan distributions were used to estimate microprotozoan grazing impact on primary producers, in particular the diatoms, in the field. The distribution of particles produced by micro- and mesoprotozooplankton (empty diatom frustules, faecal pellets, empty skeletons and loricas) and their contribution to carbon and silica vertical fluxes was also investigated.

Microprotistplankton, protozoan faecal pellets and empty diatom frustules were counted in water samples, collected during two transects between the 4th and 30th of October (transect 1 and transect 5). Transect 1 started at 57° S 38°51' W and proceeded eastward along the ice edge of the southern Antarctic Circumpolar Current (ACC) and into the ice-covered ACC/Weddell Gyre Boundary (AWB) until the 6° West Meridian. Transect 5 was carried out along the 6° W Meridian, from the ice edge at 56° S across the open water of the southern ACC into the Polar Frontal region (PFr) till 47° S.
Larger microprotozoa (> 64 µm) and mesoprotozoa were sampled with a multinet at five depth intervals (between 0 and 500 m depth) during transect 11. This transect took place between the 10th and 20th November and extended from the northern rim of the Weddell Gyre (59° S) to the PFr (48° S) along the 6° West Meridian.

Along transect 1, chlorophyll a concentrations decreased eastward, ranging from 0.5 µg l^{-1} at 38°51' W to < 0.2 µg l^{-1} at stations in the AWB (Bathmann et al., 1997). Along transect 5, chlorophyll a concentrations were low (~ 0.2 µg l^{-1}) at the southern ACC and increased in the PFr with a peak of 1.6 µg l^{-1} at 49°S (Bathmann et al., 1997). Carbon standing stocks of microphytoplankton was dominated by diatoms. During both transects, microphytoplankton standing stocks, integrated over the upper 100 m of the water column, followed changes in chlorophyll a and ranged between 77 and 3964 mg C m^{-2} in the AWB and PFr, respectively. Microprotozoan stocks

ranged between 60 mg C m^{-2} and 665 mg C m^{-2} in the AWB and PFr, respectively, and were correlated to both chlorophyll and microphytoplankton stocks. Distinct differences in microprotozoan assemblages were observed between the different regions investigated (AWB, ice edge and open southern ACC water and PFr, respectively). These differences were related to factors other than food supply, i.e. ice cover, water mass characteristics and possibly zooplankton grazing.

Maximum specific growth rates of the Antarctic dinoflagellate *Protoperidinium cf. pellucidum* ranged between 0.09 and 0.14 d^{-1} in growth and feeding experiments using the diatom *Thalassiosira antarctica* as food. *P. cf. pellucidum* showed a maximum ingestion rate of 51 pg carbon ind^{-1} h^{-1}, a maximum clearance rate of 0.84 µl $ind.^{-1}$ h^{-1} and half-saturation constant of 62 µg C l^{-1}. Cell yields of *P. cf. pellucidum* ranged between 58 and 87% and were higher than those found for temperate species at higher temperatures.

Grazing rate by microprotozoa estimated for ANT X/6 showed that microprotozoa consume a significant fraction of primary production, including the diatoms (3 to 22 % of primary production grazed d^{-1}, corresponding to 7 to 38 % of diatom daily production).

During transect 11, chlorophyll a concentrations were low at ice-covered stations (in the Weddell Gyre and AWB) and in the open water of the southern ACC (~ 0.2 µg l^{-1}). In the PFr, chlorophyll a had increased relative to transect 5 to > 3.5 µg l^{-1} (Bathmann et al., 1997). Tintinnids, *Protoperidinium spp. Stichoionche spp.*, foraminifera and radiolaria comprised the bulk of net (> 64 µm) protozoan assemblages. In surface layers (0 to 100 m depth), overall abundances and biomasses of net protozoa followed changes in chlorophyll a with values increasing northward from the Weddell Gyre to the PFr (0.01 to 0.40 µg C l^{-1} and 750 to 9490 ind. m^{-2} respectively). The biomass of net protozoa in the surface layers was negligible when compared to the rest of the protozoa and zooplankton. Between 100 to 200 m depth, abundances of net protozoa followed the same pattern as in the upper 100 m of the water column, but the biomass was by far dominated by larger (> 300 µm) phaeodaria, (68 to 90 %) with the highest values in the Weddell Gyre and AWB. biomass of large (> 300 µm) phaeodaria also contributed significantly to overall zooplankton biomass below 100 to 200 m depth in the Weddell Gyre and AWB.

Particles produced by micro- and mesoprotozoa during this study showed a gradient in abundance increasing from the AWB and ice edge in the southern ACC to the PFr. Both protozoan faecal pellets and empty diatom frustules showed very high abundances as compared to radiolarian skeletons and empty tintinnid loricas. Comparison with zooplankton faecal pellet abundances studied in the same area indicate that contribution of protozoan faecal pellets and empty diatom frustules to total vertical fluxes should be significant. However, previous deep sediment trap studies in oceanic areas of the southern ACC have recorded very low sedimentation rates. Therefore, it is likely that microprotozoa contribute significantly to dissolved pools in the Circumpolar Deep Water. Given their low carbon content, microprotozoan faecal pellets and empty diatom frustules should mainly contribute to the redistribution of silica in the Southern Ocean.

ZUSAMMENFASSUNG

Die vorliegende Arbeit basiert auf der Untersuchung von Proben und Experimenten mit Organismen, die während der Southern Ocean-Joint Global Ocean Flux Study (SO-JGOFS)-Fahrt ANT X/6 der R/V Polarstern gewonnen wurden.
Verteilung und Zusammensetzung von Mikrophytoplankton, Mikroprotozooplankton (> 20 µm) und Netz-Protozooplankton (> 64 µm) wurden entlang der Eiskante des südlichen antarktischen Zikumpolarstromes (ACC, Antarctic Circumpolar Current) und zwischen dem eisbedeckten Weddellwirbel und der Polarfront untersucht. Das Freßverhalten des antarktischen Dinoflagellaten *Protoperidinium cf. pellucidum* wurde in Abhängigkeit der Futterkonzentration unter kontrollierten Bedingungen untersucht. Die Ergebnisse dieser Experimente wurden zusammen mit den Felddaten über Mikrophyto- und Mikrozooplankton für Berechnungen des Fraßdruckes von Mikrozooplankton auf die Primärproduzenten (insbesondere auf die Diatomeen) im Untersuchungsgebiet verwendet. Die Verteilung von Partikeln, die von Mikro- und Netzprotozooplankton produziert wurden, wie leere Diatomeenschalen, Protozoen-Kotballen, leere Skeletteile und Loricae wurde untersucht und der Anteil dieser Partikel an den Vertikalflüssen von Kohlenstoff und Silizium diskutiert.

Mikroprotozoen, Protozoen-Kotballen und leere Diatomeenschalen wurden aus Wasserproben, die während der Transekte 1 und 5 genommen wurden,

ausgezählt. Tansekt 1 führte entlang der Eiskante des südlichen antarktischen Zirkumpolarstromes zwischen 57°S 38°51´W und 56°S 9°33´W und der eisbedeckten Grenze zwischen ACC und dem Weddellwirbel (AWB, ACC/Weddell Gyre Boundary) entlang des 6°W-Meridians. Transekt 5 erstreckte sich entlang des 6°W-Meridians von der Eiskante bei 56°S über den südlichen ACC bis in die Polarfrontzone bei 47°S. Größere (> 64 µm; Netz-) Protozoen wurden auf Transekt 11, das zwischen dem 10. und 20. November 1992 von der nördlichen Grenze des Wedellwirbels bei 59°S bis zur Polarfront bei 48°S befahren wurde, mit einem Multinetz aus den oberen 500 m der Wassersäule gesammelt.

Die Chlorophyll-a-Konzentrationen auf Transekt 1 erreichten bei 57°S 38°51´W Werte um 0,5 µg l^{-1} und nahmen ostwärts bis auf Werte unter 0,2 µg l^{-1} ab (Bathmann et al., 1997). Auf Transekt 5 wurden im ACC niedrige Werte (um 0,2 µg l^{-1}) gemessen, an der Polarfront bei 49°S erreichte die Chlorophyll-a-Konzentration in einer Diatomeenblüte 1,6 µg l^{-1} (Bathmann et al., 1997). Die über die oberen 100 m der Wassersäule integrierte Biomasse des Mikrophytoplanktons korrelierte auf beiden Transekten mit den Chlorophyll-a-Konzentrationen, sie erreichte Werte zwischen 77 und 3964 mg Kohlenstoff m^{-2}. Die Chlorophyll-a-Konzentrationen auf Transekt 11 zeigten dasselbe Muster wie auf Transekt 5, mit den niedrigsten Werten an den eisbedeckten Stationen des Weddellwirbels und des AWB, und dem höchsten Chlorophyll-a-Gehalt an der Polarfrontzone.

Die Biomassen der Mikroprotozoen erreichten Werte zwischen 60 und 665 mg Kohlenstoff m^{-2} und wurden im wesentlichen von choreotrichen Ciliaten und Dinoflagellaten dominiert. Die Mikroprotozoen-Biomassen korrelierten sowohl mit den Chlorophyll-a-Konzentrationen als auch mit den Mikrophytoplanktonkonzentrationen. Deutliche Unterschiede zwischen Mikroprotozoen-Gemeinschaften konnten in Abhängigkeit der Phytoplanktonbestände, des Zooplankton-Fraßdruckes, der Wassermassenverteilung, der Eisbedeckung sowie der Zeit der Probennahme beobachtet werden.
Zum Einfluß heterotropher antarktischer Organismen auf das Phytoplankton wurden exemplarisch Versuche mit *Protoperidinium cf. pellucidum* durchgeführt. Die Wachstum- und Fraßraten dieses heterotrophen Dinoflagellaten in Abhängigkeit von Nahrungskonzentrationen wurde untersucht. *Protoperidinium cf. pellucidum* erreichte die höchsten spezifischen Wachstumsraten (0,093-0,14 pro Tag), wenn die Diatomeenart

Thalassiosira antarctica als Futter verwendet wurde. Dabei wurden eine maximale Ingestionsrate von 52 pg Kohlenstoff pro Individuum und pro Stunde, eine maximale Klärungsrate von 0.84 µl pro Individuum und pro Stunde und eine Halbsättigungskonstante von 62 µg Kohlenstoff pro Liter ermittelt.

Berechnungen der Fraßraten von Mikroprotozoen während der Fahrt ANT X/6 zeigten, daß Mikroprotozoen einen beträchtlichen Anteil der täglichen Gesamtprimärproduktion (3-22%, entsprechend 7-38 % der täglichen Diatomeenproduktion) konsumierten.

Die Zusammensetzung und Biomassen der Netzprotozoen-Gemeinschaft (> 64 µm) schwankten stark in vertikaler und horizontaler Richtung. Zwischen 0 und 100 m folgten die Vorkommen und Biomassen der Netzprotozoen im allgemeinen Änderungen der Chlorophyll-a-Konzentration, die Biomassewerte stiegen vom Weddellwirbel nordwärts bis zur Polarfrontzone an mit 0,01 bis 0,4 µg Kohlenstoff pro Liter (750 bis 9490 Individuen pro m^2). Die Biomasse der Netzprotozoen in den Oberflächenschichten (0-100 m) war im Vergleich zu den restlichen Protozoen und dem Mesozooplankton verschwindend gering. Auch zwischen den Netzprotozoen-Gemeinschaften der verschiedenen Wassermassen und Regionen des Untersuchungsgebietes bestanden deutliche Unterschiede. Diese Unterschiede konnten mit Änderungen sowohl der Phytoplankton- als auch der Zooplanktonbiomassen sowie der Tiefe, der Meereisbedeckung an den südlichsten Stationen und den Einfluß des subantarktischen Wassers nördlich des AWB in Zusammenhang gebracht werden. Unterhalb von 100 bis 200 m Wassertiefe folgte das Auftreten der Netzprotozoen demselben Muster wie in den oberen 100 m. Die Biomassen der Netzprotozoen unterhalb von 100-200 m Wassertiefe waren im Gegensatz zur Oberflächenschicht mit 68-90% Anteil deutlich von größeren (>300 µm) Phaeodarien dominiert, wobei die höchsten Werte im Weddellwirbel und im AWB erreicht wurden.
Die von Mikroprotozoen und Netzprotozoen gebildeten Partikel wie leere Diatomeenschalen, Protozoen-Kotballen, leere Skeletteile und Loricae nahmen vom Weddellwirbel und der Eiskante im südlichen ACC zur Polarfrontzone hin zu. Protozoen-Kotballen und leere Diatomeenschalen waren wesentlich stärker vertreten als Radiolarienskelette und leere Tintinniden-Loricae. Trotz geringer Sinkraten von Protozoen-Kotballen und leerer Diatomeenschalen sollte ihr Beitrag zum Gesamtfluß im

Untersuchungsgebiet von Bedeutung sein. Da aber nur ein geringer Teil der durch Protozoen verursachten Partikelflüsse das Sediment erreicht, muß man davon ausgehen, daß sich der größte Teil dieses Materials auf dem Weg durch die Wassersäule auflöst. Deshalb ist anzunehmen, daß Protozoen in erheblichem Maße zu den gelösten Substanzklassen im zirkumpolaren Tiefenwasser beitragen. Wegen ihres geringen Kohlenstoff- und hohen Silikatgehaltes beeinflussen Protozoen-Kotballen und leere Diatomeenschalen dabei wahrscheinlich vor allem die Umverteilung von Silikat im antarktischen Ozean .

1 INTRODUCTION

1.1 Historical aspects of protozooplankton research and the evolving role of protozoa in the marine pelagic system.

Heterotrophic unicellular organisms (protozoa) occurring in the plankton have been grouped under the term protozooplankton by Sieburth et al. (1978) as a means to establish a coherent group within the heterotrophic compartments of the plankton in terms of life cycle, metabolic and growth rates. The protozooplankton has been further divided into size classes that are also currently used for the phytoplankton:
-Nano: 2-20 μm
-Micro: 20-200 μm
-Meso: 0.2-2.0 mm.
These size classes, introduced by Schütt (1832) and latter Lohmann (1811) and redefined by Sieburth et al. (1978) for protozoa and autotrophic protists, do not only correspond to different metabolic capacities but are also assumed to roughly represent trophic and taxonomic groups (Caron and Finlay, 1994): the nanoprotozooplankton include mainly flagellates and dinoflagellates, the microplankton mainly ciliates and dinoflagellates, and in the larger size fraction (> 60 μm), the sarcodines. The mesoprotozooplankton comprises primarily large sarcodines (Fig.1).

Observations on marine protozoa date back to the invention of the first microscope by Antoni van Leeuwenhoek in the 17th century. In the following two hundred years, protozoa in freshwater and marine environments were qualitatively described in monumental monographs such as Ehrenberg's "Die Infusionsthierchen als vollkommene Organismen" (1838) or Haeckel's (1887) description of radiolaria from the Challenger expedition.

The first work that dealt with the whole of protozoa in a marine environment was the exhaustive quantitative description of the seasonal cycle of heterotrophic protists in the Kiel Bight by Lohmann in 1908. This work built upon the foundation of quantitative biological oceanography laid by Victor Hensen in the late 19th century at Kiel (Mills,1989).
In spite of Lohmann's observations little or no attention was paid to this group of organisms in the next 60 years. By that time the seasonal cycles of the phyto- and metazooplankton had been demonstrated from various regions.

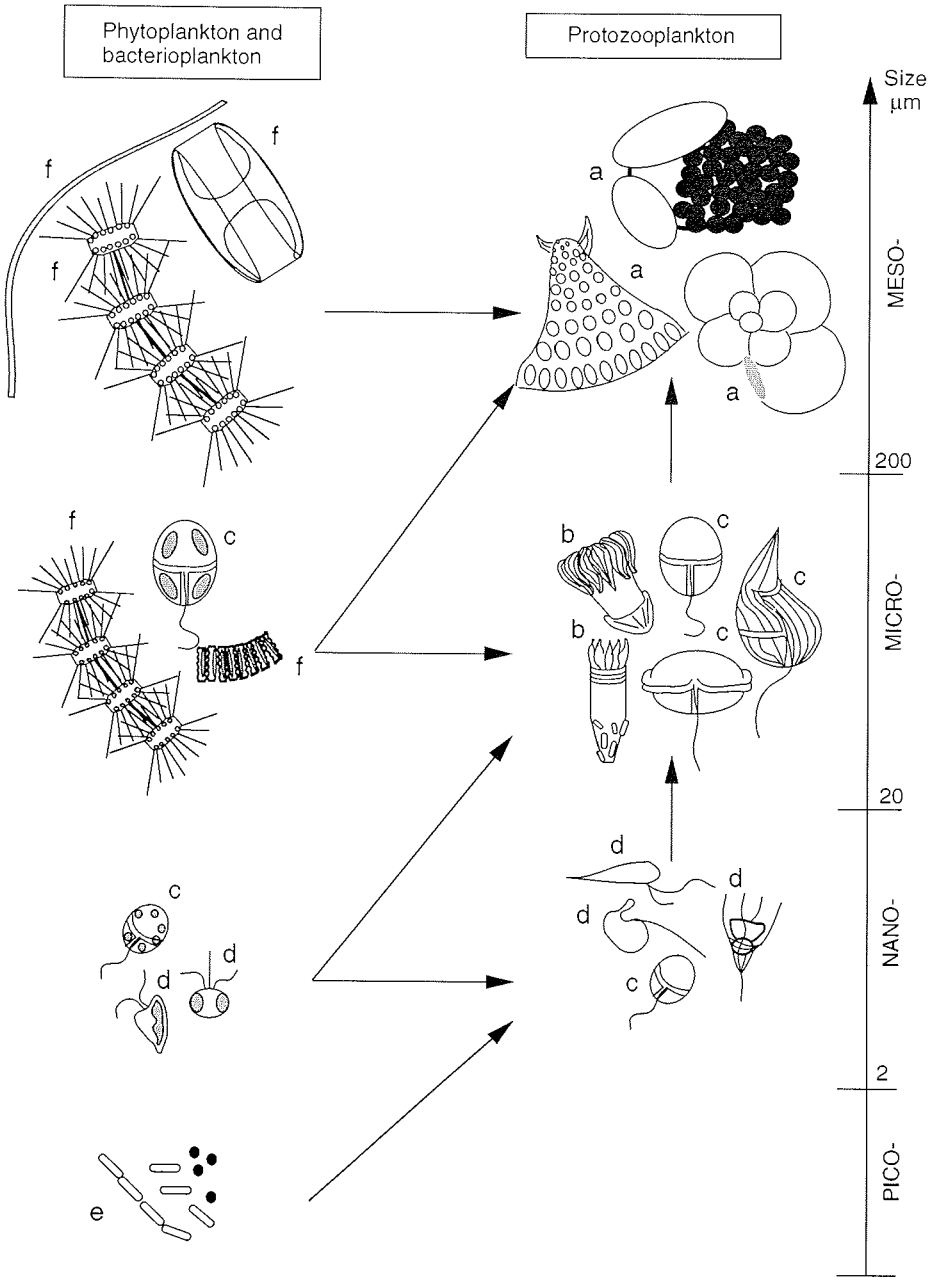

Figure 1. Illustration of the composition and trophic relationships between the different size classes of the bacterioplankton, phytoplankton and protozooplankton. Redrawn after Fenchel (1987). a: large sarcodines, b: ciliates, c: dinoflagellates, d: other flagellates, e: bacteria and cyanobacteria, f: diatoms.

The explanations for the seasonal variations in phytoplankton standing stocks were based on concepts borrowed from agriculture and physiology and more attention was paid to bottom-up control of productivity (nutrients and light) rather than food chain or food web interactions.

The work carried out in Kiel was further developed in the Plymouth Marine Laboratory by H. W. Harvey and collaborators who studied the seasonal plankton cycle in the English Channel off Plymouth. The results of this study published in 1935 emphasised the role of grazing as an important factor controlling primary production. However their conclusion was based on the study of net samples and referred mainly to metazoan grazing. Although Harvey mentioned protozoa, he considered their importance mainly as decomposers of detrital material (Harvey, 1928; Harvey et al., 1935).

The rediscovery of the importance of protozoa in marine food webs can be traced back to the works of Johannes (1965), J. R. Beers and G. L. Stewart (1967; 1969 and 1970) and Sorokin (1969). Johannes (1965) showed the importance of protozoa in nutrient regeneration whereas J. R. Beers and G. L. Stewart (1967; 1969 and 1970) and Sorokin (1969) attracted attention to their importance in terms of biomass and distribution. Sorokin (1969; 1977) also showed the importance of bacteria during the seasonal succession in lakes and the open ocean. During the same period Heinbokel (1978a, 1978b) and Heinbokel and Beers (1979) demonstrated the fast growth and grazing potential of tintinnid ciliates. These studies, combined with the discovery of the importance of the dissolved organic matter (DOM) pool, bacteria and nanoplankton production in pelagic systems, lead to the formulation of a new paradigm for planktonic food webs by L. R. Pomeroy (1974) latter refined by Azam et al. (1984) under the name of "microbial loop".

The microbial loop concept emphasises the importance of a dissolved organic matter (DOM) reservoir in marine environments (5 to 50% of primary production) which provides the substrate for bacteria. Bacteria are consumed by nanoplanktonic protozoa which are in turn consumed by microprotozoa (mainly ciliates). In this concept the protozoa constitute a major link between primary production and large zooplankters such as copepods and euphausids via the DOM reservoir and nanoplankton. In addition to providing a link between primary production and zooplankton, protozoa are also largely responsible for nutrient regeneration and thus for providing nutrients

again to the phytoplankton (Azam et al., 1984). The importance of protozoa in nutrient remineralisation as well as in transferring primary production to higher trophic levels caused controversy as to their role in marine systems. Namely, do protozoa act as a "sink" for primary production, by remineralising most of it, or as a "link", by transferring most of the primary production to higher trophic levels? (Porter et al., 1979; Ducklow et al., 1986; Sherr et al., 1986; Caron, 1991).

The microbial loop was coupled with "regenerating" or "retention systems" (Smetacek and Pollehne, 1986; Peinert et al., 1989) in which a significant part of the primary production is based on regenerated nutrients (primarily ammonium as a nitrogen source) and is dominated by pico- and nanoplankton grazed upon by protozoa and copepods. By contrast "new" or "export systems" are based on "new" or nitrate based production and dominated by larger phytoplankton (diatoms) which are partially consumed by large zooplankton but generally end up, when all nutrients are exhausted, in mass sedimentation of the phytoplankton cells (Smetacek, 1984a; Smetacek and Pollehne, 1986).

The role of protozoa in the microbial loop and in "retention systems" has been inferred from a food-web model where prey:predator size ratios are thought to be about 1:10 (Fenchel, 1988). It was assumed that microprotozoa graze primarily nanoplankton. Sorokin (1977) and Smetacek (1981, 1984b) who counted protozoa in water samples instead of net samples, showed the importance of dinoflagellates and aloricate ciliates in the microprotozooplankton. Smetacek (1981, 1984b) also attracted attention to the fact that in his samples dinoflagellates as well as aloricate ciliates where often seen with ingested diatoms at least as big as themselves. Despite the observations of Smetacek (1981) the view that microprotozoa (primarily dinoflagellates, apochlorotic flagellates and choreotrich ciliates) graze mainly bacterioplankton and nanoplankton remained fixed for quite some time (Moloney and Field, 1991; Ducklow and Taylor, 1991).

Choreotrich ciliates are known to graze on organisms of sizes up to 40% the size of their own oral diameter (Spittler, 1973, Heinbokel, 1978b; Johnsson, 1986). More recent studies have shown that several groups of dinoflagellates can engulf particles at least as big as themselves (Hansen, 1992; Hansen et al., 1994; Strom and Strom, 1996). Other dinoflagellates, including the armoured species, have complex feeding behaviours and apparatus that

enable them to feed on prey larger than themselves (Jacobson and Anderson, 1986; Drebes, 1988; Drebes and Schnepf, 1988; Hansen, 1991a; Jeong, 1994a). Prey:predator biovolume ratios greater than 1:1 have also been observed in flagellates (Suttle et al., 1986; Schnepf et al., 1990; Kühn et al., 1995). Large sarcodines have also been shown to prey on a wide variety of particles ranging from detritus to copepods (Anderson, 1983; Gowing, 1989; Hemleben et al., 1989; Nöthig and Gowing, 1991; Swamberg and Caron, 1991).

Protozoa have also been shown to contribute substantially to vertical fluxes through the production of faecal pellets or "minipellets" (Gowing and Silver, 1985; Nöthig and von Bodungen, 1989; Riemann, 1989; González, 1992; Buck and Newton, 1995), cysts (Reid, 1987; Antia et al., 1993) and through the release of empty skeletons and shells (Takahashi, 1991).

From these new findings it appears that micro and mesoprotozoa are much more diverse in their feeding behaviour than previously thought. The fact that protozoa can feed on diatoms indicates that they are not restricted to the microbial loop or "regenerating systems", but can also impact diatom blooms and hence influence biogeochemical cycles.

1.2 The Southern Ocean

The importance of the Southern Ocean in biogeochemical cycles has been stressed in studies of silica deposition (DeMasters, 1981) and in several models of carbon-cycle (Knox and McElroy, 1984; Sarmiento and Toggweiler, 1984). However, despite high nutrient concentrations, primary production in the Southern Ocean is mainly based on recycled nitrogen and is dominated by cells in the nano-size range (von Bröckel, 1981; Hewes et al., 1985; Holm-Hansen, 1985; Smetacek et al., 1990, Dugdale and Wilkerson; 1991; Jacques, 1991; Owens et al., 1991). Diatom blooms occur mainly in areas under the influence of continental land masses and in frontal zones (Laubscher et al., 1993; Sullivan et al., 1993).

The overall low phytoplankton standing stocks in the Southern Ocean combined with the fact that primary production is mainly based on regenerated nitrogen (ammonium) rather than nitrate have been attributed to lower growth rates due to deep mixing of surface waters (i.e. low light regime; Sakshaug

and Holm-Hansen, 1984) and iron deficiency (Martin et al., 1991). It has been suggested that low concentrations of iron and other trace elements might affect mainly larger phytoplankton species (diatoms) explaining the predominance of smaller cells (nanoplankton) which preferentially take up regenerated nitrogen (Martin et al., 1991; Buma et al., 1991). However, no matter how low phytoplankton growth rates are, loss rates must compensate for the production rates to prevent biomass accumulation (Banse, 1992). Sediment trap studies in the Southern Ocean also show remarkably low vertical fluxes in the oceanic areas and higher values in coastal areas and the Polar Front (Fischer et al., 1988; Wefer and Fischer, 1991). The low losses due to sedimentation point to the importance of grazing in maintaining the low nanophytoplankton standing stocks and in preventing diatom bloom formation in the open waters surrounding Antarctica (Hewes et al., 1985; Smetacek *et al.*, 1990; Frost, 1991). Smetacek et al. (1990) described the pelagic system in open waters of the Southern Ocean as an efficient "retention system" in which protozoan and copepod grazing contributes to retaining both nutrients and carbon in surface layers and to maintaining low levels of primary production. Superimposed on this system are the blooms, dominated mainly by larger phytoplankton such as diatoms or the colony forming *Phaeocystis*. Blooms, rather than being a constant feature of the Southern Ocean pelagic system, are local and transient features of the system not under control of the grazers (mainly larger zooplankton), leading to high sedimentation fluxes.

One of the first studies on protozoan distribution in the Southern Ocean (von Bröckel, 1981) showed their importance in terms of biomass as compared to other compartments of the plankton. In his review, Garrison (1991) showed that protozoa can contribute significantly to total micro- and nanoplankton carbon (<7 to >75%). In various localities, protozoa have been found to equal phytoplankton biomass in spring, summer, autumn and winter (Nöthig,1988; Garrison and Buck, 1989; Garrison et al., 1993; Scharek et al., 1994). Hewes et al. (1985) and later Bjørnsen and Kuparinen (1991) showed that micro- and nanoprotozoa might have a significant grazing impact on nanophytoplankton production. A few studies done on larger protozoa (> 400 µm) have also shown that the sarcodine, especially phaeodaria radiolaria, can also built-up important stocks in summer and winter (Gowing, 1989; Nöthig and Gowing, 1991; Abelmann and Gowing, 1996). These results together with the more recent studies on protozoan feeding behaviour discussed in section 1.1, indicate that they might have an important impact in controlling primary production including the larger fraction of the

phytoplankton (the diatoms). Additionally, Nöthig and von Bodungen (1989) and González (1992) showed that faecal pellets of protozoan origin might constitute an important part of diatom fluxes in the Southern Ocean.

Protozoa constitute an important component of pelagic assemblages in the Southern Ocean and are likely to play a role within the "retention system" characteristic of most oceanic areas of the Southern Ocean (Smetacek et al., 1990) as well as in "new" or "export systems". Hence their impact on biogeochemical cycles in the Southern Ocean should be significant.

1.3 Aims of this thesis

One of the aims of this work was to extend our knowledge on protozoan communities by describing and quantifying microprotozoa and net (> 64 µm) protozoa assemblages in relation to environmental factors, in an area of the Southern Ocean where they were not previously investigated. Furthermore, the feeding behaviour of an Antarctic dinoflagellate (*Protoperidinium cf. pelucidum*), in relation to food concentration, was studied under controlled conditions. These experimental results, together with the field results on microprotozoan distribution, were used to estimate microprotozoan grazing impact on primary production, in particular the diatoms, in the area investigated. Additionally, the distribution of particles produced by micro and net protozoa: empty diatom frustules, faecal pellets, empty skeletons and loricas, was investigated and their importance in vertical fluxes of carbon and silica discussed. This thesis concludes with an overview on the role of microprotozoa and net (> 64 µm) protozoa on the silica and carbon cycles in the Southern Ocean.

This investigation was carried out during the Southern Ocean-Joint Global Ocean Flux Study (SO-JGOFS) cruise ANT X/6 on board *R/V Polarstern*. The area surveyed extended from the ice edge in the southern Antarctic Circumpolar Current (ACC) at 38°51' W to the ice-covered Weddell Gyre at 6° W, and between the ice edge in the southern ACC and the Polar Frontal region (PFr) along the 6° W Meridian.
Hitherto, protozoan studies in the Southern Ocean comprise either detailed descriptions of a few specific groups (mainly tintinnids) or the whole community without differentiation according to taxonomic composition, size and feeding ability. Because of the highly diverse feeding behaviour of

protozoa, more detailed descriptions of the protozoan community are necessary in order to understand their impact on primary production, phytoplankton assemblage composition and vertical fluxes. Additionally, studies on protozoa in the Southern Ocean have been restricted to a few particular regions, namely, coastal areas, the ice edge of the Weddell-Scotia Confluence, the Weddell and Bellingshausen Seas.

Microprotozoa and microphytoplankton were counted in water-bottle samples taken along the ice edge of the Southern ACC and the ice-covered Weddell Gyre, following the eastward gradient from the productive Weddell-Scotia Confluence and the land remote region along the 6° W Meridian. Further, microprotozoa and microphytoplankton were investigated in water samples taken from the different oceanic regions between the ice-covered ACC-Weddell Gyre Boundary (AWB) and the PFr along the 6° W Meridian. Larger (> 64 µm) protozoa were counted in net samples from a transect extending from the ice-covered Weddell Gyre to the PFr along 6°W. Only protists larger than 20 µm were considered in this study. Nanoprotist distribution in the area studied are described by Becquevort (1997) and Detmer and Bathmann (1997).

The identification of protists is often difficult and requires specific preparation for each group of protozoa. Protozoa (> 20 µm) were identified to species level when possible but more often to genus or order level only. Results on standing stock distribution and composition of protozoan (> 20 µm) assemblages were compared and discussed as a function of physical, chemical and biological parameters of the water column (Results section 3.1.1 to 3.1.4 and 3.2.1). Factors influencing protozoan (> 20 µm) biomass distribution and seasonality as well as the importance of protozoa (> 20 µm) as compared to other compartments of the pelagic assemblage are discussed in the light of literature data (Discussion section 4.1). Factors influencing protozoan (> 20 µm) assemblage composition are discussed in conjunction with other data sets in the Discussion section 4.2.

Up to now only a handful of studies were carried out on protozoan grazing rates in the cold waters surrounding Antarctica (Bjørnsen and Kuparinen, 1991; Reitmeier, 1994; Burkill et al., 1995; Archer et al., 1996b). They all point out the importance of protozoan grazing in regulating phytoplankton stocks in the Southern Ocean. Among those few studies, only the work of Bjørnsen and Kuparinen (1991) examines the growth and feeding response of a nanoplanktonic heterotrophic dinoflagellate (*Gymnodinium* sp.) under

controlled conditions. In order to enlarge our knowledge of Antarctic protozoan feeding behaviour to the larger component (> 20 µm) of the protozoan assemblage, and give estimates of protozoan grazing rates in the field, experiments to determine the growth and grazing response of an Antarctic heterotrophic microdinoflagellate as a function of food concentration were done. Growth and grazing rates of *Protoperidinium cf. pellucidum* (Larsen, pers. comm.), isolated during ANT X/6, were studied at 0°C, at different concentrations of the diatom *Thalassiosira antarctica* (Results section 3.3). Grazing impact of microprotozoa during ANT X/6 was determined by combining these experimental studies to the field data on microprotozoan distribution and composition (Results section 3.4). As diatoms play a major role in new production and vertical flux in the sea, it is necessary to separate microprotozoa capable of feeding on them from those only capable of feeding on nanophytoplankton. Microprotozoa counted in the field samples were grouped as a function of feeding behaviour and size (Results section 3.1.4 and 3.4). These results enabled the assessment of microprotozoan grazing rates on the different size classes of phytoplankton and thus, on the diatoms which dominate microphytoplankton (Results section 3.4). These results are discussed for the period investigated as well as for other seasons as inferred from literature data (Discussion section 4.3).

In today 's oceans, phytoplankton aggregates and zooplankton faecal pellets are thought to dominate vertical fluxes (Honjo, 1990). A few recent studies have demonstrated that particle production by protozoa can at times dominate fluxes (Nöthig and von Bodungen,1989; Takahashi, 1991; Buck and Newton, 1995). However, up to now, the types of particles associated with protozoan activity were shells or empty skeleton and the small membrane bound faecal pellets described by Gowing and Silver (1985), Nöthig and von Bodungen (1989) and Buck et al. (1990). The discovery that protozoa can also feed on diatoms without releasing membrane bound pellets (Stoecker, 1984; Jacobson and Anderson, 1986; Hansen, 1991a; Schnepf and Elbrächter, 1992; Kühn, 1995) and that unlike the metazoa, protozoa digest the diatoms without crushing the frustules suggests that they might also contribute significantly to the release of intact, empty diatom frustules.

The importance of particles of protozoan origin in vertical fluxes was investigated by describing the abundance of those particles in the water column. Protozoan faecal pellets and empty diatom frustules were counted in

the same water-bottle samples as the microprotists (Results section 3.1.5). In order to investigate particle production by the larger protozoa (> 64 µm) empty tintinnnid loricas and radiolarian skeletons were counted in the same samples as their living producers (Results section 3.2.2). The relationship between these particles and standing stocks of microprotozoa, diatoms, microprotozan grazing impact and region investigated is discussed (Discussion section 4.4). These results are compared to earlier studies on vertical particle flux and sedimentation rates of particles of protozoan origin in the Southern Ocean, and the importance of particles produced by protozoa (> 20 µm) in the framework of silica and carbon cycles is discussed (Discussion section 4.4).

Finally all results are combined in a general discussion redefining the role of microprotozoa and net (> 64 µm) protozoa on carbon and silica biogeochemical cycles in the Southern Ocean (Discussion section 4.5).

2 MATERIALS AND METHODS

2.1 Area of study

The investigation was carried out during the Southern Ocean-Joint Global Ocean Flux Study (SO-JGOFS) cruise ANT X/6 on board *R/V Polarstern.* The cruise track (Fig. 2) first followed the retreating ice edge in the southern Antarctic Circumpolar Current (southern ACC) until the 6° W meridian along which several transects were done between the ice edge and the Polar Front region (PFr).

Samples for microprotist determination were collected during two transects (transect 1 and transect 5). Sampling during transect 1 started at 57° S 38°51' W on the 4th October 1992 and proceeded along the ice edge of the southern ACC and into the ice covered Weddell Gyre, until the 6° West Meridian was reached on the 12th October (Fig. 3). Transect 5 was carried out between the 24th and the 30th of October, along the 6° W Meridian. The transect extended from the ice edge at 56° S across the open waters of the southern ACC into the Polar Frontal region (PFr) till 47° S (Fig. 4).

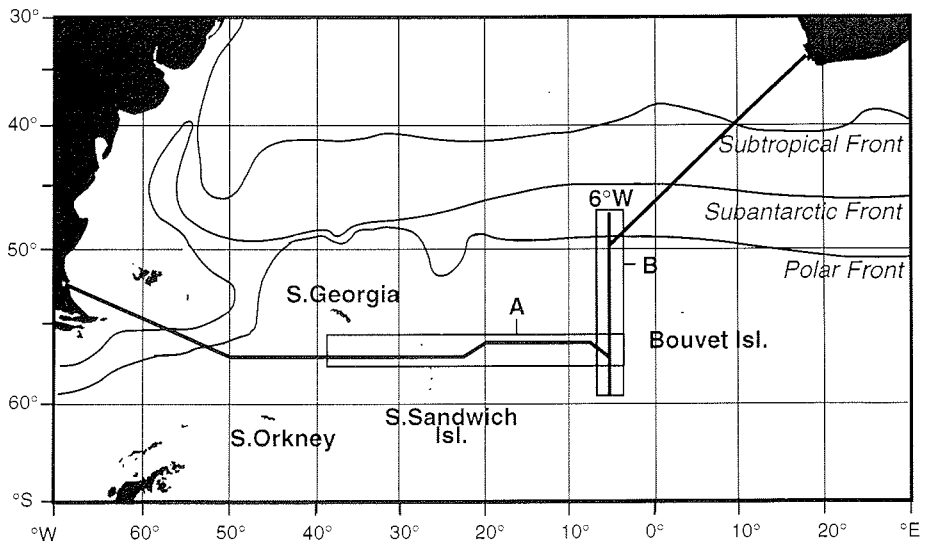

Figure 2. Cruise track of the *R/V. Polarstern* during the SO-JGOFS expedition ANT X/6. Box A: transect 1. Box B: transects 5 and 11. Redrawn from Bathmann et al. (1997).

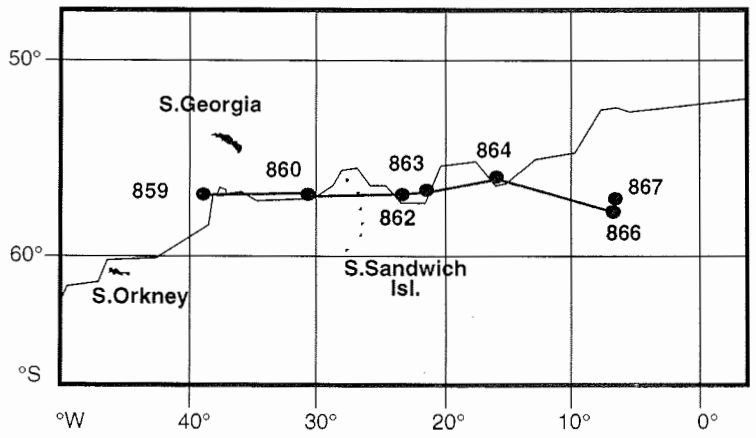

Figure 3. Location of stations indicated by symbols (●) and station number along transect 1. Sea ice extent is indicated by the shaded area. Geographical location of transect 1 is given in Fig. 2.

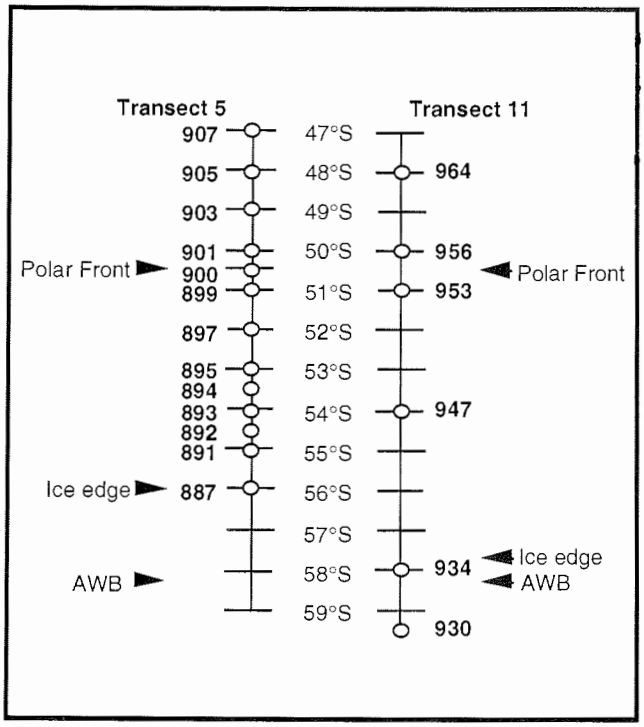

Figure 4. Location of stations indicated by symbols (O) and station number, along the 6° W meridian, during transects 5 and 11. Geographical location of the transects is given in Fig. 2.. The Polar Front region was situated north of 50°30' S. During transect 5, the ice edge was located at 56°S but had retreated to 57°45' S during transect 11. During transect 11, the ACC-Weddell Sea Boundary (AWB) was crossed at 58°15' S.

Larger protozoa (> 64 µm) were sampled on transect 11 between the northern rim of the Weddell Sea at 59° 30'S, and the PFr up to 48° S (Fig. 4). Sampling during this transect took place between the 10th and the 20th November 1992.

2.2 Determination of microprotistplankton, empty diatom frustules and protozoan faecal pellets.

2.2.1 *Biomass and composition of microprotistplankton*

Water samples for counting microprotists (auto- and heterotrophic protists > 20 µm), empty but intact diatom frustules and minipellets were collected at five discrete depths (20, 40, 60, 80 and 100 m) with Niskin or GoFlo bottles mounted on a Seabird SBE 9 plus CTD rosette. Samples were preserved with 0.6% hexamine-buffered formalin (transect 1) or 1% alkaline Lugol's iodine (transect 5) and stored at 4°C in dark bottles. 50 to 100 ml were settled and counted after the method of Utermöhl (1958) following the recommendations of Venrick (1978) and Edler (1979). Before settling, Lugol-preserved samples were decoloured with a few drops of sodium thiosulfate (Pomeroy, 1984; Sherr and Sherr, 1993) for recognition of cytoplasmic organelles. Organisms over 20 µm size were classified as autotrophs or heterotrophs on the basis of genus and by the presence or absence of chloroplasts, observed in living organisms with the help of video recordings taken at the time of collection. All ciliates except *Mesodinium rubrum* were counted as heterotrophs.

The Utermöhl method does not allow a reliable discrimination of autotrophic and heterotrophic flagellates (including dinoflagellates). Incorrect classification of auto- and heterotrophs is likely to occur especially within the smaller size groups (< 40 µm). In uncertain cases organisms were always counted as phytoplankton. Also, since autotrophic flagellates and dinoflagellates are often mixotrophs (Sanders and Porter, 1988; Jacobson and Andersen, 1994), the heterotrophic fraction will have been underestimated (Davis and Sieburth, 1982).

Faecal pellets counted during this study had different forms. The following two types were attributed to protozoa: - Olive green spherical to ellipsoidal pellets of 10 to 50 µm diameter as described by Gowing and Silver (1985). These "minipellets" generally contained a matrix of fine material unidentifiable with light microscopy. - The second type of pellet attributed to protozoa were

membrane bound, of variable shape and size (10 to >100 µm length), and contained intact diatom frustules (Buck et al. 1990; González, 1992).

Carbon (C) biomass of microprotists was obtained by measuring the organisms with an ocular micrometer and calculating cell volumes after Edler (1979). The following carbon to volume conversion factors were then applied: 0.11 pg carbon μm^{-3} for diatoms and flagellates (Strathmann, 1967), 0.13 pg carbon μm^{-3} for armoured dinoflagellates (Smetacek, 1975) and 0.08 pg carbon μm^{-3} for ciliates (Beers and Stewart, 1970).

2.2.2 *Size composition of microprotistplankton and empty diatom frustules*

In order to investigate trophic relationships between microprotozoa and phytoplankton, in particular diatoms, microprotists and empty diatom frustules were grouped into size classes of 20 µm interval. These counts were very time consuming and only done for stations along transect 5 which includes the three important regions investigated during the cruise, namely, the ice edge, the open waters of the southern ACC and the PFr. Heterotrophic protist counts in size classes larger than 60 µm were pooled together since the abundances in the samples were low (0 to 17 individuals counted per sample) Ciliates were size-classified according to their diameter and flagellates according to body length in order to account for the differences in the prey size spectrum consumed by the two groups.

The peristome diameter and lorica diameter set the upper size limit of prey for the dominant ciliates in the samples the aloricate choreotrichs (Jonsson, 1986) and tintinnids respectively (Heinbokel, 1978b). For dinoflagellates and other flagellates, prey to predator size ratios tend to be variable and depend on feeding behaviour. In unarmoured dinoflagellates and other flagellates the average size of prey ingested can be considered to correspond to the predator length (Hansen et al., 1994). Armoured dinoflagellates of the genus *Protoperidinium* and members of the "Diplopsalis group" (Dodge, 1982) tend to feed on particles much larger than themselves by extruding a membrane (the pallium) which can engulf whole diatom chains (Jacobson and Anderson, 1986). Thus, size constraints are difficult to estimate and these two groups are treated separately. Autotrophs and empty diatom frustules were classified according to the size of their largest cell dimension (length or diameter),

without taking into account the presence of colonies since the Lugol's iodine did not preserve their structure (personal observation).

2.3 Determination of net protozooplankton (> 64 μm)

Large protozooplankton were sampled using a multinet (Hydrobios, 64 μm mesh size) at five depth intervals: 0-25, 25-50, 50-100, 100-200 and 200-500 m. Samples were fixed with 0.6 % hexamine buffered formalin. Larger phaeodaria (> 300 μm) were counted with a dissecting microscope (x25) in the whole sample. Protozoa between 64 and 300 μm in one dimension were counted in settling chambers using a Zeiss inverted microscope equipped with fluorescent light. Prior to counting 70 μl of a stock DAPI (4',6 diamidino-2-phenylindole) solution were added in order to stain the nucleus (Porter and Feig, 1980; Nöthig and Gowing, 1991). Cells with a nucleus were considered alive at the time of capture. Aliquots were counted up to a minimum of 50 cells of the most abundant species or a total of 300 cells.

Dinoflagellates, tintinnids, heliozoa and phaeodarian radiolaria were identified to genus or to species when possible, polycistine radiolaria were separated into nassellaria and spumellaria and foraminifera were separated into spinose and non-spinose forms.
Cell volumes were estimated by measuring cells with an ocular micrometer and converting cell dimensions into volume using approximately geometrical shapes. Carbon content was estimated using cell volume to carbon conversion factors of 0.13 pg carbon μm^{-3} for thecate dinoflagellates (Smetacek, 1975) and 0.08 pg carbon μm^{-3} for the other protozoans (Beers and Steward, 1970; Nöthig and Gowing, 1991). Carbon content of larger (> 300 μm) phaeodaria was calculated with a factor of 0.08 pg carbon μm^{-3} for the nucleus and phaeodium and 0.08/3 pg carbon μm^{-3} for the cytoplasm (Nöthig and Gowing, 1991).

2.4 Statistical analysis

Statistical analysis of microprotozoan distribution among stations of transect 1 and 5 was done with normalised microprotozoa standing stocks (mg C m^{-2}) using a square root-square root transformation (Field et al. 1982). Cluster analysis was done with the transformed data and stations were grouped by an

average linkage cluster method. Difference between stations was also analysed using principal component analysis (PCA) of the correlation matrix of standardised transformed microprotozoan standing stocks and physico-chemical data.

2.5 Growth and grazing experiments with the heterotrophic dinoflagellate *Protoperidinium cf. pellucidum*

2.5.1 *Isolation*

Plankton samples were collected using a 20 µm mesh plankton net at 50° S 6° W, during the SO-JGOFS cruise ANTX/6 of *R/V Polarstern* in the Antarctic Circumpolar Current. Before isolation samples were maintained in 70 ml tissue culture bottles, on a rotating wheel (~1rpm), at 0°C for several weeks for enrichment. The dominant heterotroph in these enrichment cultures was *Protoperidinium cf. pellucidum* (Larsen, pers. com.) which feeds on phytoplankton by means of a "pallium" (Jacobson and Anderson, 1986). *Protoperidinium* cf. *pellucidum* cells were isolated with a drawn pipette and transferred to new culture bottles with the diatom *Thalassiosira antarctica* as food. These isolates were incubated for several weeks in the dark to avoid growth of phytoplankton. The isolation procedure was repeated several times in order to obtain clean, non axenic, cultures of the dinoflagellate.

2.5.2 *Culturing*

The routine maintenance of cultures was done in the same way as the isolation: at regular intervals individual dinoflagellate cells were transferred with a drawn pipette to new tissue culture bottles containing exponentially growing *T. antarctica.* Bottles were incubated on a rotating wheel at 0°C in the dark. Both *P. cf. pellucidum* and *T. antarctica* were maintained in Antarctic seawater passed through 0.2 µm nitrocellulose Sartorius filters. Nutrients and trace metals were added to the seawater after von Stoch and Drebes (1964) adapted by Baumann (1990) for Arctic cultures.

2.5.3 *Growth and grazing experiments*

For all of the following experiments incubations were done in the dark at 0°C on a rotating wheel (~1 rpm) and with *T. antarctica* strain SK-12 as food. This strain was chosen because it did not form colonies.

Experiment 1

In order to determine acclimation time and growth rates of *P. cf. pellucidum* under balanced growth conditions, cultures of *P. cf. pellucidum* where food was almost exhausted were transferred to 2 l acid-washed polycarbonate bottles containing new media and exponentially growing cultures of *T. antarctica* added to three different end concentrations: 100, 2000 and 8000 cells ml^{-1}, respectively. Three replicate incubations were done per treatment. Samples were taken at regular intervals of 2 days for the first 6 days of incubation and later at time intervals of 3 to 4 days for about a month. Samples were fixed with 1% Lugol's iodine, settled and counted with an inverted microscope. For each treatment 100 diatoms where measured at the beginning of the experiments with an ocular micrometer. Their carbon content was calculated after Edler (1979) using appropriate geometrical shapes to estimate cell volume multiplied by 0.11 to estimate cell carbon (Strathmann, 1967). Food concentration was checked on each sampling day. When necessary, food concentration was readjusted to the target concentration by adding new, exponentially growing, *T. antarctica* cells.

Experiment 2

Individual cells of *P. cf. pellucidum* from experiment 1 were transferred to 30 ml polycarbonate tubes with exponentially growing *T. antarctica* at the same concentration as the treatment of origin (Table 1). Additionally three new treatments were done with cultures of *P. cf. pellucidum* when food was almost exhausted. These were transferred into 40 ml tissue culture flasks with initial food concentrations of 50, 500 and 1500 *T. antarctica* ml^{-1} (Table 1). Parallel control tubes of *T. antarctica* culture without *P. cf. pellucidum* were also incubated for all treatments in order to check for diatom growth and mortality under the experimental conditions. At varying intervals depending on treatment, 3 to 4 tubes per treatment were collected and fixed with 1% Lugol's iodine, settled and counted with an inverted microscope.

For each treatment 30 to 100 dinoflagellates and 100 diatoms, respectively, were measured with an ocular micrometer at the end of the experiments. Cell volume was calculated using appropriate geometrical shapes. Carbon

content was estimated after Edler (1979) using a volume to carbon conversion factor of 0.11 (Strathmann, 1967) for *T. antarctica* and 0.14 for the *P. cf. pellucidum* (Lessard, 1991).

Table 1. Initial food concentrations for the six treatments in experiment 2.

Target concentration (cells ml^{-1})	*Initial food concentration* (cells ml^{-1})	*Food volume* ($mm^3 l^{-1}$)	*Carbon concentration* ($\mu g\ C\ l^{-1}$)
100	99	0.49	20
2000	2065	10.67	421
8000	8213	44.30	1738
50	60	0.67	25
500	665	6.23	243
1500	2318	23.16	880

2.5.4 *Calculation of growth and grazing rates*

For experiment 1, specific growth rates were calculated between each sampling interval in the linear portion of the growth curve ln (dinoflagellate concentration l^{-1}) against time, using the exponential growth equation (1)

$$\mu = \frac{1}{t_2 - t_1} \ln \frac{Nt_2}{Nt_1} \qquad (1)$$

where μ = specific dinoflagellate growth rate (d^{-1}), N = dinoflagellate abundance (cells ml^{-1}), t_1 and t_2 = time of sampling.

For experiment 2 growth rates were determined by regression in the linear portion of the growth curve ln (dinoflagellate concentration l^{-1}) against time. Grazing rates of *P. cf. pellucidum* on *T. antarctica* were determined by assuming that the variations in phytoplankton concentration can be modelled by the equation (2)

$$\frac{dP}{dt} = -I\,N \qquad (2)$$

where P = phytoplankton abundance (cells ml^{-1}); t = time; I = specific ingestion rate of individual grazer cells (d^{-1}) and N = grazer abundance (cells ml^{-1}).

Equation (2) was integrated assuming an exponential growth of the grazers:

$$I = \mu \frac{P_{t2} - P_{t1}}{N_{t1} - N_{t2}} \quad (3)$$

where I = specific ingestion rate (d^{-1}); P = phytoplankton abundance (cells ml^{-1}); N = grazer abundance (cells ml^{-1}); μ = grazer specific growth rate (d^{-1}) and t_1 and t_2 = time of sampling.

This model assumes that no phytoplankton growth occurs and mortality is exclusively due to grazing. Since all incubations of experiment 2 were carried out in the dark, diatoms did not grow. However, in the treatment with highest diatom concentration, mortality in the control incubations (diatoms without grazers) did occur. To calculate grazing in this treatment, equation (3) was used with diatom abundances corrected for the mortality in the controls.

Feeding and growth rate response of protozoa to food concentration (often called "functional response") follows a hyperbolic function which can be modelled by a Michaelis Menten type kinetics (4):

$$V = V_{max} \frac{P}{(K_m + P)} \quad (4)$$

Where V = specific ingestion or growth rate (d^{-1}), V_{max} = maximum specific ingestion or growth rate (d^{-1}), K_m = half saturation constant (μg carbon l^{-1}) and P = food concentration (μg carbon l^{-1}).

The parameters K_m and V_{max} can be estimated by different linear transforms of the Michaelis-Menten equation (Dowd and Riggs, 1965; Eppley et al., 1969). For the ingestion and growth curves of *P. cf. pellucidum* feeding on *T. antarctica* these parameters were calculated by using the linear transform in (5):

$$P = V_{max}\left(\frac{P}{V}\right) - Km \qquad (5)$$

Km and Vmax together with their 95% confidence intervals were estimated through regression analysis. This transform of the Michaelis-Menten equation was chosen because it gave the better spread of the experimental results.

2.5.5 *Starvation experiment*

In order to follow the mortality of *P. cf. pellucidum* under starvation conditions, one treatment of experiment 1 (food concentration of 8000 cell ml^{-1}) was further incubated for twenty days without adding new food. Food levels during this period decreased to 29 cells ml^{-1}. Individual *P. cf. pellucidum* cells were then pipetted out and transferred to a bottle containing culture medium in order to reach a concentration of about 1 dinoflagellate ml^{-1}. After gentle mixing, the medium containing the dinoflagellates was distributed to individual 70 ml tissue culture flasks, incubated in the dark. Two culture flasks were taken after intervals of 2,4, 8, 16, 20, 30 and finaly 36 days and fixed with 1% Lugol's iodine and counted with an inverted microscope. During this experiment, motility in *P. cf. pellucidum* in the incubation bottles was regularly checked with a dissecting microscope.

2.6 Grazing impact of microprotozoa during ANT X/6

The functional response of protozoa found by Bjørnsen and Kuparinen (1991) and in this study were used in order to estimate the grazing rates of microprotozoan assemblage during ANT X/6.
For transect 1 and 5 grazing impact was estimated by applying the functional responses to protists and microprotozoan abundances found during the cruise. Since those are the only functional response studies for Southern Ocean protozoa, I applied it to all the microprotozan community. It is likely that by doing so grazing impacts are somewhat underestimated since ciliates tend to have higher growth and feeding rates than dinoflagellates (Strom, 1991; Hansen, 1992; Buskey et al., 1994; Montagnes, 1996). Food levels used corresponded to the average protistplankton standing stocks in the upper 100 m of the water column, and comprised the sum of nanoplankton (own data and

data from Becquevort, 1997) and microplankton both autotrophic and heterotrophic. During transect 5, nanoprotozoa and nanophytoplankton standing stocks were only calculated at 20 m depth (Becquevort, 1997) but were assumed to be constant throughout the upper 100 m of the water column. Bacteria were not considered since both tintinnids, aloricate choreotrichs and microdinoflagellates do not efficiently feed on them (Jonsson, 1986; Rassoulzadegan et al., 1988; Kivi and Setälä, 1995; Hansen, 1992; Nakamura et al., 1992). The percentage of primary production grazed was calculated using phytoplankton stocks grazed per day divided by the primary production rates measured at the same stations (data in Jochem et al., 1995).

For transect 5 a second estimate of grazing impact was calculated. This time grazing estimates by, and on, each size classes were done. Size classes were taken according to the classification described in section 2.2.2. Since *Protoperidinium* species and the "Diplopsalis group" do not seem to have same size constraints as most other protozoa, they were pooled with the larger size class of protozoa (> 60 µm). The functionnal response of Bjørnsen and Kuparinen (1991) was studied on a dinoflagellate of about 10 µm diameter and was applied to microprotozoa between 20 and 40 µm. The functional response found during this study (for *P. cf. pellucidum*, 42-50 µm diameter) was applied to the microprotozoan fraction larger than 40 µm. The size fractions grazed by the microprotozooplankton included the nanoplankton (Becquevort, 1997) and all protists (including heterotrophs) smaller or in the same size class than the grazers. The percentage of primary production grazed was again calculated using phytoplankton standing stocks grazed per day divided by the primary production rates measured at the same stations (Jochem et al., 1995). Additionally grazing impact on the size classes of larger phytoplankton (20 to 40, 40 to 60 and> 60 µm, respectively) was estimated assuming non-selective feeding by microprotozoa: each size class of phytoplankton was grazed in proportion to its contribution to nano- and microprotistplankton standing stocks.

3 RESULTS

The following results have not been organised in accordance with the principal questions of this thesis but by presenting sets of stations (or transects) in order to facilitate the comparison between biological and hydrographical characteristics. Also, for each set of stations (or transects) a brief description of the hydrography and physico-chemical conditions are given before describing the results. The last section of the results contains the experimental data and grazing estimates.

3.1 Microprotist, faecal pellet and empty diatom frustule distribution.

3.1.1 *Hydrography*

The first transect followed the receding ice edge along the southern ACC (stations 859 to 864) before turning south to the ACC-Weddell Gyre Boundary (AWB) well into the pack ice (stations 866 and 867). The vertical structure between stations 859 and 864 was characterized by a layer of homogeneous temperature, salinity and nutrient concentrations corresponding to the Antarctic Surface Water (AASW) and extending down to depths varying from 60 to 100 meters (Veth et al., 1997; Bakker and Fritsche, unpublished). Below 100 m depth, steep gradients of temperature, salinity and nutrients marked the transition between the AASW and the upper regime of the Circumpolar Deep Water (UCDW, Veth et al., 1997; Bakker and Fritsche, unpublished). At stations 866 and 867 salinities around 34.10 and higher nutrient concentrations than in the southern ACC (Table 2) were characteristic of the Circumpolar Deep Water (CDW) reaching the surface in this area (Veth et al., 1997). At those two stations, potential temperature, salinity and nutrients were uniform down to 80 and 60 m depth. Below, potential temperature, salinity and nutrient gradients marked the transition between the UCDW and the lower regime of the Circumpolar Deep Water (LCDW) (Veth et al., 1997; Bakker and Fritsche, unpublished).

Transect 5 extended from the ice edge in the southern ACC at 56°S to 47°S in the Polar Frontal region (PFr). The southernmost station at 56°S was situated in a tongue of dispersing ice in the outer ice edge (ice coverage of about 30%; van Franeker, 1994), the other stations were in open water.

Table 2. Number, position and surface physical and chemical characteristics of stations during transects 1 and 5. θ (c) potential temperature in ° C, nutrients in µmol l^{-1}, chlorophyll a in µg l^{-1}.

Transect number	Station number	Latitude South	Longitude West	Surface					§% Ice cover
				# θ (c)	#Salinity	+Silica	$^{+}NO_3$	$^{+}PO_4$	
1	859	57°00'	38°51'	-1.30	33.94	54.3	28.7	2.01	0
	860	56°59'	30°27'	-1.76	33.80	62.5	28.0	2.00	10
	862	57°00'	23°19'	-1.02	33.80	45.7	27.6	1.97	0
	863	56°51'	21°21'	-1.78	33.80	55.8	27.7	1.98	100
	864	56°09'	15°26'	-1.70	33.80	42.5	27.7	1.93	0
	866	57°45'	06°28'	-1.80	34.10	60.1	29.1	2.01	100
	867	57°18'	06°13'	-1.81	34.07	60.8	29.0	2.03	90
5	887	55°59'	06°04'	-1.77	33.90	50.5	28.2	1.96	30
	891	55°02'	06°00'	-1.64	33.90	39.9	27.1	1.82	0
	892	54°03'	06°00'	-1.50	33.92	41.9	27.1	1.85	0
	893	54°00'	06°01'	-1.47	33.91	41.8	27.0	1.84	0
	894	53°30'	06°01'	-1.02	33.96	42.2	27.3	1.86	0
	895	53°00'	06°00'	-	-	-	-	-	0
	897	52°00'	06°00'	-0.02	33.96	28.5	28.3	1.90	0
	899	51°00'	06°00'	0.20	33.95	28.6	26.6	1.85	0
	900	50°30'	06°00'	1.04	33.94	20.9	25.9	1.72	0
	901	50°00'	05°59'	1.28	33.90	18.7	25.9	1.66	0
	903	49°00'	06°00'	1.55	33.87	11.7	23.8	1.23	0
	905	48°00'	06°00'	2.41	33.86	14.7	23.9	1.64	0
	907	46°59'	05°57'	2.54	33.86	14.0	23.2	1.59	0

Veth et al. (1997)
+ Bakker and Fritsche (unpubl.)
§ Van Franeker (1994)

The vertical structure between 56°S and 51°S was characterized by a layer of homogeneous temperature, salinity and nutrient concentrations corresponding to the AASW and extending down to 150 m depth (Veth et al., 1997; Bakker and Fritsche, unpublished). At 56°S, a narrow melt-water lens extending down to 60 m depth was observed. Below 150 m, a temperature, salinity and nutrients gradient marked the transition between the AASW and the UCDW (Veth et al., 1997). Between the southern ACC and the southern limit of the PFr a latitudinal gradient in silica concentration was observed (from 60 to 20 µmoles l^{-1}) while other nutrient levels (nitrate and phosphate) remained constant (Bakker and Fritsche, unpublished). The southern limit of the Polar Front was evident north of 51°S by the sloping isopycnals from the surface down to 200 m as well as an increase in temperature and a decrease in nutrient concentrations (Veth et al., 1997; Table 2). Vertical temperature and nutrient stratification extended from the surface to the UCDW (Veth et al., 1997; Bakker and Fritsche, unpublished).

3.1.2 *Microprotist standing stocks*

Chlorophyll a concentrations exceeded 0.5 µg l^{-1} at the first station of transect 1 (station 859, west of the South Sandwich Islands) and decreased towards the East to levels > 0.2 µg l^{-1} at station 866 and 867 in the AWB (Bathmann et al., 1997). During transect 5, chlorophyll a concentrations were low (~ 0.2 µg l^{-1}) at the southern ACC and increased in the PFr with a peak of 1.6 µg l^{-1} at 49°S (Bathmann et al., 1997).

Integrated carbon biomass of microphytoplankton followed changes in chlorophyll a during transect 1, with maximum values in ice-free water at station 859 and decreasing westwards (Table 3; Fig. 5). During the whole transect, the diatom assemblage was dominated by *Thalassiosira* spp. Other important diatom species were *Corethron criophilum* which peaked at stations 860 and 867 and species of the genus *Pseudonitzschia* at station 859.

During transect 5, microphytoplankton biomass was higher than in Transect 1 and varied little in the southern ACC, with the lowest value at station 887 in the ice edge (Fig. 5, Table 3). At the southern limit of the Polar Front (50°30'S) an abrupt increase in microphytoplankton standing stocks was found. Microphytoplankton standing stocks remained high in the PFr with a peak at

Table 3. Carbon standing stocks (C) in mg C m^{-2} and percentage (%) of carbon standing stocks of microprotists during transect 1 and transect 5. Values were integrated in the upper 100 m of the water column. (Aut.) autotrophs, (Cil.) ciliates excluding *Mesodinium rubrum*, (Het. flag.) heterotrophic flagellates including the dinoflagellates and (Tot. het.) total heterotrophs (ciliates + heterotrophic flagellates).

Transect	Water	Station	Latitude	Longitude	Aut.		Cil.		Het. flag.		Tot. het.	
number	mass	number	South	West	C	*(%)*	C	*(%)*	C	*(%)*	C	*(%)*
1	*Southern ACC*	859	57°00'	38°51'	316	*65*	78	*16*	94	*19*	171	*35*
		860	56°59'	30°27'	199	*64*	55	*18*	58	*19*	113	*36*
		862	57°00'	23°19'	102	*37*	46	*16*	129	*47*	174	*63*
		863	56°51'	21°21'	77	*38*	48	*23*	80	*39*	128	*62*
		864	56°09'	15°26'	98	*39*	42	*17*	110	*44*	151	*61*
	AWB	866	57°45'	06°28'	97	*52*	19	*8*	73	*39*	89	*48*
		867	57°18'	06°13'	101	*63*	17	*10*	43	*27*	60	*37*
5	*Southern ACC*	887	55°59'	06°04'	215	*52*	108	*26*	89	*22*	197	*48*
		891	55°02'	06°00'	292	*43*	271	*40*	117	*17*	388	*57*
		892	54°03'	06°00'	309	*55*	169	*30*	84	*15*	253	*45*
		893	54°00'	06°01'	371	*50*	258	*35*	111	*15*	369	*50*
		894	53°30'	06°01'	475	*69*	132	*19*	83	*12*	215	*31*
		895	53°00'	06°00'	266	*38*	244	*35*	189	*27*	434	*62*
		897	52°00'	06°00'	495	*70*	92	*13*	119	*17*	211	*30*
		899	51°00'	06°00'	414	*61*	128	*19*	132	*20*	259	*39*
	PFr	900	50°30'	06°00'	1509	*84*	51	*3*	231	*13*	282	*16*
		901	50°00'	05°59'	1745	*84*	106	*5*	217	*10*	323	*16*
		903	49°00'	06°00'	3964	*86*	82	*2*	584	*13*	665	*14*
		905	48°00'	06°00'	1933	*84*	111	*5*	255	*11*	366	*16*
		907	46°59'	05°57'	1877	*84*	66	*3*	286	*13*	352	*16*

49°S dominated by the diatoms *Fragilariopsis kerguelensis* and *Thalassionema nitzschioides* (Fig. 5, Table 3). Autotrophic biomass (> 20 µm) was dominated by diatoms along both transects (50 to 89%) but the total phytoplankton assemblage was dominated by pico- and nano-sized protists in the AWB and the southern ACC and by larger diatoms (> 20 µm) north of 50°S (Becquevort; 1997; Detmer and Bathmann, 1997).

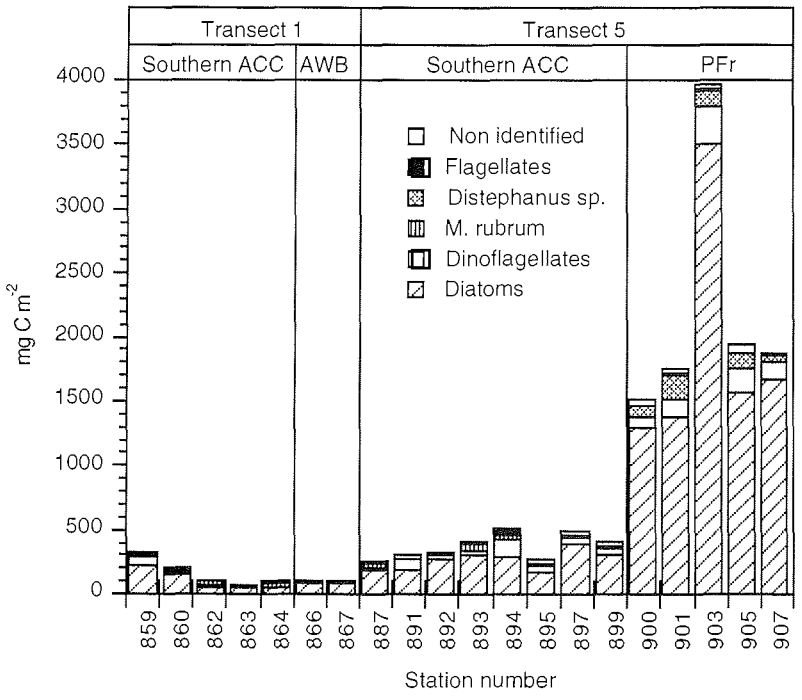

Figure 5. Standing stock and composition of autotrophic protists in the microplankton. Values integrated over the upper 100 m of the water column.

Ciliate biomass was generally higher at the surface (20 m depth) although a subsurface peak was often observed in the AWB and southern ACC. standing stocks were extremely low at stations 866 and 867 of transect 1 and increased towards the west with maximum values in open water at station 859 (Table 3; Fig. 6). The highest ciliate standing stocks were found in the southern ACC and the ice edge during transect 5. In the PFr, ciliate standing stocks were on average lower than in the southern ACC (Mann-Whitney U tests, $P<0.05$). Differences in ciliate standing stocks were found to be significant between stations of transect 1 and transect 5 (Mann-Whitney U tests, $P<0.05$).

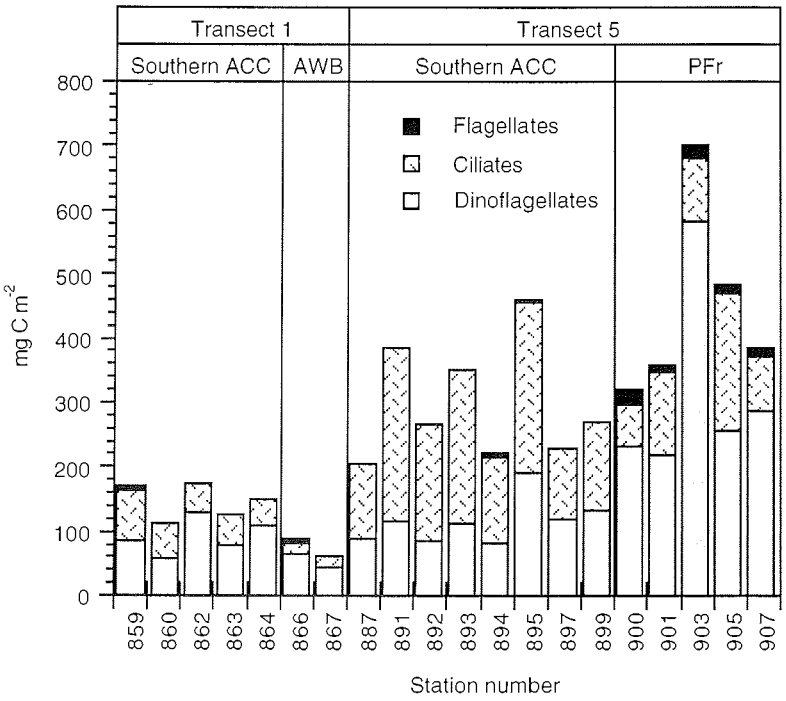

Figure 6. Standing stock of heterotrophic protists in the microplankton. Values integrated over the upper 100 m of the water column.

Integrated ciliate standing stocks were positively correlated to microautotrophic standing stocks but not with chlorophyll a and primary production (Table 4). When both transects are examined separately, ciliate standing stocks showed positive correlation with chlorophyll a (0.857, $P<0.05$) but no significant correlation with microautotrophic biomass (mainly diatoms) during transect 1. During transect 5, no significant relationship was found between ciliate stocks and chlorophyll a, microautotrophic and zooplankton stocks.

Microheterotrophic flagellate biomasses tended to be higher at the surface in the ice-covered areas and in the PFr. In open water of the southern ACC, biomasses were more or less uniformly distributed from the surface down to 100 m depth. Standing stocks of microheterotrophic flagellates (including the dinoflagellates) showed less variability between stations of transect 1 and

transect 5, in the southern ACC and AWB (Fig. 6, Table 3), but values for transect 1 were slightly lower than during transect 5. No significant differences were observed between AWB, Ice-edge and open water stations of the southern ACC (Mann-Whitney U tests, $P>0.05$). The PFr was marked by a significant increase in heterotrophic flagellate biomass (Mann-Whitney U tests, $P<0.05$). Microheterotrophic flagellates showed a positive correlation with microphytoplankton chlorophyll a, primary production and zooplankton standing stocks (Table 4).

Table 4. Spearman rank correlation coefficient between ciliates, heterotrophic flagellates (including the dinoflagellates) and total microprotozoa (ciliates + heterotrophic flagellates) standing stocks (mg C m^{-2}) in the microplankton and §Chlorophyll a (mg m^{-2}), microautotrophs (mg C m^{-2}), +primary production (mg C m^{-2} d^{-1}, and # zooplankton standing stocks (mg AFDW). All values integrated in the upper 100 m of the water column. Significance levels are given: (*) $P<0.05$ and (**) $P<0.01$.

	§ Chlorophyll a	Microautotrophs	+Primary production	#Zooplankton
Ciliates	0.333	0.495*	0.073	0.397
Flagellates	0.784**	0.765**	0.800*	0.653*
Total microprotozoa	0.709**	0.768**	0.536	0.538*

§ Bathmann *et al.* (1997)
# Fransz and González (1997)
+ Jochem *et al.* (1995)

Microprotozoan standing stocks constituted an important fraction of total microprotist standing stocks during transect 1 and in the Southern ACC during transect 5 (30-63%). In the PFr, the contribution of heterotrophic microprotozoa to microprotist standing stocks decreased to 14 to 16 %. Heterotrophic dinoflagellates still made up 10 to 13 % of total standing stocks whereas ciliates only constituted a few percent of the microprotist assemblage (Table 3, Fig. 6).
Microprotozoan biomass constituted about 30% of total protozoan biomass (Becquevort, 1997).

3.1.3 *Microprotozooplankton composition*

Except for station 899 just south of the PFr, during both transects, the ciliate assemblage was dominated by aloricate choreotrichs of the genera

Strombidium, *Laboea* and *Strobilidium* (52 to 99% of total ciliate carbon). Holotrich ciliates represented an important fraction of standing stocks at the two stations in the AWB (37 to 47 %) as well as at stations near the ice edge in the Southern ACC (3 to 9%). At some stations in the southern ACC, species of the genus *Didinium* that feed on other ciliates also made a significant contribution to ciliate biomass, indicating complex food web structures. A sharp boundary was observed at 51°S due to a marked increase in tintinnids at station 899 and in the PFr (8 to 54% of ciliate biomass, Fig. 7). *Cymatocilis caliciformis* dominated tintinnid assemblages at stations 899 and 901. A mixed assemblage of *Cymatocilis caliciformis, C. antarctica, Codonellopsis gaussii, Codonellopsis* spp., *Acanthostomella norvegica* and a species described by Laackmann (1910) as *Tintinnus costatus* was found at the other stations in the PFr.

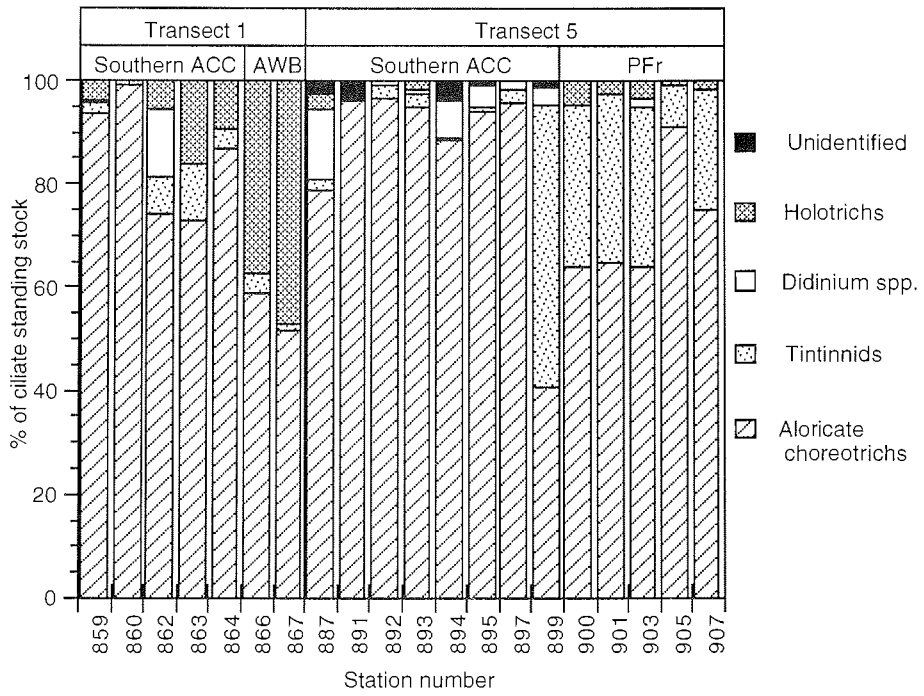

Figure 7. Ciliate community composition given as percentage of ciliate standing stocks (mg C m^{-2}). All ciliates found in the sample were included except *Mesodinium rubrum*.

The flagellate assemblage of transect 1 was dominated by two species of thecate dinoflagellates, namely *Protoperidinium applanatum* and

Protoperidinium defectum. Unarmoured dinoflagellates of the genera *Gymnodinium/Gyrodinium* and *Amphidinium* also contributed significantly to heterotrophic flagellate standing stocks (11 to 34 % and 12 to 25% respectively).

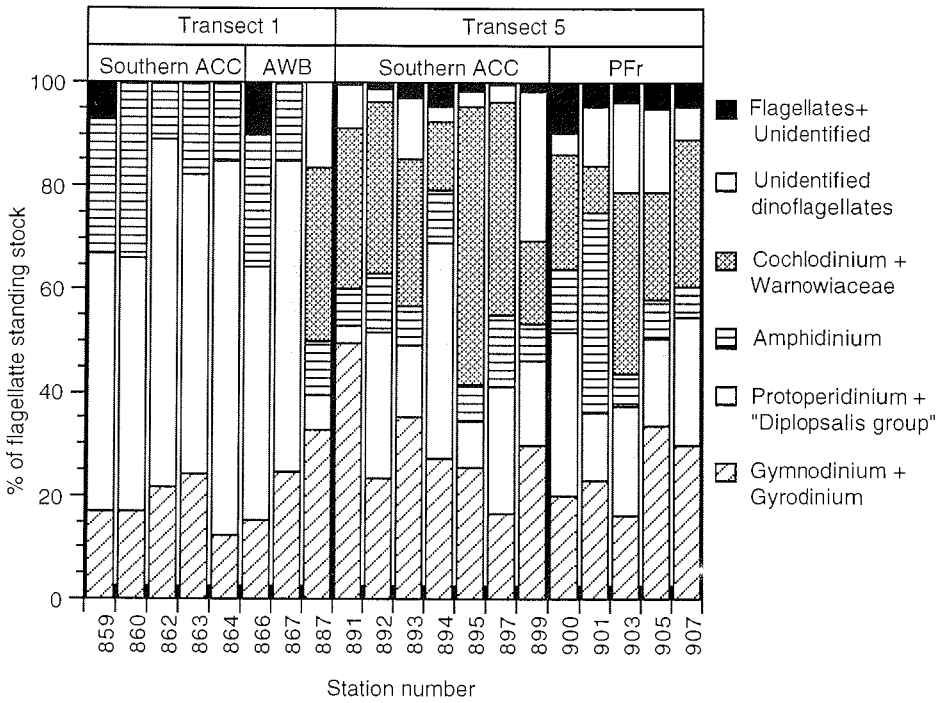

Figure 8. Heterotrophic flagellate community composition given as percentage of heterotrophic flagellate standing stocks (mg C m^{-2}).

During transect 5 unarmoured dinoflagellates dominated flagellate assemblages. The most important genera represented in all stations were *Gyrodinium*, *Gymnodinium*, *Amphidinium* and a group consisting of *Cochlodinium* spp. and members of the family *Warnowiaceae* (Fig. 8). Dinoflagellates of the *Protoperidinium* genus and a few species of the "Diplopsalis group" (Dodge, 1982) also contributed significantly to flagellate carbon except at the two southernmost stations (stations 887 and 891). No clear dominance of any of these genera could be found in any station of transect 5, also no significant differences were observed between the PFr and the southern ACC during this transect. The other heterotrophic flagellates contributed little to the total flagellate standing stock during both transects (0 to

10%), with higher values in the PFr (Fig. 8). Heterotrophic flagellates other than dinoflagellates might, however, be underestimated since they generally belong to the smaller size fraction counted (20 to 40 µm; see section 2.2.1).

Factorial and cluster analysis

Principal Component Analysis (Fig. 9) and Cluster analysis (Fig. 10) produced three to four major groups of stations that correspond to the four main areas investigated namely the AWB, the ice edge in the Southern ACC, the open water of the southern ACC and the PFr. The first principal component axis accounts for 54% of the variance (Table 5) and separates the stations of the PFr from those in the southern ACC and transect 1. This first region is defined by lower nutrient concentrations, higher temperatures and high phytoplankton standing stocks. Characteristic of this area are the high standing stocks of tintinnids, heterotrophic flagellates and dinoflagellates, naked heterotrophic dinoflagellates and heterotrophic armoured dinoflagellates other than *Protoperidinium* spp. and members of the "Diplopsalis group".

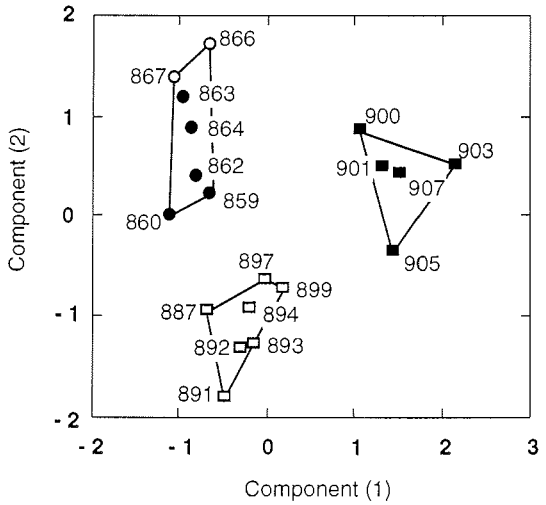

Figure 9. Station scores plotted on the first and second principal component axis from the analysis of transect 1 and transect 5. (●) AWB, (○) ice edge of the southern ACC during transect 1, (□) southern ACC (transect 5), (■) PFr.

The second principal component axis (17% of the variance) separates the southern ACC stations of transect 5 from stations of transect 1. Ice coverage, higher standing stocks of Holotrichs, *protoperidinium* spp. and members of the "Diplopsalis group" characterise stations of transect 1, in a sequence going

from open-water stations in the southern ACC to the ice-covered stations in the AWB. The stations of transect 5, in the southern ACC, were characterized by higher standing stocks of aloricate choreotrich ciliates and *Didinium* spp.

Table 5. Principal component analysis based on the Pearson correlation matrix for transect 1 and 5. Component loadings are given for the first two principal component axes. Analysis is based on standing stocks integrated in the upper 100 m of the water column of heterotrophic microprotozoan groups, microautotrophs and diatoms (in mg C m^{-2}), chlorophyll a (mg m^{-2}) and physico-chemical properties of the surface water (Table 2). Total ciliates: all ciliates except *Mesodinium rubrum*. Total dinoflagellates: all heterotrophic dinoflagellates. Armoured dinoflagellates: all heterotrophic armoured dinoflagellates except *Protoperidinium* spp. and species of the "diplopsalis group". Unarmoured dinoflagellates: all heterotrophic unarmoured dinoflagellates except *Amphidinium* spp. Flagellates: all heterotrophic flagellates other than dinoflagellates. Total autotrophs: all autotrophic protists > 20 µm. Diatoms: all diatoms > 20 µm.

	Component 1	Component 2
Total ciliates	0.373	-0.883 *
Aloricate choreotrichs	0.251	-0.892 *
Tintinnids	0.728 *	0.112
Didinium spp.	-0.123	-0.656 *
Holotrichs	0.059	0.545 *
Total dinoflagellates	0.933 *	0.041
Protoperidinium +"diplopsalis group"	0.392	0.631 *
Armoured dinoflagellates	0.863 *	-0.088
Amphidinium	0.572 *	-0.883 *
Unarmoured dinoflagellates	0.877 *	-0.341
Flagellates	0.858 *	-0.084
Total autotrophs (>20 µm)	0.977 *	-0.074
Diatoms	0.973 *	-0.064
Chlorophyll a	0.901 *	0.040
Silica	-0.939 *	0.153
Nitrate	-0.909 *	0.080
Phosphate	-0.933 *	0.056
Potential temperature	0.938 *	0.070
Salinity	-0.079	0.123
Ice cover	-0.433	0.590 *
% of total variance explained	54	17

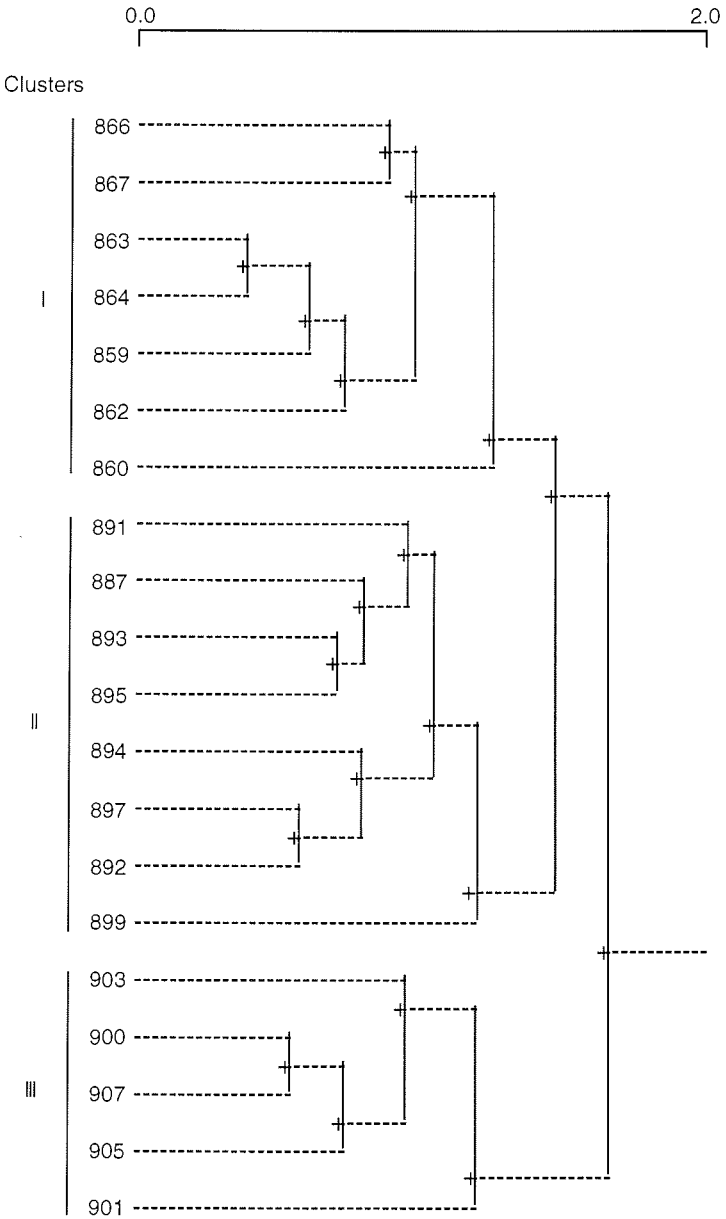

Figure 10. Dendrogram from the average-linkage cluster analysis on stations of transect 1 and transect 5. Variables for the analysis were standing stocks (mg C m^{-2}) of the different heterotrophic microprotozoa groups found in the samples (see figures 7 and 8). Distance metric is euclidean distance.

3.1.4 *Microprotist size composition during transect 5*

At the PFr, higher biomasses of all size classes of autotrophic microplankton were observed as compared to the southern ACC and ice edge. However, the proportion of smaller diatoms (20 to 60 µm) was significantly larger in the PFr (Fig. 11). The differences in size composition of autotrophs between the southern ACC and the PFr reflected the changes in diatom abundance and assemblage composition. South of 51°S, species larger than 60 µm (*Nitzschia closterium*, *Pseudonitzschia* spp., *Corethron criophilum* and *Rhizosolenia* spp.) contributed 36 to 58% of the microphytoplankton assemblage. Smaller chain-forming pennate diatoms (*Thalassionema nitzschioides* and *Fragilariopsis kerguelensis*) dominated in the PFr (66 to 86%) but very high abundances of *Corethron criophilum* were also found at 50°30' S and 47°S. The size composition of the microprotozoa exhibited a much stronger gradient along the transect. With the exception of one station at 50°S the larger size fractions of ciliates (> 60 µm) decreased in the PFr and disappeared north of 49°S (Fig. 11). The contribution of large unarmoured dinoflagellates (> 60 µm) was also significantly lower in the PFr than in the southern ACC and the ice edge and AWB (respectively 5 to 13% and 15 to 39%; Fig. 11). No significant correlation was found between microprotozoan and microautotrophic biomass in the different size classes.

3.1.5 *Standing stocks of microprotozoan faecal pellets and empty diatom frustules*

The abundance of protozoan faecal pellets (> 10 µm) varied a great deal from station to station, ranging from 0 to 1.33 10^8 m^{-2} (Fig. 12). However, stations along the ice edge had on average lower faecal pellet stocks than stations in open water. Faecal pellet abundances were also higher in the open water of the southern ACC than in the PFr during transect 5. Protozoan faecal pellet abundance was significantly correlated with ciliate standing stock (Table 6). The estimates of microprotozoan faecal pellet volume varied between 0 and 2.57 10^3 mm^3 m^{-2} (Fig. 13). The lowest values were found along transect 1. Faecal pellet volume increased in the open water of the southern ACC and peaked at station 903, in the PFr, where the highest microprotist standing stock was found. Due to the high variability of the results, differences in faecal pellet volume were found to be significant only between the ice-edge stations and the PFr (Mann-Whitney U test, $P < 0.05$).

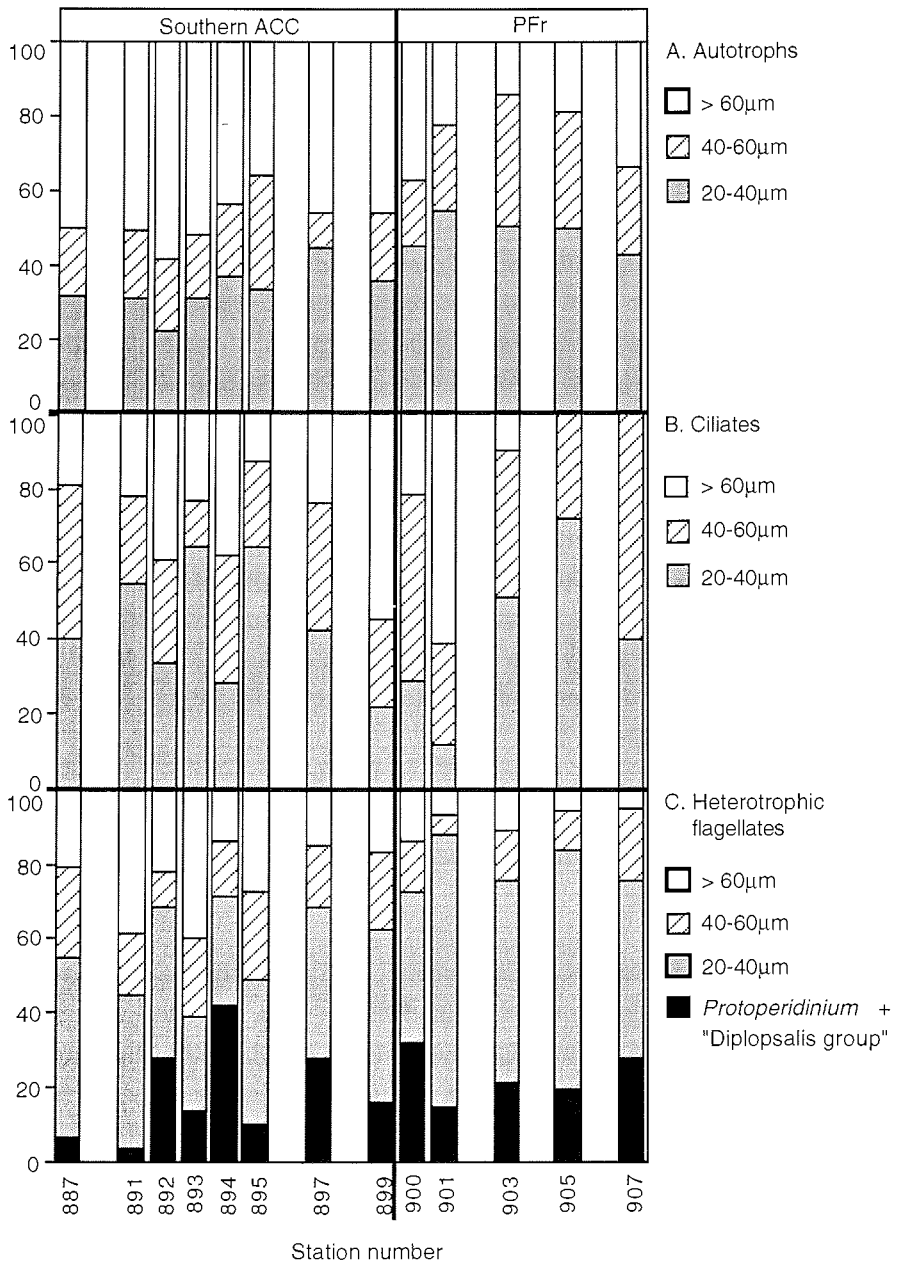

Figure 11. Size composition of microprotist assemblage. Values are given as percentage of standing stock (mg C m^{-2}). (A) diatom, (B) ciliates (except *M. rubrum*) and (C) heterotrophic flagellates including the dinoflagellates.

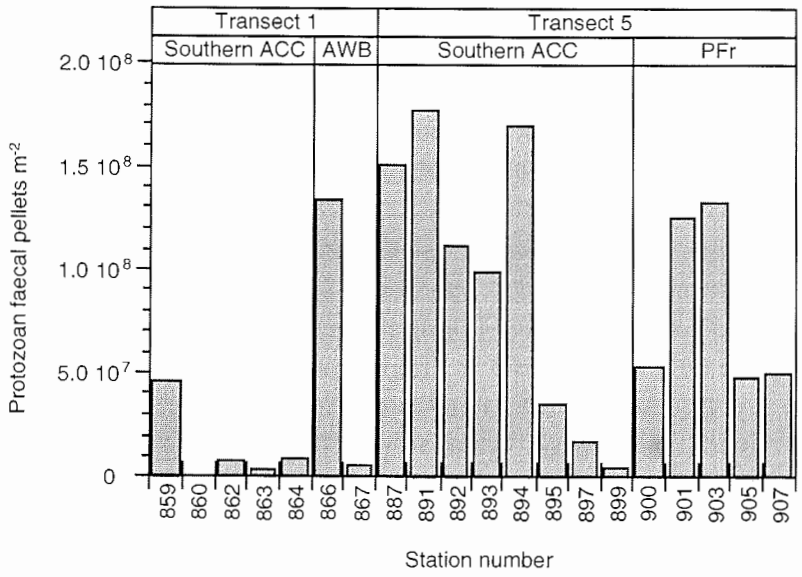

Figure 12. Abundance of protozoan faecal pellets (>10 μm). Values integrated over the upper 100 m of the water column.

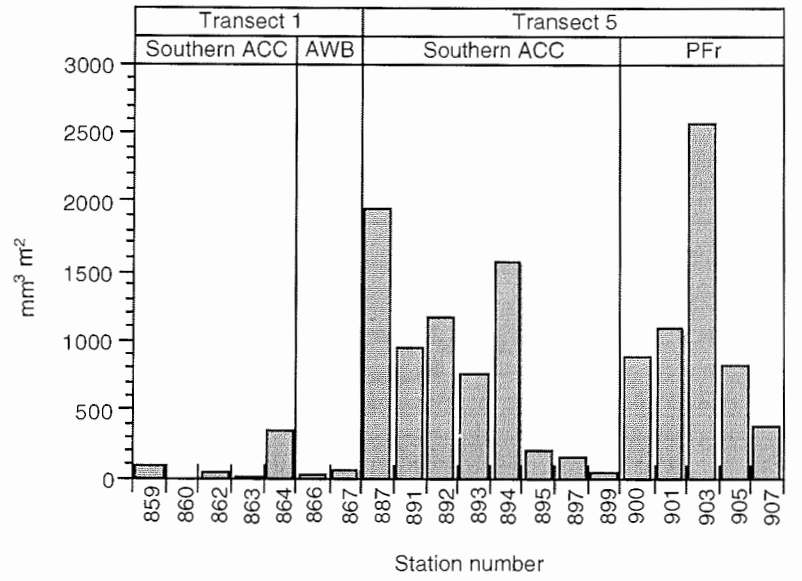

Figure 13. Protozoan faecal pellet volume integrated over the upper 100 m of the water column.

Faecal pellet volume was significantly correlated with diatom as well as microprotozoan standing stocks (Table 6). Estimates of pellets carbon standing stocks, using an average conversion factor of pellet volume to carbon of 0.0114 pg C μm^{-3} (Buck et al., 1990), varied between 0 and 29.1 mg C m^{-2}, corresponding to 0 to 10 % of microautotrophic standing stocks or 0 to 12 % of primary production (Jochem et al., 1995).

The abundance of empty diatom frustules larger than 20 µm showed marked variations between the ice edge, open water of the Southern ACC and the PFr (Fig. 14). Concentrations were low at stations in the AWB and the ice edge ($7.04\ 10^7$ to $3.63\ 10^8$ frustules m^{-2}) and increased in the open water of the southern ACC ($6.56\ 10^8$ to $1.14\ 10^9$ m^{-2}). The highest empty diatom frustule concentrations were found in the PFr ($2.78\ 10^9$ to $4.70\ 10^9$ m^{-2}), their contribution to total frustule concentrations (empty+full; Fig. 15) was, however, on average lower in that region (22%) than in the open water of the southern ACC (34%, Mann-Whitney U test, $P<0.05$) and in the ice-edge and AWB (33%). A significant correlation was found between empty diatom frustule abundance and the standing stocks of flagellates, total microprotozoa, zooplankton and full (or live) diatoms, respectively (Table 6).

Table 6. Spearman rank correlation coefficients between protozoan faecal pellet abundances (ind. m^{-2}) and volume (mm^3 m^{-2}), empty diatom frustules (ind. m^{-2}) and abundances of living diatoms, microheterotrophic flagellates (including the dinoflagellates), ciliates (excluding *M. rubrum*), total microheterotrophic protozoa (Tot. microprot.) and zooplankton. (N.S.) not significant. (A) abundance in ind. m^{-2}, (C) carbon standing stocks in mg C m^{-2} and in mg AFDW for the zooplankton.

	Live diatoms		Flagellates		Ciliates		Tot. microprot.		#zooplankton	
	A	C	A	C	A	C	A	C	A	C
Faecal pellet abundance	N.S.	N.S.	N.S.	N.S.	N.S.	0.460*	N.S.	N.S.	N.S.	N.S.
Faecal pellet volume	0.633+	0.546*	N.S.	0.459*	N.S.	0.528*	N.S.	0.598+	N.S.	N.S.
Empty frustules	0.866+	0.888+	0.839+	0.803+	N.S.	N.S.	0.881+	0.720+	0.976+	0.847+

* $P<0.05$

+$P<0.01$

Franzs and González (1997)

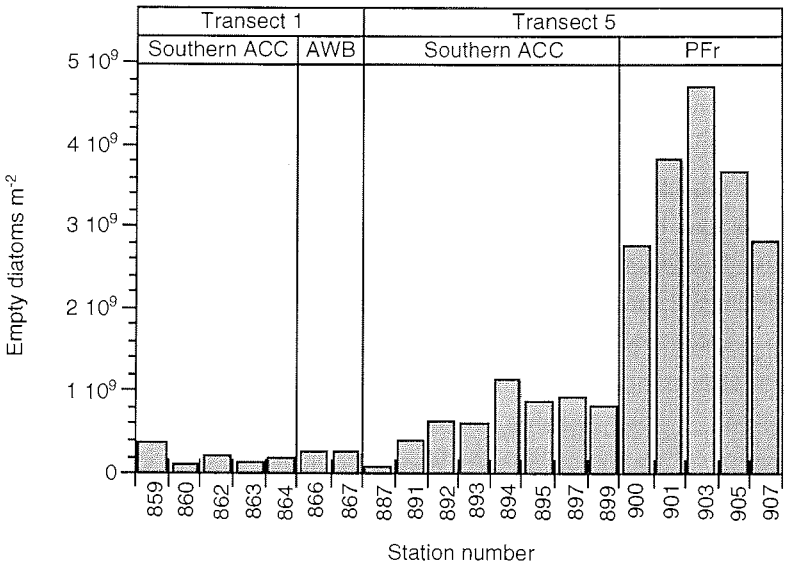

Figure 14. Abundance of empty diatom frustules integrated over the upper 100 m of the water column.

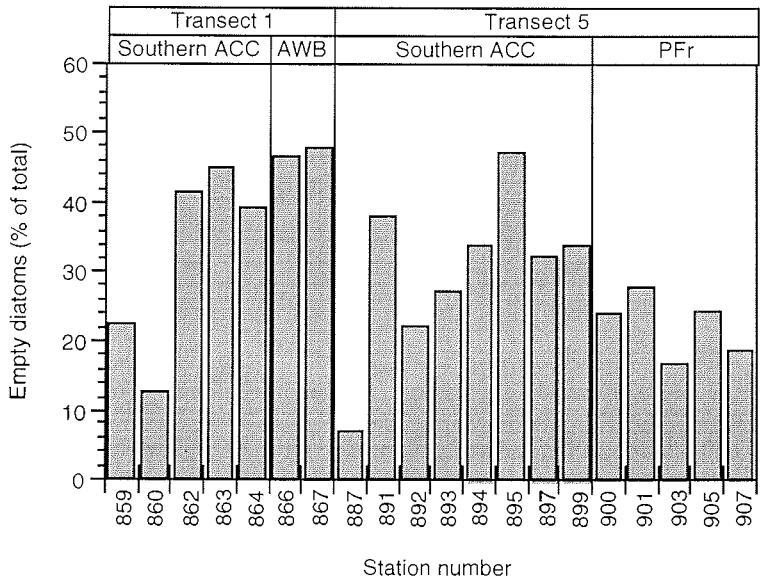

Figure 15. Percentage of empty diatom frustules calculated as % of abundance (ind. m^{-2}) of empty frustules + full frustules (live diatoms).

3.1.6 *Size composition of empty diatom frustule assemblage during transect 5*

Ratios of empty diatom frustule abundance to total frustule abundance (empty+full) were significantly different between the smaller diatoms (20 to 40 µm) and the two other size groups: 40 to 60 µm and > 60 µm, (Wilcoxon rank test, $P<0.05$). Ratios were higher for the smaller size class (20 to 40 µm), and similar for the larger size classes (Table 7). Additionally the ratios of empty diatom frustule to total frustule (empty+full) within each size class changed significantly between the southern ACC and the PFr (Mann-Whitney U tests, $P<0.05$). The southern ACC was characterised by higher empty/(empty+ full diatom frustules) ratios than the PFr for all the three size classes. Correlation between abundance of empty diatom frustules 20 to 40 µm in size and abundance of live diatoms, microprotozoa 20 to 40 µm in size, total microprotozoa and zooplankton was significant (Table 8). Empty diatom frustule abundance 40 to 60 µm in size and < 60 µm were correlated with live diatom, microprotozoa between 20 and 40 µm, total microprotozoa and zooplankton abundance. Empty frustules < 60 µm were also significantly correlated with the larger protozoa (> 40 µm and > 60 µm). No significant corrrelation was found between empty frustules of the larger diatoms (> 60 µm) and the other parameters.

Table 7. Ratio of empty diatom frustule to total frustule (empty + full or live diatoms). Values used for the calculation are abundances integrated over the upper 100 m of the water column (ind. m^{-2}).

	Station number	Latitude South	> 60 µm	40-60 µm	20-40 µm
Southern ACC	887	55°59'	35	30	54
	891	55°02'	29	51	38
	892	54°03'	19	25	22
	893	54°00'	20	18	38
	894	53°30'	37	35	29
	895	53°00'	47	44	53
	897	52°00'	16	23	38
	899	51°00'	13	29	41
PFr	900	50°30'	11	22	26
	901	50°00'	21	25	30
	903	49°00'	21	9	20
	905	48°00'	14	21	27
	907	46°59'	5	15	24

Table 8. Spearman rank correlation analysis between size composition of empty diatom frustule assemblages, full or live diatom assemblages, microprotozoa and (Zoop.) zooplankton during transect 5. Significant correlation coefficients are shown: (**) P< 0.01; (*) P< 0.05; (N.S.) not significant. Values used for the analysis are abundances integrated over the upper 100 m of the water column (ind. m^{-2}).

Empty frustules	Live diatoms			Microprotoza					§Zoop.
	20-40 µm	40-60 µm	>60 µm	20-40 µm	40-60 µm	>60 µm	>40 µm	>20 µm	
20-40 µm	0.912**	-	-	0.714*	N.S.	N.S.	N.S.	0.676*	0.881*
40-60 µm	-	0.874**	-	0.621*	N.S.	N.S.	N.S.	0.599*	0.768*
< 60µm	-	-	-	0.685*	N.S.	0.625*	0.592*	0.713*	0.976**
> 60 µm	-	-	N.S.	N.S	N.S.	N.S.	N.S.	N.S.	N.S.

§ Franzs and González (1997)

3.2 Distribution of net (>64 µm) protozoa

3.2.1 *Hydrography and biotic conditions during transect 11*

During transect 11 three fronts were crossed: the ACC - Weddell Gyre Boundary (AWB), the southern ACC Front and the Polar Front (Veth et al., 1997). The different water masses investigated can be seen in the physico-chemical properties of suface waters (Table 9). Stations 930 and 934 were located in the Weddell Gyre and AWB, respectively. Stations 947 and 953 were located in the southern ACC, north of the ACC Front, and stations 956 and 964 in the Polar Front region. In the Weddell Sea, AWB and southern ACC, temperatures, salinities and nutrients were homogeneous from the surface down to 100 m depth. This layer corresponds to the Antarctic Surface Water (AASW) where a seasonal stratification had not yet been established (Bakker et al., 1994; Veth et al., 1997). Below, a temperature, salinity and nutrient gradient corresponding to the upper regime of the Circumpolar Deep Water (CDW) extended down to about 200 m depth, shoaling at 58°15' S in the AWB. Below the UCDW the gradient extended down to 1500 m corresponding to the lower regime of the Circumpolar Deep Water (LCDW) (Veth et al., 1997). The PFr was marked by the sloping isopycnals down to 200 m depth accompanied by marked vertical gradients of temperature and nutrients observed from the surface to the LCDW.

Stations 930 and 934 were characterised by low phytoplankton standing stocks and high particulate organic carbon (POC) /Chlorophyll a ratios of 540

and 257, respectively (Quéguiner et al., 1997). Phytoplankton standing stocks at stations 947 and 953 were similar to stations 930 and 934 but POC/Chlorophyll a ratios were lower: 226 and 113, respectively Quéguiner et al. (1997). In the PFr, phytoplankton concentrations were high and dominated by diatoms (Bathmann et al., 1997). Peak concentrations of the diatom *Fragilariopsis kerguelensis* were found at station 956 extending down to over 150 m depth, the large *Corethron criophilum* dominated the assemblage at station 964 with high concentrations up to 150 m depth. In the PFr, POC/Chlorophyll a ratios were much lower (around 130 at both stations).

Table 9. Number, position and surface physical and chemical characteristics of stations during transect 11. θ (c) potential temperature in ° C, nutrients in µmol l^{-1}, chlorophyll a in µg l^{-1} and distance from the ice edge in Km.

Station	Latitude	Longitude	Surface						Distance from
number	South	West	# θ (c)	#Salinity	+Silica	$^{+}NO_3$	$^{+}PO_4$	£Chl a	ice-edge
930	59°30'	06°00'	-1.83	34.29	78.7	28.5	2.07	0.20	- 216
934	58°00'	06°01'	-1.54	34.06	69.9	28.2	2.01	0.40	- 27
947	54°00'	06°00'	-1.10	33.91	42.1	26.9	1.86	-	417
953	51°00'	06°01'	0.72	33.94	26.5	26.2	1.85	0.24	748
956	50°01'	05°59'	2.00	33.87	5.5	23.9	1.07	1.42	860
964	48°00'	06°00'	3.80	33.81	0.8	19.9	1.30	2.06	1083

Veth et al. (1997)
+ Bakker et al. (1994)
£ Bathmann et al. (1997)

3.2.2 *Abundance and standing stocks of net protozoa (> 64µm)*

Abundance of living net protozoa

Total abundance of net protozoa (> 64 µm) ranged from 750 to 9490 ind. m^{-3} between 0 and 100 m depth, 856 and 3493 ind. m^{-3} between 100 and 200 m depth and 569 to 1740 ind. m^{-3} between 200 and 500 m depth. For the upper 100 m of the water column abundances increased northward with maximum values at the PFr (station 964; Table 10). Between 100 and 200 m depth, no significant changes were observed between stations. Below 200 m depth, in the CDW, abundances were again higher in the PFr but high net protozoan concentrations were also found at the AWB. Integrated abundance between 0

Table 10. Range of abundance (individuals m^{-3}) of the net (> 64 µm) protozoa at the different depth intervals sampled. (*Protop.* spp.) *Protoperidinium* spp., (*Stichol.* spp.) *Sticholonche* spp., (Foram.) foraminifera, (Nassell.) nassellaria, (Spumell.) spumellaria, (Phaeod.) phaeodaria, (WG) Weddell Gyre, (AWB) ACC-Weddell Gyre Boundary. (ACC) open water of the southern ACC and (PFr) Polar Front region.

Water Mass	Depth Interval	Tintinnids	*Protop.* spp.	*Stichol.* spp.	Foram.	Nassell.	Spumell.	Phaeod. < 300 µm	Phaeod. > 300 µm
	0-25	6-14	24-26	0-7	9-179	28-281	8-51	4-250	0-0.6
WG	25-50	10-142	40-42	75-307	13-30	97-439	21-50	34-300	0.6-3.8
+	50-100	16-357	45-48	96-717	13-20	105-282	32-72	51-183	0.3-0.8
AWB	100-200	3-45	5-820	823-1531	13-39	129-249	87-109	119-129	0.6-7.8
	200-500	2-8	0-101	309-324	2-13	147-162	52-85	23-219	5-8
	0-25	114-162	2-159	0	129-408	16-41	26-59	20-62	0
	25-50	36-251	3-143	8-9	45-95	3-47	14-17	0-127	0
ACC	50-100	279-3239	8-138	0	238-303	17-62	40-63	20-51	0
	100-200	4-370	252-671	0	333-351	60-66	41-98	85-281	0-0.3
	200-500	1-5	0-68	0	62-196	45-59	49-99	314-416	1.4-2.2
	0-25	88-146	219-744	0-29	2379-4211	1316-569	439-584	73-511	0
	25-50	140-372	315-2281	0	1529-5260	658-1210	400-698	93-500	0
PFr	50-100	0-637	80-275	0-1512	2337-6118	962-1248	1100-1116	962-1541	0
	100-200	8-66	0-33	0-431	563-1137	461-489	381-425	621-1401	0-0.2
	200-500	6-34	6-11	0-307	64-295	102-511	32-136	230-443	1.7-2.2

and 100 m depth was found to be significantly correlated with primary production (Spearman rank correlation, $P < 0.05$) but not with POC and chlorophyll a stocks in the euphotic zone (data in Bathmann et al., 1997, Quéguiner et al., 1997; and Jochem et al., 1995). Below 100 m depth no significant correlation was found with any biological parameter.

Tintinnids were more abundant between the AWB and the southern part of the PFr. The highest concentrations were found at station 953, exactly at the same position as the tintinnid peak from transect 5 (Results, section 3.1.3). Tintinnids were abundant from 0-100 m depth. Maximum values were found between 25 and 100 m depth except at stations 930 and 964 were large numbers were also found at the surface. *Protoperidinium* spp. increased in abundance from the Weddell Gyre to the PFr with the exception of station 953 were very low values were found at the surface. These armoured dinoflagellates were abundant from the surface down to 200 m depth. Peak values were found at 50-200 m depth except at station 930 and the PFr stations where maxima were found above 100 m depth. The heliozoan *Sticholonche* spp. was always more abundant below 50 m depth down to 500 m depth. High abundances of *Sticholonche* spp. where found in the Weddell Gyre and in the AWB but also at station 964 in the PFr. Foraminifera showed the same pattern as *Protoperidinium* spp. with the exception of station (station 953) were maximal values were found at the surface. Nassellaria showed higher abundance in the PFr stations followed by the stations in the Weddell Gyre and AWB. Lower values were found in the open water of the southern ACC. At stations with lower nassellarian abundance (934, 947 and 953) higher concentrations were found below 50 m depth. At stations 930 in the Weddell Gyre and in the PFr, with higher abundances, maximum abundances were found in the upper 100 m of the water column. Spumellaria radiolaria were less abundant than the nassellarian in the Weddell Gyre and AWB. Abundances remained similar in the open water of the southern ACC but increased significantly in the PFr. Spumellaria radiolaria were also found to be abundant from the surface down to 500 m depth with higher values generally below 50 m depth except at the two Polar Front stations where they were more abundant in the upper 100 m of the water column. Smaller Phaeodaria (< 300 µm) abundances did not change markedly between the Weddell Gyre and the open water of the southern ACC. However, maximum abundances in the Weddell Gyre (station 930) were found from the surface down to 200 m depth whereas in the AWB and open water of the southern ACC higher abundances were found below 100 m depth. The highest abundances were found at stations in the PFr between 50 and 100 m depth. Larger phaeodaria (> 300 µm) were more

abundant in the Weddell Gyre and AWB. Higher abundances were found below 100 m depth in the Weddell Gyre and below 200 m depth at other stations.

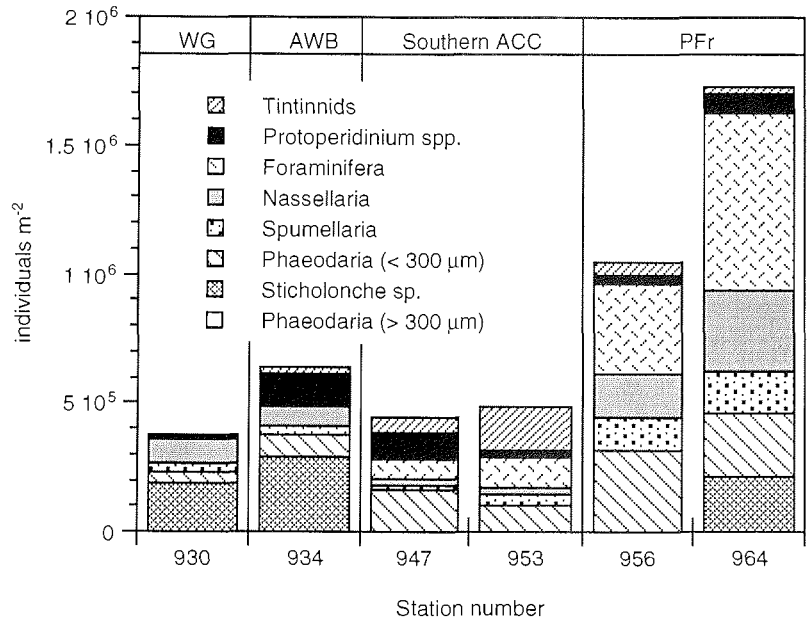

Figure 16. Abundance of larger protozoa (> 64 µm) along transect 11. Values integrated over the upper 500 m of the water column.

In terms of abundance the heliozoan *Sticholonche spp.* dominated the assemblage in the two southernmost stations, 930 and 934, in the Weddell Gyre and AWB respectively (Fig. 16), followed by the nassellaria, *Protoperidinium cf. antarcticum* and the smaller (< 300 µm) phaeodaria (mainly *Challengeron bicornis* and *Protocystis tridens*). No spinose foraminifera were found at these two stations and the tintinnid assemblage was dominated by *Cymatocylis affinis/convallaria*. Although total protozoan abundance did not vary significantly, a radical change in the assemblage was observed in the southern ACC (stations 947 and 953, Fig. 16): the heliozoan *Sticholonche* spp. disappeared and the nassellarian radiolaria decreased significantly; tintinnids (mainly *Cymatocylis affinis/convallaria* and *C. calyciformis*), spinose and non-spinose foraminifera increased together with the smaller phaeodaria (< 300 µm, mainly *Phaeodina antarctica*, *P. harstoni*,

C. bicornis, *P. tridens* above 200 m depth, *Phaeodina antarctica* and *Euphysetta* sp. below 200 m depth). Armoured dinoflagellate assemblage was still dominated by *P. cf. antarcticum* . Stations in the PFr were characterised by a further increase in the abundance of spinose and non-spinose foraminifera, polycystine and smaller (< 300 µm) phaeodaria radiolaria (mainly *Protocystis swirei* above 200 m depth and *P. swirei*, *P. tridens* and *Euphysetta sp.* below 200 m depth). The heliozoan *Sticholonche* spp. were also abundant at station 964. The Aulacanthidae and *Coelechinus wapiticornis* dominated the larger (> 300 µm) phaeodaria assemblage at stations 930 and 934 whereas *Aulacanthis* spp. dominated at the other stations.

Abundance of empty tintinnid loricas and radiolarian skeletons

Standing stocks of empty radiolaria skeletons and tintinnid loricas varied between 1.97 10^4 and 1.85 10^5 skeletons m^{-2}, 3.42 10^4 and 2.49 10^6 empty loricas m^{-2} (Fig. 17), and increased from the Weddell Gyre to the PFr.

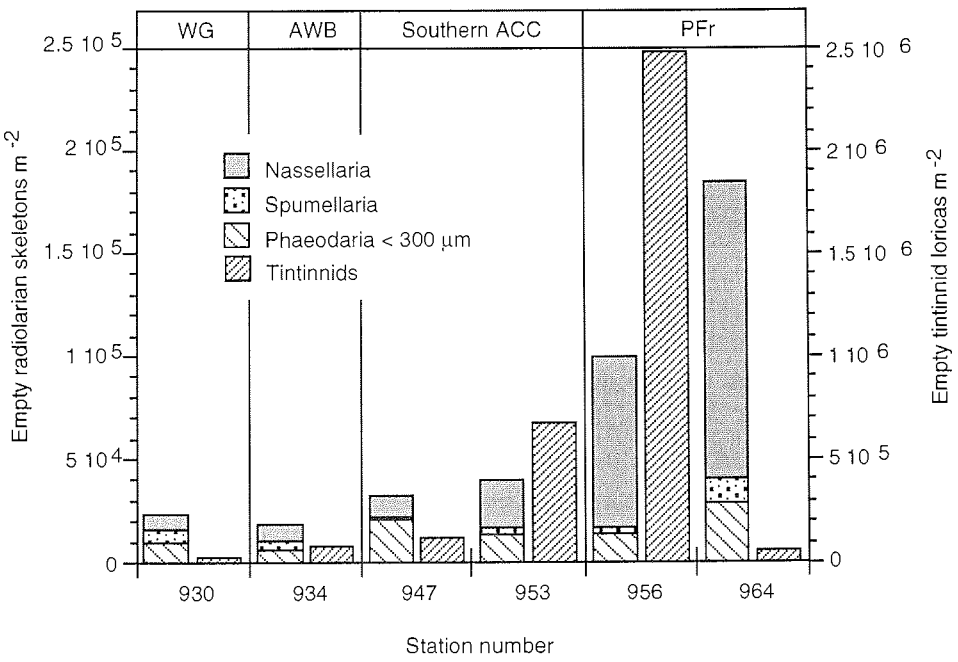

Figure 17. Abundance of empty radiolarian skeletons and tintinnid loricas. Values integrated over the upper 500 m of the water column.

Percentage of empty tintinnid loricas during the transect averaged 84% of full+empty loricas for the whole water column, for each depth values varied between 46 and 100% with maximum proportion of empty loricas always in the deeper layer (200 to 500 m). Empty radiolarian skeletons constituted on average and for the whole water column 27, 8 and 11 % of the population of nassellaria, spumellaria and smaller phaeodaria, respectively. Values at individual depth intervals varied between 0 and 55 % for the nassellaria, 0 and 24 % for the spumellaria and 0 to 50 % for the smaller (< 300 µm) phaeodaria. The abundance of empty tintinnid loricas, nassellarian and smaller phaeodarian (< 300 µm) skeletons were significantly correlated with abundance of live organisms. When integrated over the whole water column, only empty tintinnid lorica standing stocks (from the surface to 500 m depth) were correlated with standing stocks of live tintinnids. The percentage of empty tintinnid loricas, spumellarian and smaller phaeodarian (< 300 µm) skeletons were correlated with depth (Spearmann rank correlation, $P < 0.05$) with maximum values between 200 and 500 m. Percentage of empty spumellarian and smaller phaeodarian (< 300 µm) skeletons were also negatively correlated with chlorophyll a (Spearmann rank correlation, $P < 0.05$). The proportion of empty nassellarian skeletons was positively correlated with zooplankton biomass but not with depth. However, maximum empty skeleton abundances were also found below 200 m depth.

Biomass of living net protozoa

Integrated carbon standing stocks of larger protozoa varied between 1 to 40 mg C m^{-2} in the upper 100 m of the water column (Fig. 18). Values increased northward from the Weddell Gyre (station 930) to the PFr (station 964). Between 100 and 200 m depth no clear trend was observed and stocks were less variable than in the surface layer (6 to 17 mg C m^{-2}). Below 200m depth standing stocks of large protozoa were generally higher than at other depth intervals (23 to 202 mg C m^{-2}). Highest biomass occurred in the AWB (station 934) and the lowest values were found in the southern ACC (station 947). No significant correlation was found between integrated biomass for each depth interval and primary production, POC and Chlorophyll a stocks in the euphotic zone (data in Bathmann et al., 1997; Quéguiner et al., 1997; Jochem et al., 1995).

In terms of biomass, the composition of the total net protozoan assemblage was always dominated by the larger (> 300 µm) phaeodaria (50 to 94% of total net protozoan biomass, Figs. 19 and 20). Assemblage composition showed

significant differences between the different depth intervals (from the surface down to 500 m depth) at stations in the Weddell Gyre and AWB. Nassellaria and phaeodaria dominated biomass in the upper 100 m in the Weddell Gyre, but foraminifera also contributed significantly to biomass in the upper layer (0-25 m depth). Below 200 m depth large phaeodaria (> 300 µm) contributed over 90 % of the biomass.

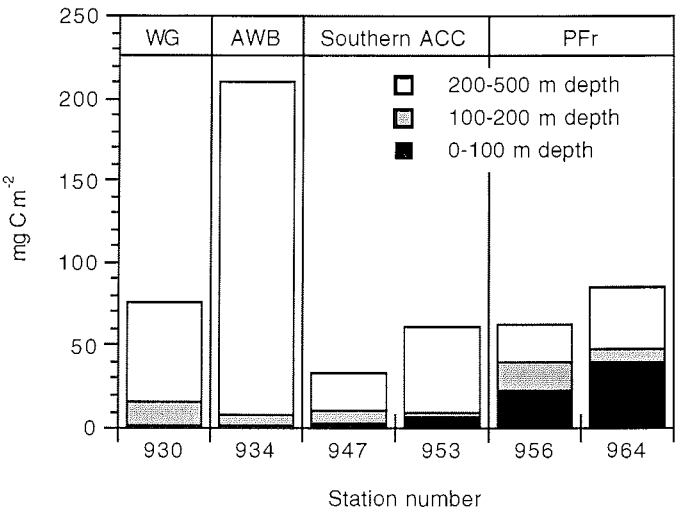

Figure 18. Total standing stocks of larger protozoa (> 64 µm). Values integrated over the upper 500 m of the water column.

At the station in the AWB, foraminifera followed by tintinnids, *Protoperidinium* spp. and nassellaria dominated the upper layer (0 to 25 m depth). Larger (> 300 µm) phaeodaria dominated between 25 to 50 m depth, *Sticholonche* spp. and tintinnids between 50 and 100 m depth, *Sticholonche* spp., *Protoperidinium* spp. and large (> 300 µm) phaeodaria between 100 and 200 m depth. In southern ACC, net protozoan assemblage composition did not vary markedly from the surface down to 200 m depth at station 947 and was dominated by tintinnids, *Protoperidinium* spp. and foraminifera. At station 953 net protozoan assemblage was dominated by tintinnids, and foraminifera, between 0 to 100 m depth. Between 100 and 200 m depth, tintinnids disappeared and *Protoperidinium* spp and foraminifera were dominant. In the

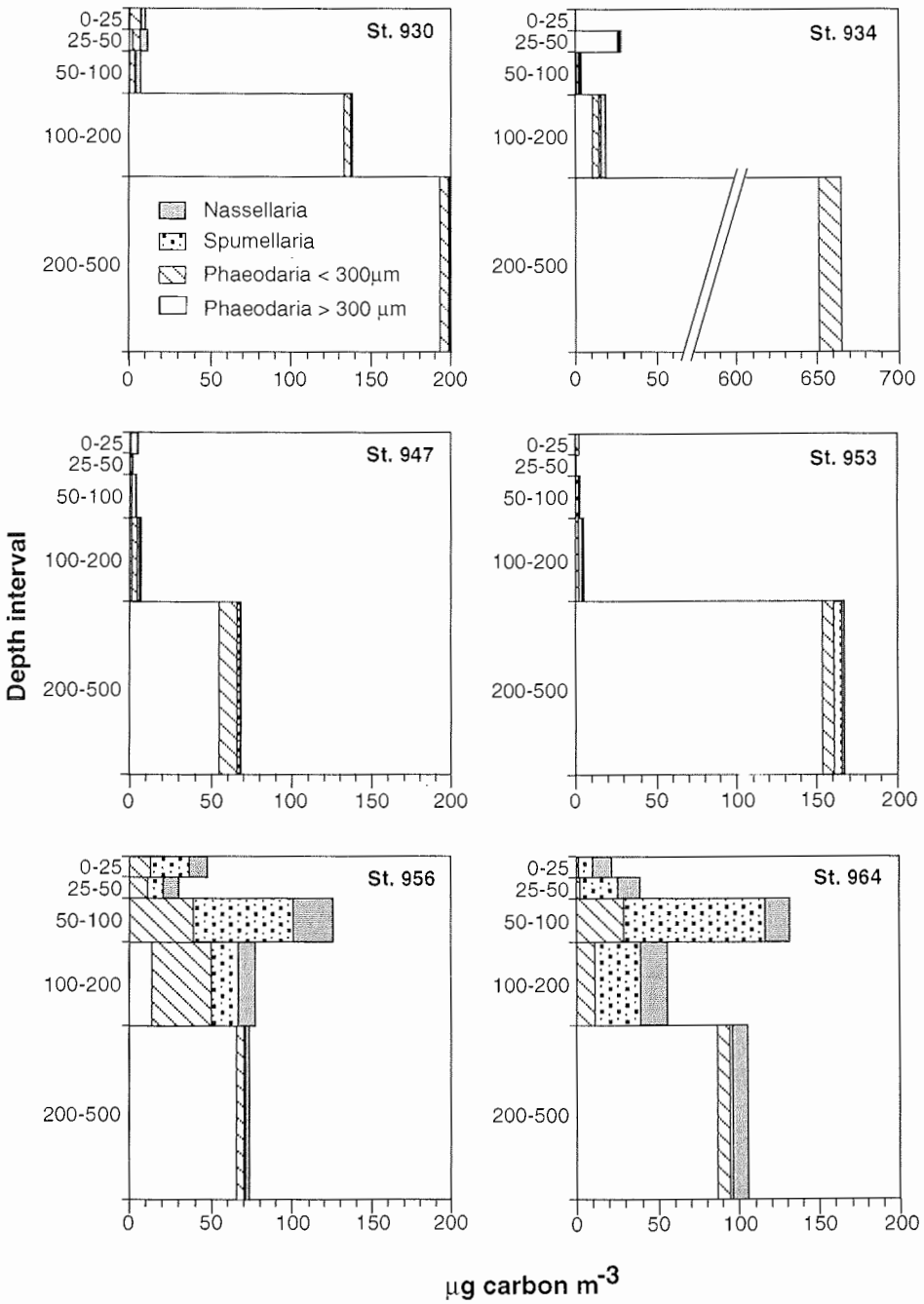

Figure 19. Depth distribution of nassellaria, spumellaria and phaeodaria radiolarian biomass. Note changes in scaling for station 934. Depth in meters.

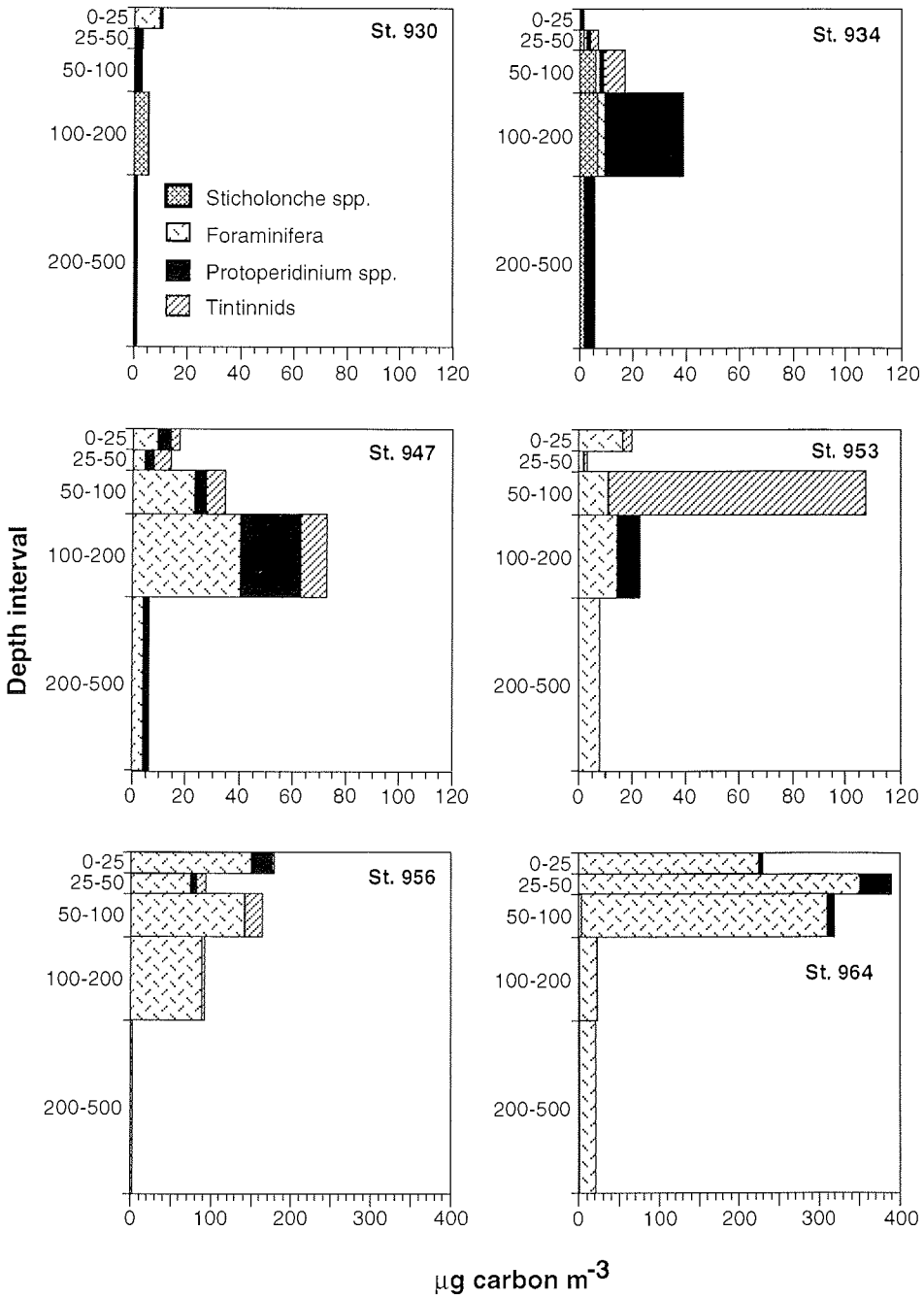

Figure 20. Depth distribution of the heliozoan *Sticholonche* spp., tintinnids, *Protoperidinium* spp. and foraminiferan biomass. Note changes in scaling for stations in the PFr. Depth in meters.

PFr, the upper 100 m of the water column showed similar net protozoan assemblage composition dominated by foraminifera. Between 100 and 200 m depth spumellaria and phaeodaria also contributed significantly to biomass. Between 200 and 500 m depth larger (> 300 μm) phaeodaria dominated at all stations (68 to 97 % of the biomass), although foraminifera contributed a sizeable 16 % at the last station (964) in the PFr.

Table 11. Spearman rank correlation analysis for net protozoan (>64 μm) biomass. Values of correlation coefficients for significant correlations are shown. (N.S.) not significant. (*) P> 0.05 and (**) P> 0.01. Values of all sampling depth intervals were used. Weighted average values for each depth intervals were used for the following parameters: depth, potential temperature, salinity, silica and chlorophyll a Protozoan biomass (μg C m^{-3}), depth (m), θ (c) potential temperature (° C), silica (μmol l^{-1}), (Chl a) chlorophyll a in (mg m^{-3}) and (Zoop) zooplankton biomass (mg C m^{-3}).

	Depth	# θ (°c)	#Salinity	+Silica	£Chl a	aZoop.
Tintinnids	-0.402*	N.S	-0.490**	-0.401*	0.648**	N.S.
Protoperidinium spp.	N.S.	N.S.	-0.430*	N.S.	0.466*	N.S.
Sticholonche spp.	N.S.	N.S.	N.S.	0.417*	N.S.	N.S.
Foraminifera	N.S.	0.653**	- 0.774**	-0.830**	0.598**	0.725**
Nassellaria	N.S.	0.423*	N.S.	-0.413*	0.409*	0.743**
Spumellaria	N.S.	0.704**	- 0.518**	- 0.648**	N.S	0.777**
Phaeodaria (< 300 μm)	0.463*	0.432*	N.S.	N.S.	N.S.	0.614**
Phaeodaria (> 300 μm)	0.728**	N.S.	0.886**	0.793**	- 0.595**	N.S.

Veth et al. (1997)
+ Bakker et al. (1994)
£ Bathmann et al. (1997)
a Franzs and González (1997)

Of the large protozoan groups found in the samples, the tintinnids, *Protoperidinium* spp., nassellarian and foraminiferan biomasses were higher at the PFr and significantly correlated with chlorophyll a, (Table 11, Figs. 19 and 20). Spumellarian biomass at the different depth intervals did not show significant correlation with chlorophyll a however a significant increase in biomass was also found in the upper 100 m of the water column at stations in the PFr. Tintinnids biomass showed negative correlation with depth being higher in the surface 100 meters. The biomass of the heliozoan *Sticholonche* spp., *Protoperidinium* spp., foraminifera, the nassellaria and spumellaria radiolaria did not show significant correlation with depth and peak values were found between 0 and 200 m depth, depending on station. Smaller (< 300

μm) phaeodarian biomass were marginally correlated with temperature and depth with higher biomass generally between 50 and 200 m. Biomass of the larger (> 300 μm) phaeodaria were also significantly correlated with depth, salinity and silica concentrations with maximum biomass below 200 m depths in the Weddell Gyre and AWB. The biomass of larger phaeodaria (> 300 μm) also showed a significant negative correlation with chlorophyll a and was higher in the Weddell Gyre and AWB.

3.3 Grazing, Growth and starvation experiments with *Protoperidinium cf. pellucidum*

3.3.1 *Experiment 1*

During the first growth vs food concentration experiment, *Protoperidinium cf. pellucidum* growth lagged for a period of 2 to 6 days (Fig. 21). After this acclimation phase the dinoflagellate grew exponentially in the three treatments. The specific growth rates varied from 0.11 d^{-1} to 0.14 d^{-1} increasing with food concentration (Table 12).

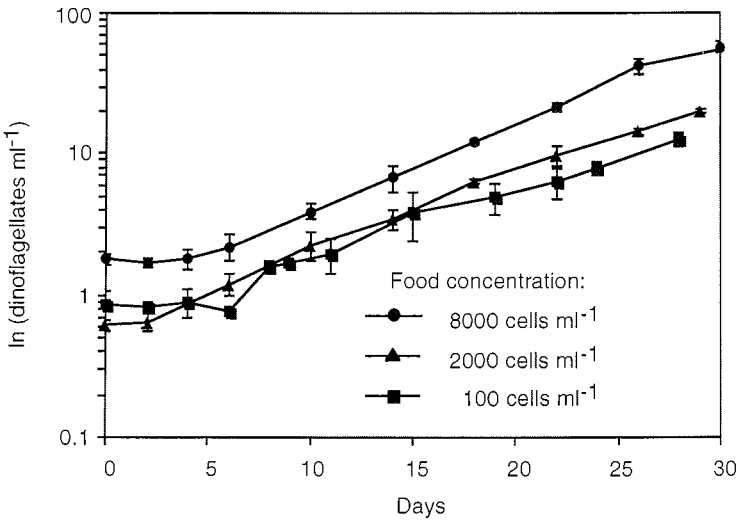

Figure 21. Growth curves of *P. cf. pellucidum* at different food concentrations during experiment 1.

Table 12. Specific growth rates of *P.cf pellucidum* at different food concentrations in experiment 1. Growth rates are given with 95 % confidence interval.

Food concentration: T. antarctica (µg Cl $^{-1}$)	*Food concentration: T. antarctica (cells ml^{-1})*	*Specific growth rate (day^{-1})*
20	100	0.11 ± 0.02
407	2000	0.12 ± 0.01
1693	8000	0.14 ± 0.02

3.3.2 *Experiment 2*

During the second set of experiments *P. cf. pellucidum* grew exponentially after an acclimation period of 3 to 5 days except for the treatment at food concentration of 25 µg C l^{-1} (Table 13). In this treatment *P. cf. pellucidum* did not show balanced growth, consequently growth and ingestion rates from this treatment were not used to determine the parameters Vmax and Km of the Michaelis-Menten kinetics for the growth and ingestion rates as a function of food concentration (Materials and Methods, section 2.5.4).

Table 13. Specific growth rates and ingestion rates of *P. cf. pellucidum* during experiment 2. Growth rates are given with 95% confidence intervals and ingestion rates with standard deviations.

Food concentration µg C l^{-1}	Growth rate d^{-1}	ingestion rates Pg C ind^{-1} h^{-1}
20	0.066 ± 0.030 *	25 ± 10
25	ns†	-
243	0.072 ± 0.017 **	37 ± 15
421	0.113 ± 0.043 **	44 ± 21
880	0.068 ± 0.014 **	48 ± 6
1738	0.093 ± 0.013 **	51 ± 12

(**) Calculated with linear regression significance level P<0.001
(*) Calculated with linear regression significance level P<0.05
(†) Calculated with linear regression, P not significant.

Growth rates of *P. cf. pellucidum* increased with food concentration, varying from 0.66 to 0.13 d^{-1} (Table 13; Fig. 22). Parameters of the Michaelis-Menten kinetics estimated by linear regression together with their 95% confidence interval were 0.86 ± 0.34 d^{-1} and 13 ± 354 µg C l^{-1} for the maximal specific growth rate and the half saturation constant (Km), respectively, (Fig. 22). At

comparable food concentration the growth rates obtained during experiment 1 were significantly higher than during experiment 2 (Tables 12 and 13). This difference cannot be attributed to variability in sample handling since the sampling time, volume of sample counted and the number of organisms counted per sample were similar for both experiments. Differences appear rather to be related to the experimental incubation conditions. Protozoa, in general, are known to be sensitive to manipulation and culturing method, also the differences observed between the two experiments seem rather due to differences in incubation procedure in particular to the incubation volumes/vessels: large 2 l bottles vs 30 ml tubes.

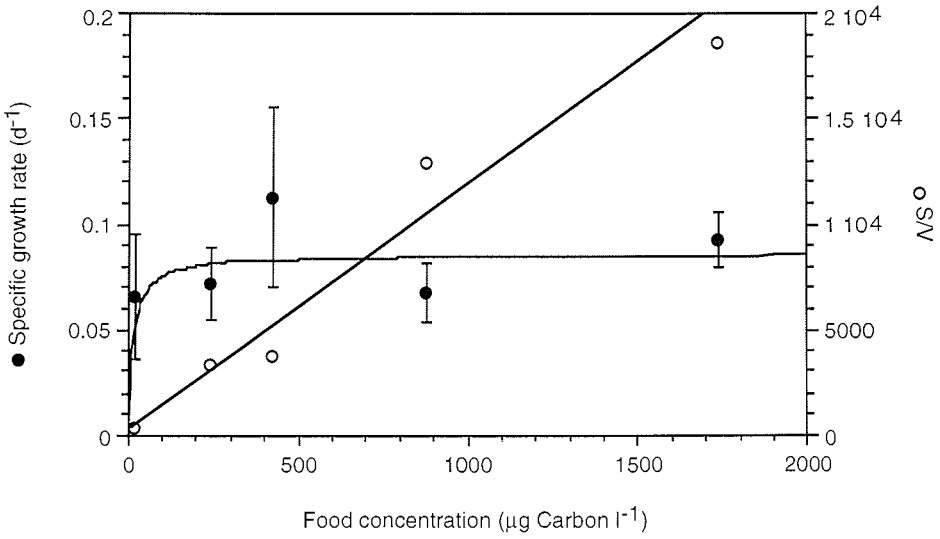

Figure 22. Specific growth rate of *P. cf. pellucidum* as a function of *T. antarctica* concentration. Error bars represent the 95% confidence interval of the specific growth rates obtained by linear regression. Data are fitted to a Michaelis-Menten type kinetics. The constants of the Michaelis-Menten equation Vmax and Km, respectively, are given as the slope and the negative intercept of the linear regression of S/V (ratio of the food concentration to specific growth rate) as a function of food concentration.

Ingestion rates of *P. cf. pellucidum* during experiment 2 also increased with increasing food concentration and ranged from 25 to 51 pg C ind.$^{-1}$ h^{-1} (Table 13, Fig. 23). Parameters of the Michaelis-Menten kinetics estimated by linear regression together with their 95% confidence interval were 52 ± 4 pg C ind.$^{-1}$ h^{-1} and 62 ± 73 µg Carbon l^{-1} for the maximal ingestion rate and the half saturation constant (Km), respectively (Fig. 23). Feeding of *P. cf. pellucidum* saturated at a concentration of approximately 300 µg C l^{-1}.

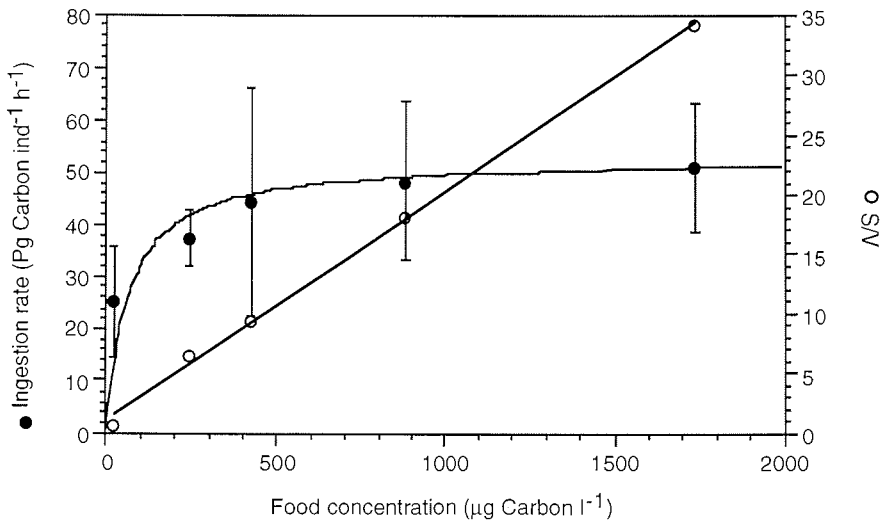

Figure 23. Ingestion rates of *T. antarctica* by *P. cf. pellucidum* as a function of *T. antarctica* concentration. Error bars represent standard deviations. Data are fitted to a Michaelis-Menten type kinetics. The constants of the Michaelis-Menten equation Vmax and Km, respectively, are given as the slope and the negative intercept of the linear regression of S/V (ratio of the food concentration to ingestion rate) as a function of food concentration.

Maximum clearance rate (C_{max}) could be estimated using the maximum ingestion rate (I_{max}) and the Michaelis Menten half saturation constant (K_m) for ingestion rates following equation (6):

$$C_{max} = \frac{I_{max}}{K_m} \qquad (6)$$

The maximum clearance rate predicted by this relationship is 0.84 µl ind.$^{-1}$ h^{-1}.

Diameter of *P. cf. pellucidum* ranged from 49.5 to 42.2 µm between treatments of experiment 2 and did not change significantly with food concentration (Fig. 24). Gross Growth Efficiency defined as the ratio between the increase in *P. cf. pellucidum* biomass and the biomass of *T. antarctica* ingested ranged from 0.49 to 0.87 and showed no trend with increasing food concentration.

3.3.3 *Starvation experiment*

After transfer to tissue culture bottles without food, the population of *P. cf. pellucidum* remained stable during the first two weeks (Fig. 25) and from then

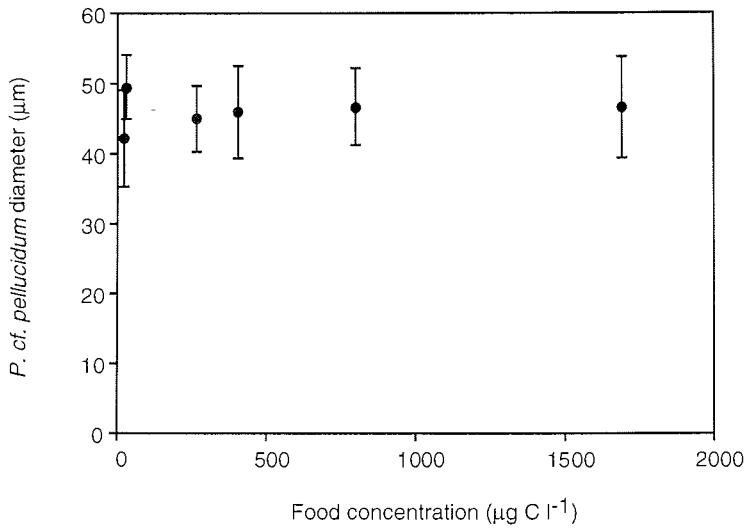

Figure 24. Cell diameter of *P. cf. pellucidum* as a function of food concentration. Error bars represent the standard deviations.

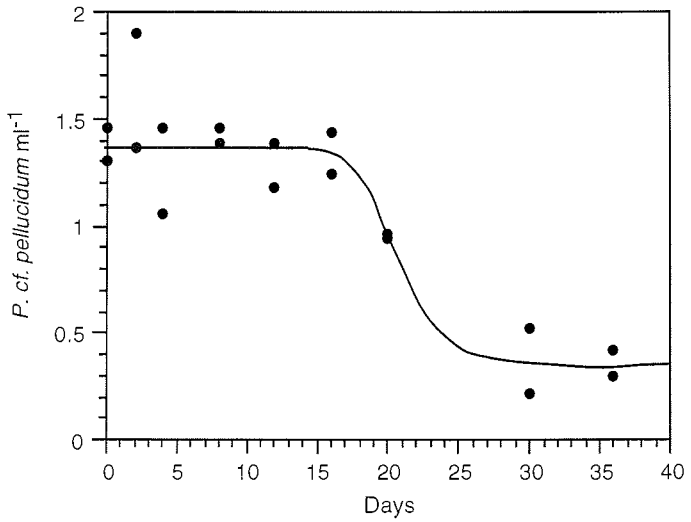

Figure 25 Changes in the concentration of *P. cf. pellucidum* (cells ml^{-1}) under starvation conditions.

on started declining. The intensity of *P cf. pellucidum* coloration with Lugol's iodine decreased from the beginning of the experiment showing that energy reserves in the form of starch were being used. After 34 days incubation, swimming *P. cf. pellucidum* cells were still seen in the bottles. At 36 days incubation intact cells of *P. cf. pellucidum* were still observed but none of them swam.

3.4 Grazing impact of microprotozoa during ANT X/6

The functional relationship found in this study (Results section 3.3) was used to calculate grazing impact of the microprotozoan assemblage on phytoplankton standing stocks for transect 1 and transect 5. These estimates of grazing rates range from 3 to 6 % of the primary production grazed m^{-2} day^{-1} at the ice edge and AWB, 3 to 9 % in open water of the southern ACC and 3 to 12 % in the PFr (Fig. 26).

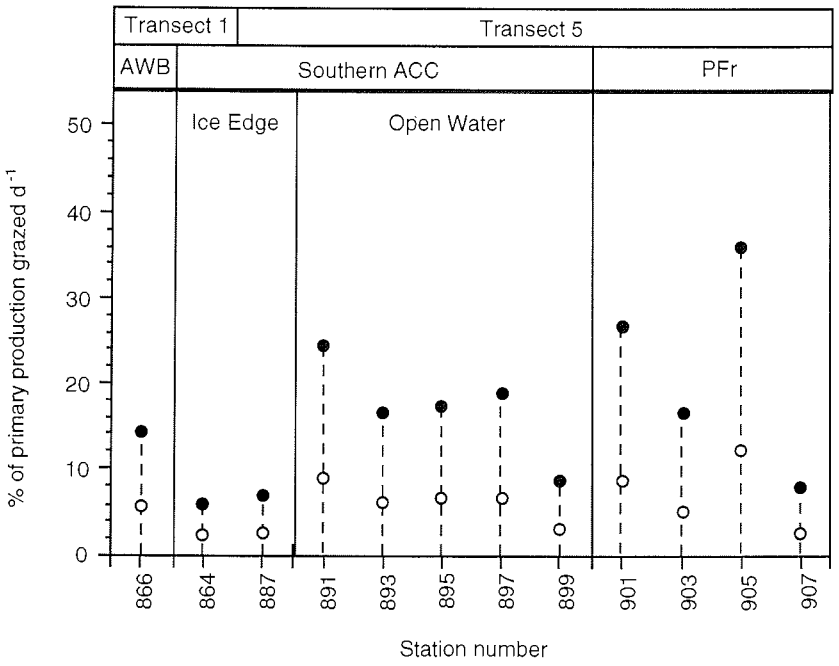

Figure 26. Grazing impact of microprotozoa calculated in percent of daily primary production grazed day^{-1}. Calculations were made on the integrated values of grazing and primary production for the upper 100 m of the water column. (O) estimates obtained using the functional relationship found in this study (see Results section 3.3), (●) estimates obtained using the relationship of Bjørnsen and Kuparinen (1991).

The same calculations using the functional response found by Bjørnsen and Kuparinen (1991) gives estimates which are about twice as high: 6 to 15, 7 to 25 and 8 to 36 % of the primary production grazed day^{-1} for the ice-edge and AWB, open water of the southern ACC and PFr, respectively (Fig. 26). These values suggest that grazing impact in the ice edge areas is less than in open water of the southern ACC and PFr. Hence, although the fraction of heterotrophs in the microplankton assemblages is less in the PFr than in the southern ACC and AWB, their grazing impact can be higher in the PFr due to higher food and microprotozoan standing stocks. Also, despite similar grazing impact, growth rates of microprotozoa should increase from the ice-covered areas investigated to the PFr.

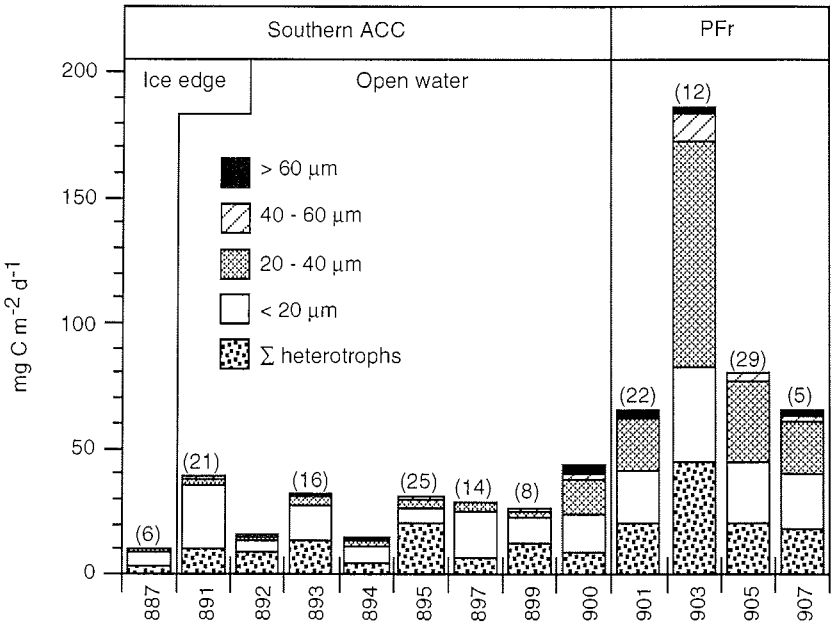

Figure 27. Grazing rates in mg C m^{-2} d^{-1} of the microprotozoan assemblage during transect 5. Grazing on the different size classes of larger Autotrophs (20 to 40, 40 to 60 and > 60 µm respectively) as well as on nanophytoplankton + nano- and microheterotrophs assuming non selective grazing are presented. Values in brackets represent total grazing impact (on auto- and heterotrophic standing stocks) in % of daily primary production.

The second estimate for transect 5, as calculated from the phytoplankton fraction grazed d^{-1} over daily primary production, gives intermediate values of grazing impact, ranging from 4 to 15 % of primary production consumed day^{-1} for the ice edge and open water of the southern ACC, with the lowest values at

the ice edge (station 887). Values in the PFr are similar, ranging from 4 to 22%. The fraction grazed corresponding to the larger phytoplankton (> 20 µm) vary between 2 and 103 mg C m^{-2} day^{-1} in the ice edge (station 887) and PFr (station 903, Fig. 27), respectively. Estimates of the percentage of microphytoplankton production grazed day^{-1} could only be calculated at four stations where size fractionated primary production was measured (Jochem et al., 1995). At stations 887, 895, 901 and 905, respectively, microprotozoa grazed 7, 21, 17, and 38 % of the daily production by microphytoplankton (essentially diatoms) and 3, 6, 14 and 14 % of the primary production due to nanophytoplankton, assuming no selective feeding behaviour. These values show the same trend with the lowest values at ice-covered stations, and somewhat higher but variable values in the southern ACC and in the PFr. They also indicate that if the microprotozoa do not graze on a particular size class of food, their grazing impact should be higher on the microphytoplankton than on nanophytoplankton.

4 DISCUSSION

The following discussion is organised according to the principal questions of this thesis. First, micro- and net (> 64 µm) protozoan assemblages are presented in relation to factors influencing their biomass, abundance, distribution and seasonality. This section is followed by a discussion of factors influencing community composition. Next, the impact of microprotozoan grazing rates on primary production rates, with special emphasis on diatoms, and the importance of particles produced by protozoa > 20 µm are presented and discussed in the framework of carbon and silica fluxes. The discussion ends with an overview of the role of protozoa in carbon and silica biogeochemical cycles in the Southern Ocean together with some concluding remarks and perspectives.

4.1 Importance, seasonality and factors influencing microprotozoan standing stocks in the Southern Ocean.

Factors influencing microprotozoan standing stocks during ANT X/6

Phytoplankton standing stocks found along the ice edge, at the AWB and in the open water of the southern ACC remained at low levels during the whole cruise and were dominated by nanoplankton. The very low phytoplankton stocks found along the ice-edge stations of the southern ACC and below pack ice in the AWB are comparable to values found in other ice-covered areas of the Weddell Sea and Weddell-Scotia Confluence, in late winter-early spring (Becquevort et al., 1992; Garrison et al., 1993; Scharek et al., 1994). Thus, east of the South Sandwich Islands, the "typical" ice-edge blooms described in the WSC and in the Ross Sea (Smith and Nelson, 1986; Nelson et al., 1987; Mathot et al., 1992; Sullivan et al., 1993) do not seem to be the rule (Bathmann et al., 1997). Microphytoplankton standing stocks in open water of the southern ACC, during transect 1 and 5 were slightly higher than in ice-covered areas but did not change during the whole cruise (Bathmann et al., 1997). In the PFr, several blooms were found, dominated by diatoms (Bathmann et al., 1997).

In the AWB and southern ACC, microprotozoa constituted an important fraction of microprotist biomass (30 to 63 %). In the PFr, microprotozoan biomass was also higher than in the southernmost stations. The ratio of microprotozoa to microphytoplankton was however significantly lower in the

PFr than in the AWB and southern ACC. The bloom in the PFr developed from levels of 0.7 µg chlorophyll a l^{-1} to values of 1.9 µg chlorophyll a l^{-1}, during transect 5, in a period of 12 days, corresponding to a net population growth rate of 0.08 d^{-1}. For the lowest biomass levels of phytoplankton present in the PFr, microprotozoan specific growth rates estimated in the experiments carried out with *Protoperidinium cf. pellucidum* (Results, section 3.3.2) and from the functional response determined by Bjørnsen and Kuparinen (1991) range between 0.04 and 0.12 d^{-1}, respectively. With these growth rates microprotozoan biomass should keep pace with that of phytoplankton. Thus, either the microprotozoan growth rates were lower than phytoplankton rates of increase, in the PFr, at the beginning of the growth season, or microprotozoa have been removed through grazing. As the following discussion will show both conditions are likely to have occurred.

By using the functional response of *Protoperidinium cf. pellucidum* (this study) and assuming that microphytoplankton growth follows the exponential growth equation, it is possible to calculate the proportion of microprotozoan biomass (in percent of total microprotist biomass) necessary to consume microphytoplankton at rates such that microphytoplankton net specific growth rates equals microprotozoan specific growth rates (Fig. 28).

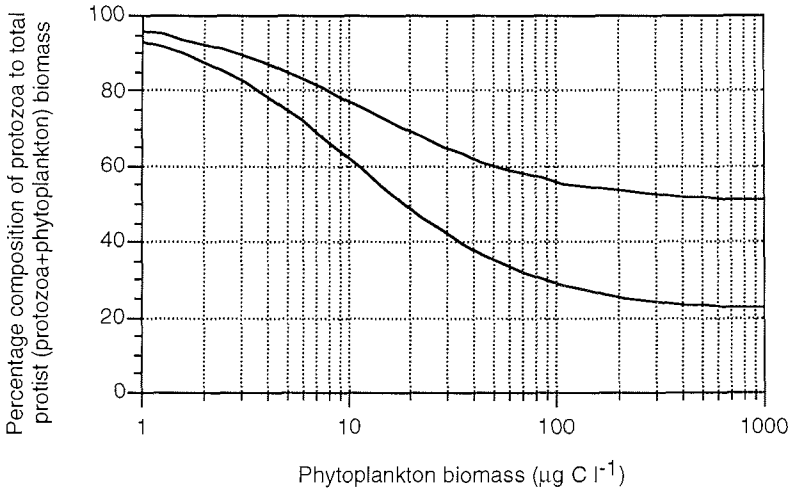

Figure 28. Relative abundance of protozoa, in % of phytoplankton + protozoan biomass as a function of phytoplankton biomass, necessary to attain an equilibrium situation in which the net rate of increase of phytoplankton equals that of protozoa. Both curves are presented for phytoplankton specific growth rates of 0.3 d^{-1}. Upper curve was calculated using the functional response of *P. cf. pellucidum* found in this study. Lower curve was calculated using the functional response of Bjørnsen and Kuparinen (1991) for a small *Gymnodinium* species.

By assuming that at the beginning of the growth season in the PFr, microphytoplankton biomasses were similar to those found in the open water of the southern ACC, microphytoplankton biomass should not have exceeded 5 μg C l^{-1} (this study). The curves shown in Fig. 28 indicate that for these biomass levels and a phytoplankton specific growth rate of 0.3 d^{-1}, microprotozoan concentrations should correspond to 75 to 85 % of microprotist biomass in order to show similar rate of increase to the microphytoplankton. This assuming no mortality of the microprotozoa and also that microprotozoa only graze microphytoplankton. Present knowledge on protozoan and zooplankton feeding behaviour indicates that this assumptions are unrealistic (Stoecker et al., 1981; Stoecker and Evans, 1985; Atkinson, 1996). At the beginning of the growth period, in the PFr, microphytoplankton (essentially diatoms) net rates of increase should have been, therefore, higher than those of microprotozoa, leading to the differences in contribution of microprotozoan to total microprotist stocks observed between the PFr and stations south of it.

In the PFr, copepod biomass was double that found in the southern ACC (Fransz and González, 1997). Egg production of the dominant copepod species (*Calanoides acutus* and *Rhincalanus gigas*) were 5 to 20 eggs d^{-1} in the PFr. Much lower egg production values were found in the southern ACC (Fransz and González, 1997). Phytoplankton carbon (PPC) ingestion rates by copepods determined with the gut fluorescence method varied between 1 and 3 μg PPC $ind.^{-1}$ d^{-1} for *Calanoides acutus* and *Rhincalanus gigas* in the PFr (Dubischar and Bathmann, 1997). Measurements of respiration rates in active Antarctic copepods have been made, in November-December, in the Antarctic Peninsula region for four of the main copepods also present during our cruise, *Calanoides acutus*, *Metridia gerlachei*, *Calanus propinquus* and *Rhincalanus gigas* (Schnack et al., 1985). The lowest respiration rates measured, 3.1, 4.2, 5.0 and 7.7 μg C $ind.^{-1}$ d^{-1} for *Calanoides acutus*, *Metridia gerlachei*, *Calanus propinquus* and *Rhincalanus gigas* respectively (Schnack *et al.*, 1985), should correspond approximately to the minimum energy requirements of active copepods. The feeding rates on phytoplankton measured at the PFr by Dubischar and Bathmann (1997) would not cover those energy requirements and cannot explain the high rates of egg production found in the PFr by Fransz and González (1997). Thus, copepods in the PFr must have food sources other than phytoplankton. Preferential grazing by copepods on microprotozoa, especially ciliates, has been shown for several temperate copepod species even under conditions where

phytoplankton dominated (Kleppel et al., 1991; Fessenden and Cowles, 1994; Jeong, 1994b). The same selective feeding behaviour has been observed in the dominant copepod species present in the PFr under low phytoplankton conditions (Atkinson, 1996). Although phytoplankton stocks in the PFr were much higher than during the study of Atkinson (1996) it is likely that copepods were preferentially feeding on protozoa, especially aloricate ciliates since their standing stocks were lower in the PFr as compared to the Southern ACC and AWB.

Seasonality of microprotozoan assemblage

In the Southern Ocean, comprehensive studies on microprotozoan assemblages have been generally limited to the eastern and western Weddell Sea and the WSC (Garrison, 1991). Furthermore, only a few studies distinguished the microprotozooplankton from the smaller members of the protozoan community.

In the ice-covered region of the northeastern Weddell Sea, Scharek *et al.* (1994) found increasing microprotozoan standing stocks towards the north (4.9 to 285 mg C m^{-2} in the upper 100m of the water column) in a transect along the Greenwich Meridian (70°30'S to 58°S) during late winter-early spring. Microprotozoan biomasses ranged from 10 to 90% of microprotist biomasses (Scharek et al., 1994). In the Weddell-Scotia Confluence (WSC), during winter, total protozoan standing stocks in the upper 100 m of the water column ranged between 177 and 410 mg C m^{-2}. Microprotozoa which constituted about 30% of the total protozoan biomass exceeded on average microautotrophic biomass (Garrison et al., 1993).

Spring to autumn microprotozoa stocks are highly variable, ranging from < 100 to > 2000 mg C m^{-2} (von Bröckel, 1981; Garrison and Buck, 1989; Becquevort et al., 1992; Boltovskoy and Alder, 1992a; Alder and Boltovskoy, 1993; Garrison et al., 1993; Kivi and Kuosa, 1994; Burkill et. al, 1995; Priddle et al., 1995) with lower values in ice-covered areas increasing towards open water. Peak concentrations have always been found associated with blooms. Percentage of microprotozoa for the growth season range between 10 and 60 % of total microprotist biomass (von Bröckel, 1981; Becquevort et al., 1992; Boltovskoy and Alder, 1992a; Alder and Boltovskoy, 1993; Garrison et al., 1993; Kivi and Kuosa, 1994; Burkill et. al, 1995; Priddle et al., 1995).

The microprotozooplankton standing stocks found during this study in the Weddell Gyre, AWB and ice-edge in the southern ACC are similar to winter

and spring/summer values in ice-covered areas around Antarctica and constitute an important fraction of microprotist biomass. Higher microprotozoan standing stocks were found in the open water of the southern ACC and the PFr. These standing stocks are comparable to the highly variable standing stocks reported from spring to autumn, and follow levels of primary production (Garrison, 1991). Higher percentages of microprotozoa occurred in ice covered areas and in the open water of the southern ACC where phytoplankton stocks remain low.

Thus, it seems that seasonality of microprotozoan standing stocks in the Southern Ocean depends on the region and is strongly related to productivity. In ice-covered areas spring and summer standing stocks remain low (around 100 mg C m^{-2}) similar to winter values and amount to an important fraction of total microprotist standing stocks (30 to 90 %). In ice-edge or open ocean areas microprotozoan seasonality is more marked and follows changes in phytoplankton standing stocks (Garrison, 1991). Microprotozoan standing stocks well over 400 mg C m^{-2} are generally restricted to areas where algal blooms have occurred. The proportion of microprotozoa in those areas is more variable than in areas were phytoplankton stocks remain low throughout the growth season, and probably depends on the stage at which sampling is done, namely, at the beginning, middle or end of a bloom phase.

In the vast oceanic belt surrounding Antarctica proportionally high standing stocks of microprotozoa seem to be maintained all year round with higher microprotozoan stocks in open water than in ice-covered areas (Garrison et al, 1993; Scharek et al.; 1994). Contribution of microprotozoa to total microprotist biomass is always significant with higher values during winter and in ice-covered areas. Microprotozoa should, therefore, be an important food source for larger zooplankton both in winter and during the growth season, particularly in areas where phytoplankton biomass remains low. Despite low primary production levels during winter, predation by metazoa on protozoa in the open water of the southern ACC should be low because of the overwintering strategies of krill and most copepod species (Marin, 1988; Smetacek et al., 1990). Thus, similar to other HNLC (high Nutrient Low Chlorophyll) areas such as the subarctic Pacific (Miller, 1993), the Southern Ocean surface water can sustain a large standing stock of protozoa through the winter until the beginning of the growth season. This might be an important factor in preventing the build-up of blooms in spring.

Net (> 64 µm) protozoa

The net protozoan assemblage, collected by vertically towed nets, during this study is more diverse at the phylum level than that of the smaller microprotozoa (20 to 64 µm). The different phyla present in the net protozoan assemblage show also a higher diversity in feeding behaviour, metabolic rates and life cycle strategies. Therefore, in the following discussion each group will be treated separately.

Transect 11, where net protozoa were studied, was sampled two weeks later than transect 5 discussed in the above section. In this period, phytoplankton stocks and assemblages in the ice edge and open water of the southern ACC did not vary markedly (Bathmann et al., 1997). In the PFr, phytoplankton biomass increased significantly as compared to transect 5, accompanied by an increase in vertical particle flux (Rutgers van der Loeff et al., 1997). However, phytoplankton community composition remained quite similar to transect 5 (Bathmann et al., 1997).

Given the scarcity of studies on large protozoa and the differences in sampling method it is difficult to discuss seasonality and factors influencing distribution at this stage of knowledge. The tintinnids are an example. Although several studies on tintinnids have been done in the Antarctic, few separate the larger (> 64 µm) component from the rest of the microprotozooplankton. During this study, tintinnid abundance and biomass roughly followed phytoplankton stocks with higher values in the upper 100 m of the water column and in open water. However, tintinnid concentrations in the PFr were not higher than in the open water of the southern ACC. When compared to winter and summer values from the Bellingshausen Sea and WSC (Alder and Boltovskoy, 1991, Gowing and Garrison, 1992; 120 to 6334 ind. m^{-3} in the upper 100 m) the spring values found between the Weddell Gyre and PFr are remarkably low (6 to 3239 ind. m^{-3}), but nevertheless much higher than winter values from the Weddell Sea (Nöthig and Gowing, 1991; <0.2 µg C m^{-3}).

In contrast to the work of Gowing and Garrison (1992) no significant numbers of *Laackmaniella* spp. were found in any of the stations during transect 11. This tintinnid group possesses a slim elongated lorica and is known to be abundant generally at ice-covered stations (Alder and Boltovskoy, 1991; Gowing and Garrison 1992). The capture method used during this study (64 µm mesh nets) might not collect these slim tintinnids quantitatively and thus tintinnid abundances may have been underestimated. Additionally, a very high percentages of empty loricas were found at all stations (46 to 100%).

These values are comparable to values found by Nöthig and Gowing (1991) who also counted multinet samples. Gowing and Garrison (1992) found much lower percentages of empty loricas in the WSC during winter, by counting reverse filtered water samples. These differences suggest that the high percentages of empty loricas might be an artifact caused by the use of nets for sampling. Furthermore, it is likely that living tintinnid abundance, biomass and distribution pattern is not properly described with the sampling method used in this study.

During this study, tintinnid abundances were higher in the upper 100 m of the water column, peak concentrations often occurring between 50 and 100 m depth. Below 100 m depth tintinnid abundances decreased significantly and only a few individuals per m^{-3} were found below 200 m depth. This distribution pattern is consistent with the winter distribution patterns found by Gowing and Garrison (1991) and Nöthig and Gowing (1991) in the WSC and Weddell Sea, respectively. These results suggest that tintinnids larger than 64 µm are primarily surface-dwelling organisms and tend to concentrate at the base of the euphotic zone.

The abundance of large (> 64 µm) heterotrophic dinoflagellates in the Southern Ocean has to my knowledge been reported only in two studies by Nöthig and Gowing (1991) and Gowing and Garrison (1992) in the Weddell Sea and the WSC, respectively. Net heterotrophic dinoflagellate assemblage seems to always be dominated by species of the genus *Protoperidinium*. The stocks found by Nöthig and Gowing (1991) in the Weddell Sea in winter are similar to the values found in spring south of the AWB (0 to 160 ind. m^{-3}; Nöthig and Gowing, 1991). In the WSC, Gowing and Garrison (1992) found higher values (0 to 599 ind. m^{-3}), similar to the abundances found in the open water of the southern ACC and in the southernmost station of the PFr (st. 956), during this study. Heterotrophic dinoflagellate abundance was higher at st. 964 in the PFr. In terms of biomass, the differences between stations were not very marked and values were only marginally correlated with chlorophyll a concentrations. Also, during the study period, large heterotrophic dinoflagellates did not show a very significant response to increases in phytoplankton standing stocks at the PFr.

Depth distribution of *Protoperidinium* spp. varied from station to station. Relatively high abundances were found at depths of 100 to 200 m in the AWB and open water of the southern ACC (252 to 820 ind. m^{-3}). In the Weddell

Gyre and PFr, higher values were found above 100 m depth. Abundances below 200 m depth were generally low although values as high as 101 ind. m^{-3} were found below 200 m depth at the AWB. Thus, contrary to the findings of Nöthig and Gowing (1991) and Alder and Boltovskoy (1993), *Protoperidinium* spp. distribution, in this study, extends deeper than that of tintinnids.

Heliozoa have rarely been studied in the Southern Ocean. Only two publications mention their distribution in the western Weddell Sea, WSC and west of the Antarctic Peninsula, in autumn and winter (Gowing, 1989; Gowing and Garrison, 1992). As in this study, the heliozoa were quite abundant under the ice, at depths of 100 to 200 m, reaching maximum values during autumn (4000 ind. m^{-3}; Gowing, 1989). During this study, their biomass varied from 0 to 6.6 µg C m^{-3} equalling and even surpassing the biomass of other large protozoa with the exception of larger (> 300 µm) phaeodaria, in the Weddell Gyre and AWB. An interesting observation of this study is the appearance of heliozoa at the PFr (st. 964) with concentrations up to 1512 ind. m^{-3}. The heliozoan *Sticholonche* spp are thought to feed at least on phytoplankton (Gowing and Garrison, 1992) but no relationship between *Sticholonche* spp. and chlorophyll a, depth or temperature was found, during this survey. Therefore, the distribution pattern of heliozoa cannot be explained by differences in phytoplankton standing stock or primary production levels. Local conditions associated perhaps with the ice in the Weddell Gyre and AWB and subantarctic influence in the PFr might be more important. In the Equatorial Pacific, Takahashi and Ling (1980) described two *Sticholonche* species in addition to *Sticholonche zanclea* . At least one of those "new" species (species A) was observed in the Southern Ocean by Gowing and Garrison (1992) and during this study. Since no attempt was made, during this study, to identify *Sticholonche* spp. to the species level, the fact that PFr individuals might belong to another species than those of the Weddell Gyre and AWB cannot be ruled out.

During this study, the distribution of polycystine radiolaria and foraminiferan biomasses and abundances followed changes in phytoplankton stocks with higher values in the PFr, from the surface to 200 m depth. Polycystine radiolaria and foraminifera also showed a significant correlation with zooplankton stocks and temperature. Boltovskoy and Alder (1992b) suggested that temperature rather than phytoplankton stocks determine polycystine distribution patterns in the Southern Ocean, with higher

abundances generally below 200 m depth associated with the warmer CDW. Since phytoplankton and zooplankton stocks and temperatures show the same trends, during this study, it is difficult to dissociate their effects on polycystine radiolaria and foraminifera distribution. However, polycystine depth distribution patterns indicates that temperature might not be determining. Spumellaria did show higher abundances at depths below 50 meters, south of the PFr, but values did not increase below 100 to 200 m depth in the CDW as observed by Boltovskoy and Alder (1992b). Also, differences in abundance and especially biomass between surface and deeper layers were not very marked. Nassellaria did not present a consistent pattern related to temperature with higher values below the AASW, as observed by Boltovskoy and Alder (1992b) in the Weddell Sea, since higher abundances and biomasses were found in surface layers in the Weddell Gyre. In the AWB and open water of the southern ACC, higher abundances were found below 50 m depth but biomasses were often higher above 200 m depth. Foraminifera were always more abundant above 200 m depth at all stations. Although temperature certainly affects polycystine and foraminiferan species and ontogenetic stages distribution (Bé, 1967; Berberich, 1996; Abelmann and Gowing, 1997) it is unlikely that this rule applies to overall polycystine and foraminiferan assemblages. Both polycystine radiolaria and foraminifera are known to feed on a wide variety of prey including phytoplankton, bacteria, other protozoa, zooplankton and probably also detritus (Anderson, 1983; Hemleben et al., 1989; Swamberg and Caron, 1991). Therefore, large-scale variations in abundance of polycystine radiolaria and foraminifera is likely to be determined by both phytoplankton and heterotrophs abundance in the water column. Also, the relatively high abundances of nassellaria in the upper 100 m of the water column in the Weddell Gyre might also be related to detritus levels in the water column as inferred by the higher POC/chlorophyll a ratios in that station (Quéguiner et al., 1997).

Winter to early spring stocks of polycystine radiolaria (the spumellaria and nassellaria) and foraminifera in the Weddell Sea are very low (Morley and Stepien, 1984; 1985; Nöthig and Gowing, 1991; Berberich, 1996). Somewhat higher winter stocks of polycystine radiolaria and foraminifera (0 to 121 m^{-3} and 0 to 187 m^{-3}, respectively; Gowing and Garrison, 1992) were found in the WSC. During spring/summer, very high biomasses and abundances of radiolaria and foraminifera (> 100 µg C m^{-3}) were found by Boltovskoy and Alder (1992b) and Alder and Boltovskoy (1993) in the WSC. Summer and autumn values for the Weddell Sea also increase significantly as compared to

the winter situation, but remain lower than in the WSC (Gowing, 1989; Boltovskoy and Alder; 1992b; Berberich, 1996). In the open water of the southern ACC and PFr, higher stocks of polycystine radiolaria were found during summer than winter values in the Weddell Sea and WSC (Morley and Stepien, 1984; 1985; Nöthig and Gowing, 1991; Gowing and Garrison, 1992; Abelmann and Gowing ,1996) but values were also lower than spring/summer abundances of the WSC (Boltovskoy and Alder, 1992b; Alder and Boltovskoy, 1993) and autumn values in the western Weddell Sea (Gowing, 1989).

During this study, in the Weddell Gyre, AWB and open water of the southern ACC, foraminifera and polycystine radiolaria stocks were higher than winter values in the Weddell Sea, WSC and west of the Antarctic Peninsula (Morley and Stepien, 1984; 1985; Gowing, 1989; Nöthig and Gowing, 1991; Gowing and Garrison, 1992, Berberich, 1996; 3 to 162 and 9 to 154 ind. m^{-3}, respectively). Spring abundances of polycystine radiolaria in the Weddell Gyre, AWB and in open water of the southern ACC were higher than summer values in the Weddell Sea (Boltovskoy and Alder, 1992b), but similar to summer abundances found in the open water of the southern ACC and PFr (Abelmann and Gowing, 1996, 21 to 335 ind. m^{-3}). During spring, foraminifera abundances in the Weddell Gyre, AWB and in open water of the southern ACC were somewhat lower than summer and autumn values found by Berberich (1996) in the coastal current of the southeastern Weddell Sea (30 to 600 ind. m^{-3}). The abundances and biomass of polycystine radiolaria and foraminifera found in the PFr, during this study, are among the highest ever recorded in the Southern Ocean, except for the spring/summer and autumn values found by Gowing (1989) and Alder and Boltovskoy (1993) in the WSC and western Weddell Sea (< 88 to 625 foraminifera m^{-3}, and 86 up to 12 10^3 polycystine m^{-3} including juveniles < 15 µm, respectively).

Polycystine and foraminiferan horizontal abundances and biomass distributions seem to show significant seasonal variation, depending on region and levels of productivity. The lowest values are always found during winter. Spring to autumn values are higher and seem to be related to productivity. In the western Weddell Sea and WSC where blooms occur during the growth season, higher stocks are found. In open water of the Weddell Gyre and southern ACC, stocks increase as compared to winter values but never reach very high numbers. In the PFr, the high productivity during spring is accompanied by a significant increase in polycystine and foraminifera stocks, but values seem to decrease in summer together with productivity to levels similar to the Weddell Gyre and open water of the southern ACC. Also, large scale abundance and biomass of foraminifera and

polycystine radiolaria seem to show distinct seasonal variations related to levels of primary and possibly secondary production.

Polycystine radiolarian abundances and biomasses showed no marked relationship with depth. In the upper 100 m of the water column in the PFr, where large phytoplankton and heterotroph standing stocks were found, polycystine radiolaria were more abundant in the upper 100 m of the water column. South of the PFr, the spumellaria were slightly more abundant below 50 m depth. The nassellaria showed the same distribution pattern except at the station in the Weddell Gyre where they were more abundant at the surface. The depth distribution pattern of polycystine radiolaria in this study is consistent with observations of Abelmann and Gowing (1996) in summer, who found peaks in abundance at the surface as well as in deeper layers depending on station. Abelmann and Gowing (1996) also observed relatively high abundances extending below 1000 m depth. Polycystine radiolaria, therefore, seem to colonise the whole of the water column with higher numbers above 500 m depth. As during previous studies, foraminifera were always more abundant in the upper 200 m of the water column (Alder and Bolstovskoy, 1993; Nöthig and Gowing,1991; Berberich, 1996) although relatively high abundances were also found in the 200 to 500 m depth layer.

Abundance and biomass of smaller (< 300 µm) phaeodaria, during this study, followed the same latitudinal pattern as the nassellaria. Highest values were found in the PFr followed by the station in the Weddell Gyre. Lowest abundance and biomass were found in the AWB and open water of the southern ACC. The biomass of smaller (< 300 µm) phaeodaria showed, however, no correlation with either phytoplankton or zooplankton and was marginally correlated with depth and temperature. As observations of Gowing (1989) have shown, smaller (< 300 µm) phaeodarian abundances or biomasses were higher at the ice-covered station in the Weddell Gyre and AWB than the open water of the southern ACC; however, higher phaeodarian abundances at ice-covered areas does not always seem to be the rule (Gowing and Garisson, 1991, Gowing and Garrison, 1992).

The highest abundance of smaller (< 300 µm) phaeodaria in the Southern Ocean were found during summer, in the open water of the southern ACC, by Abelmann and Gowing (1996; range 253 to 19052 ind. m^{-3}). The lowest abundances were found In the Weddell Sea during winter (from a few to 200 ind. m^{-3}, Morley and Stepien, 1984 and 1985; Nöthig and Gowing, 1991) and

in the PFr during summer (1 to 150 ind. m^3; Abelmann and Gowing, 1996). Higher values were found in the western Weddell Sea by Gowing (1989) during autumn and in the WSC, and west of the Antarctic Peninsula during winter (30 to 3000 ind. m^{-3}; Gowing, 1989; Gowing and Garrison, 1991; Gowing and Garrison, 1992). During spring in the WSC, smaller (< 300 µm) phaeodarian concentrations seem to be similar to winter values with average abundances of 400 ind. m^{-3} in ice-free water and 800 ind. m^{-3} in ice-covered water (Boltovskoy and Alder, 1992b).
The phaeodaria abundances and biomasses found during this study, in the Weddell Gyre, AWB and open water of the southern ACC are higher than winter values in the Weddell Sea but close to the minimum abundances present at all seasons in the WSC and in the southern ACC, during summer. In the PFr, spring stocks were higher than those found during summer in the same region (Abelmann and Gowing, 1996), but abundances were also not higher than those found in the WSC at all seasons and in the open water of the southern ACC during summer.

These results indicate that smaller (< 300 µm) phaeodaria show very different seasonal patterns depending on region. In the WSC, no clear seasonal trend could be found, from the literature data. In the Weddell Gyre, values seem to increase from winter to autumn, however, to my knowledge, no summer data is available for that area. In the southern ACC, very high abundances and biomasses are found in summer as compared to the spring situation, although levels of primary production seem to remain low in that area (Laubscher et al., 1993). The PFr seems to show earlier maxima than the Weddell Sea and open water of the southern ACC with the higher values during spring bloom events (this study). Also, smaller (< 300 µm) phaeodarian abundance and biomass seem to be primarily determined by local conditions and are not necessarily coupled to primary production. The distribution pattern along transect 11 confirms this. The wide range of food consumed by smaller (< 300 µm) phaeodarian radiolaria (Gowing, 1989, Nöthig and Gowing, 1991; Gowing and Garrison, 1992) might explain the high abundances found during summer in the southern ACC and during periods of low productivity in the WSC (Gowing, 1989).

Smaller (< 300 µm) phaeodaria were more abundant at the surface, in the Weddell Gyre, below 200 m depth, in the AWB and open water of the southern ACC, and between 50 and 200 m depth in the PFr, respectively. Thus, no distinct pattern was observed in the vertical zonation of smaller (< 300 µm)

phaeodaria. This confirms the findings of Gowing (1989) and Abelmann and Gowing (1996) that smaller (< 300 µm) phaeodaria have variable depth distributions possibly changing according to geographical location, season or assemblage composition. Also, smaller (< 300 µm) phaeodaria, like spumellarian and nassellarian radiolaria, show relatively high abundances below 200 m depth extending down to depths below 1000 m (Abelmann and Gowing 1996)

During this study, larger (> 300 µm) phaeodarian abundances and biomasses were significantly higher in the ice-covered stations of the Weddell Gyre and AWB and correlated with salinity, depth and silica concentrations. It is, at present, impossible to know whether ice, depth, silica or water mass is the most significant factor determining their distribution pattern in spring. In contrast to this study, Nöthig and Gowing (1991) found higher larger (> 400 µm) phaeodarian abundances in surface layers (above 250 m depth). Thus depth distribution possibly varies with season. The strong relationship between larger (> 300 µm) phaeodarian distribution and silica concentrations found during this study has never been mentioned in earlier studies. Although the silica concentrations in the oceans has never, to my knowledge, been proposed to explain distribution patterns of modern larger phaeodaria, north of the PFr, larger (> 300 µm) phaeodaria seem to be found mainly in deeper layers and primarily associated with upwelling areas (Meyer, 1934). Given their large size (up to 2 mm in diameter) and impressive skeletal architecture, an influence of silica on their distribution cannot be ruled out.
The abundance and biomass of larger phaeodaria (> 300 µm) found during this study is comparable to winter values found by Nöthig and Gowing (1991) in the Weddell Sea and much higher than autumn values from the western Weddell Sea (Gowing, 1989). No other reports exists on abundance and biomass of larger (> 300 µm) phaeodaria in the southern Ocean. These few studies indicate that, although regional variability exist in the distribution pattern of larger (> 300 µm) phaeodaria, phytoplankton stocks and primary production are not determining factors. This is consistent with the wide diversity of prey consumed by these organisms (Gowing, 1989; Nöthig and Gowing, 1991).

In the upper 100 m of the water column, total net protozoan biomass varied from 14 to 396 µg C m^{-3}. In this layer, net (> 64 µm) protozoa represented a negligible fraction of total microprotozoan and zooplankton stocks found during transect 11 (Scharek pers. comm., Fransz and González, 1997). In the

100 to 200 m and 200 to 500 m depth layers, net protozoan biomass was relatively high representing respectively 0.3 to 7 % and 1 to 40% of total protozoan plus metazoan biomass larger than 64μm. The highest proportion of net protozoa in these deeper layers was found in the Weddell Gyre and AWB and the lowest at stations in the PFr. Thus, net protozoa, especially the larger (> 300 μm) phaeodaria which dominated the biomass below 200 m, are an important component of deep water layer assemblages in the southernmost stations of transect 11. Although feeding and metabolic rates of larger (> 300 μm) phaeodaria have never been investigated, these results indicate that they might have an important influence on processes occurring below the euphotic zone during spring in the ice-covered areas of the Weddell Gyre and AWB. This seems true also in the surface water of the Weddell Sea in winter (Nöthig and Gowing, 1991).

4.2 Factors influencing protozoan assemblage composition during ANT X/6.

Microprotozoan composition

The first principal component axis and the cluster analysis separates the stations in the PFr from ice-covered and open water stations of the southern ACC and AWB. Characteristic of PFr stations are higher temperatures and lower nutrient concentrations associated with high diatom stocks and primary production. Stations in the PFr are also characterised by higher tintinnid, flagellate and dinoflagellate standing stocks. Despite the differences in abiotic conditions and phytoplankton assemblages composition between the open water of the southern ACC and the PFr, dinoflagellate assemblages composition, at the genus level, showed no marked differences between these two regions. Although most dinoflagellates were not identified to the species level, the distribution pattern of the few species that could be determined indicated that differences between the regions investigated should exist. Thus, the similarity observed between dinoflagellate assemblages in open water of the southern ACC and the PFr might be superficial and possibly due to the taxonomic level at which dinoflagellates were identified. However, the dinoflagellate assemblage composition (at genus level) found in the open water of the southern ACC and PFr might also be characteristic of the spring situation in open water of the Southern Ocean.

The ciliate assemblage showed marked differences between stations in the PFr and south of it, due to the important contribution of tintinnids from 51°S northward. The importance of tintinnids in the ciliate assemblage of the PFr is quite unusual when compared to other oceanic areas, generally dominated by aloricate choreotrichs (Beers et al., 1982; Sorokin et al., 1985; Booth et al., 1993; Burkill et al., 1993; Strom et al., 1993). Only Froneman and Perissinotto (1996), who studied microprotozoan assemblages in the Subtropical Convergence during winter, reported relatively high tintinnid abundances in an oceanic region. In open water of the Southern Ocean, higher tintinnid stocks than those found in the PFr have been reported around the WSC in summer and autumn (von Bröckel, 1981; Boltovskoy et al., 1989; Garrison and Buck, 1989; Boltovskoy and Alder, 1992a; Alder and Boltovskoy, 1993). Spring stocks of tintinnids in the WSC and the Bellingshausen Sea were, however, lower than in the PFr (Garrison and Buck, 1989; Alder and Boltovskoy, 1992; Alder and Boltovskoy, 1993; Kivi and Kuosa, 1994) except for two stations in the Bellingshausen Sea (Burkill et al., 1995) where very high peaks in chlorophyll (> 2 $\mu g\ l^{-1}$) and microzooplankton biomass (> 40 μg C l^{-1}) were encountered. Tintinnids, however, never contributed significantly to total ciliate biomass. Therefore, tintinnid stocks higher than the values found in the PFr, are generally found during the whole productive period close to coastal sites (Boltovskoy and Alder 1992a; Leakey et al., 1994; Priddle et al., 1995) and in open water but later in the growth season. Also, the importance of tintinnids in the ciliate assemblage in the PFr in spring seems unusual. It should be pointed out that PFr water exhibited high iron concentrations which de Baar et al. (1995) attributed to input from shelf sediments from South America or the Falkland Islands. Thus, a neritic influence cannot be ruled out. Furthermore, the occurrence of subantarctic *Codonellopsis* species with loricas aggregated with coccolithophorids in the tintinnid assemblage suggests that advection of northern water (Veth et al, 1997) influence composition of the protozoan assemblage and might introduce protozoan communities that had matured earlier then in the southern ACC and AWB. The importance of tintinnids in the ciliate assemblage of the PFr is also emphasised by the low aloricate choreotrich stocks. Therefore, it seems that local conditions in the PFr superimposed on advection, favours tintinnids and flagellates (including dinoflagellates) growth as compared to aloricate choreotrich ciliates. A likely cause might be selective grazing by copepods (see Discussion section 4.1)

Numerous studies on protozoan growth rates have shown that aloricate choreotrich ciliate growth rates are similar to those of tintinnids, but somewhat higher than those of dinoflagellates (Capriulo et al., 1991; Strom, 1991; Hansen, 1992; Buskey et al., 1994; Montagnes, 1996). Standing stocks of phytoplankton were higher in the PFr but the bulk of the biomass consisted of the colonial pennate diatom species *Thalassionema nitzschioides* and *Fragilariopsis kerguelensis* (Bathmann et al., 1997; Becquevort, 1997; Detmer and Bathmann, 1997). Observation of live plankton material from net samples taken during the cruise indicated that these diatoms built up very long chains. The size of prey consumed by choreotrich ciliates does not generally exceed 45% of their oral diameter (Splitter, 1973, Heinbokel, 1978b; Johnsson, 1986). Therefore, it is likely that long diatom chains would have been difficult to tackle for these ciliates. Thus, phytoplankton composition in the PFr might also have favoured growth of dinoflagellates rather than ciliates.

The second principal component axis and cluster analysis revealed marked differences in the dinoflagellate and ciliate assemblage between the ice edge and AWB, and open water of the southern ACC. The differences were marked by the importance of ice-dwelling ciliates (holotrich ciliates; Fenchel and Lee, 1972; Garrison and Close, 1993; Stoecker et al., 1993; Petz et al., 1995) and two species of *Protoperidinium* (*P. defectum* and *P. applanatum*) at ice-covered stations and the relatively higher stocks of aloricate choreotrichs, *Didinium* sp. and *Amphidinium* spp. in the open water of the southern ACC. Since fixation methods used for these two group of stations differed (formaline and lugol's iodine, respectively), one cannot rule out that differences between the ice edge and AWB and the open water of the southern ACC are an artefact due to the fixation methods (Choi and Stoecker, 1989; Ohman and Snyder, 1991; Leakey et al., 1994). In experiments comparing the effect of different preservatives on cell densities and volumes of choreotrich ciliates, Ohman and Snyder (1991) found that formaline caused less losses of cells upon fixation than alkaline (or neutral) lugol's iodine. However, changes in volume of cells were similar for both fixatives. These effects would rather lead to an underestimation of the choreotrich ciliate biomass in the open water of the southern ACC as compared to the AWB and ice edge. The influence of ice cover would then have a twofold effect. As the correlation analysis shows, the effect of ice in decreasing light levels and, thus, phytoplankton production in the water column, is the most likely factor determining the distribution of aloricate choreotrichs. Additionally and independently, sea ice has a significant influence on water column assemblages by introducing typical ice-

dwelling organisms, as evidenced by the increase in the contribution of holotrich ciliates with increasing ice cover during transect 1. Although no significant influence of salinity on microprotozoan assemblages was found during this study, melting of ice must have contributed to introducing ice dwelling organisms in the water column as inferred from the lower salinities found in surface water of the ice-edge stations from transect 1.
To my knowledge only two studies exist on description of dinoflagellate species distribution in relation to environmental parameters: Dodge and Priddle (1987) and McKenzie and Cox (1991). Both studies recorded the presence of *Protoperidinium applanatum*, associated with the sea-ice edge (McKenzie and Cox, 1991), but *P. defectum* is not mentioned, probably because it passes through the sampling nets. *Protoperidinium* species have been described in land-fast ice (Archer et al., 1996a) but never in sea ice (Garrison and Close, 1993; Kivi and Kuosa, 1994). Both species also constituted the entire armoured dinoflagellate assemblage at the ice edge of transect 5, although their biomass was much lower than during transect 1. There is evidence, therefore, that neither species is seeded from ice but they might constitute an early stage of seasonal succession in the water column.

An interesting result of the principal component analysis is the similarity between the ice-covered stations and the PFr relative to the second axis. This similarity is due to comparable stocks of holotrich ciliates, *Amphidinium* spp. and armoured dinoflagellates. For the last group, only *P. defectum* was found in the PFr but other species were much more abundant. Choreotrich ciliates have the most efficient mechanism for filtering high water volumes and are perfectly adapted to the pelagic environment (Fenchel, 1986; Fenchel, 1987). Holotrich ciliates have much lower specific clearance rates (Fenchel, 1986) and have to rely on higher food concentrations such as found in sediments or sea ice. The relatively high stocks of holotrich ciliates in the PFr is therefore surprising. Relatively high stocks of holotrich ciliates have also been found by Burkill et al. (1995) in open water of the Bellingshausen Sea at stations with very high phytoplankton stocks. The higher phytoplankton concentrations in the PFr might, therefore, sustain those populations in the water column.

Another interesting finding is the importance in the Southern Ocean of the ocellus-bearing unarmoured dinoflagellates belonging to the Warnowiaceae group. High abundances of this group have, to my knowledge, only been reported in the Arctic (Elbrächter, 1991b). Heterotrophic dinoflagellates of the family Warnowiaceae are widely distributed in the world's oceans but never

reach great numbers. The fact that this group, that bears a large conspicuous ocellus, contributed substantially to dinoflagellate biomass throughout the transect needs to be stressed. Little is known about the biology of these organisms and three species at least are reported to feed phagotrophically (Elbrächter, 1991a, 1991b; Hansen, 1991b). This group was not found at stations of transect 1, but a different fixative was used for the samples in this transect (formaline). Since protozoa are often more sensitive to formalin, which tends to cause bursting of cells or shape distortions and pigment bleaching, dinoflagellates belonging to the Warnowiaceae might have been overlooked during transect 1.

Net (> 64 µm) protozoan assemblage composition

The integrated abundance of net protozoa (> 64 µm) showed marked changes in assemblage composition from the Weddell Gyre to the PFr. Three distinct groups of stations could be ascertained, corresponding to the different regions investigated: stations 930 and 934 in the Weddell Gyre and AWB, stations 947 and 953 in the open water of the southern ACC and finally stations 956 and 964 in the PFr.

The integrated net protozoan assemblage composition, in terms of biomass, did not show very significant differences between different regions since larger (> 300 µm) phaeodarian radiolaria dominated at all stations. However, when the different depth intervals between 0 and 200 m depth are examined separately, distinct differences between stations and depth interval are evident. The stations in the Weddell Gyre and AWB differed significantly from each other and from stations in the southern ACC and PFr. Characteristic of the stations in the Weddell Gyre and AWB is the difference between net protozoan assemblages in the uppermost layer (0-25 m) and deeper layers (25 to 200 m depth). Since biological parameters and water mass characteristics were uniform down to about 100 m depth (Bathmann et al., 1997; Detmer and Bathmann, 1997; Fransz and González; 1997; Lochte et al., 1997; Veth et al., 1997), it is likely that the observed differences are due to sea ice influence. This is confirmed by the importance of non-spinose foraminifera the uppermost layer (0 to 25 m depth), in the Weddell Gyre, which might have been released from the sea ice where they seem to concentrate during winter (Dieckmann et al., 1991; Berberich, 1996). The station in the Weddell Gyre showed an uniform assemblage composition between 25 and 100 m depth and between 100 and 500 m depth. These two depth intervals correspond to different water masses, the AASW and the CDW, respectively (Veth et al.,

1997), marked by differences both in biotic and abiotic parameters (Bathmann et al., 1997; Detmer and Bathmann, 1997; Fransz and González; 1997; Lochte et al., 1997; Veth et al., 1997). In the AWB, all depth intervals showed different assemblage composition and the composition of the net protozoan assemblage in the AWB was different to observations from all the other stations of transect 11 except for the uppermost layer (0 to 25 m). Larger (> 300 µm) phaeodaria which tend to dominate biomass below 100 to 200 m depth constituted an important fraction of biomass in the 25 to 50 m depth layer. Tintinnid biomass was significant at the surface and then again between 50 and 100 m depth. *Protoperidinium* spp. dominated at the surface and then between 100 and 200 m depth. These differences are likely to be related to hydrodynamic processes in this divergence area, such as interleaving of water masses as inferred by the presence of sharp discontinuities in the physical characteristics in the upper 200 m of the water column (Veth et al., 1997). Net protozoan assemblage at stations in the southern ACC were significantly different from stations in the Weddell Gyre, AWB and PFr, although differences with the latter region were less marked. The two stations in the southern ACC also differed significantly from each other but again, differences were less marked than with stations in the Weddell Gyre and AWB. Characteristic of the stations north of the AWB is the importance of foraminifera above 200 m depth. Also, the influence of subantarctic water is evidenced by the increasing importance of spinose foraminifera (Hemleben et al., 1989) between the southernmost station in the southern ACC and the northernmost station in the PFr. At the southernmost station in the southern ACC, the net protozoan assemblage was uniform from the surface down to 200 m depth. At the northernmost station in the southern ACC, vertical zonation was more marked with four main layers: 0 to 50 m depth, 50 to 100 m depth and 100 to 200 m depth. Net protozoan assemblages at the two stations in the PFr were similar showing a vertical zonation with two depth layers: 0 to 50 m depth, 50 to 200 m depth. The vertical zonation of net protozoa observed during transect 11, in the southern ACC and PFr, is consistent with vertical zonation of both physical and biological parameters (Bathmann et al., 1997; Detmer and Bathmann, 1997; Fransz and González; 1997; Lochte et al., 1997; Veth et al., 1997). Below 200 m depth, in the CDW, no significant differences in the biomass composition of net protozoan assemblages were observed during the whole transect and biomass was always dominated by larger phaeodaria. In terms of abundance, the composition of net protozoan assemblages was similar to the assemblages found at the same stations

between 100 and 200 m depth, although the contribution of smaller (> 300 µm) phaeodaria was generally higher.

Thus, net protozoan assemblage composition is influenced by the presence of ice cover and follows changes in biological and physical parameters in the water column associated with different depth intervals and water masses. Since all environmental parameters are interlinked, it is difficult to separate biological effects from physico-chemical properties of the water masses and depth.

Among the factors affecting protozoan assemblage composition depth has been shown to have a marked effect both at species and group levels (Tibbs and Tibbs, 1986; Gowing, 1989; Gowing and Garrison, 1991; Nöthig and Gowing, 1991). This study and the observations of Gowing (1989) and Gowing and Garrison (1992) indicate that *Sticholonche* spp. contribute significantly to net protozoan assemblages at depths between 50 and 100 m, corresponding to the base of the euphotic zone. This pattern seems to be invariant with region, season, temperature, salinity and biological parameters (Gowing, 1989; Gowing and Garrison; 1992; this study). It should be, however, noted that the contribution of *Sticholonche* spp. to the net protozoan assemblage was less important in terms of biomass than for abundances. Tintinnid contribution to the total net protozoan assemblage was significant in the upper 100 m of the water column but tended to be higher below 25 m depth. A tendency towards higher tintinnid contribution to microprotozoan biomass in the lower part of the euphotic zone has been observed in previous studies (Boltovskoy and Alder, 1992a; Alder and Boltovskoy, 1993), however, this pattern seems to be variable depending on station and phytoplankton stocks in the water column (Boltovskoy et al., 1989; Gowing and Garrison, 1991; Boltovskoy and Alder, 1992a; Alder and Boltovskoy, 1993). During this study, *Protoperidinium* spp., foraminifera, nassellaria, spumellaria, and smaller (< 300 µm) phaodaria did not show any pattern related to depth and contributed significantly to net protozoan assemblage from the surface down to 500 m depth in terms of abundance, and down to 200 m depth in terms of biomass, depending on station (see also Discussion section 4.1; Gowing and Garrison, 1991; Gowing and Garrison, 1992). Larger (> 300 µm) phaeodarian biomass was significant mainly below 200 m depth during this study but not during winter in the Weddell Sea and WSC (Nöthig and Gowing, 1991; Gowing and Garrison, 1992).

Water mass characteristic (temperature and salinity) are known to affect species distribution of protozoa (Anderson, 1983; Dodge and Priddle, 1987; Hemleben et al., 1989; McKenzie and Cox, 1991; Boltovskoy and Alder, 1992a; Abelmann and Gowing, 1997). At group level, latitudinal shifts in large protozoan assemblage associated to water mass characteristic have also been observed for the radiolaria, with an increasing importance of the phaeodarian radiolaria at high latitudes in the northern hemisphere (Bernstein et al., 1990); this pattern has been related to the influence of temperature on polycystine radiolaria distribution (Boltovskoy and Alder; 1992b). During this study, nassellarian contribution to net protozoan abundances did not differ significantly from the phaeodaria both in the Weddell Gyre and AWB and in the PFr. In terms of biomass, nassellaria, spumellaria and phaeodaria contributed equally to total protozoan stocks independent of depth during all stations of transect 11 except in the Weddell Gyre where spumellarian contribution was markedly lower. In most studies done south of the PFr, phaeodaria, however, tended to dominate the radiolarian assemblage (Gowing, 1989; Nöthig and Gowing, 1991; Gowing and Garrison, 1991; Gowing and Garrison, 1992). However, this does not seem to be the case in the open water of the southern ACC, PFr and subantarctic water (Abelmann and Gowing, 1996; this study). Thus, although phaeodaria can built up much higher stocks than polycystine radiolaria south of the Polar Front (see Discussion section 4.1; Abelmann and Gowing, 1996) their relative contribution to net protozoan assemblage composition depends on season rather than on the physical properties of the water column. Additionally no latitudinal gradient seems to exist as observed in the Northern Hemisphere (Bernstein et al., 1990). Although overall net protozoan assemblage in the different regions investigated during transect 11 showed significant differences related to water mass, the assemblages found differed from studies done in the same water masses in other regions and seasons (Gowing, 1989; Nöthig and Gowing, 1991; Gowing and Garrison 1991; Gowing and Garrison, 1992; Abelmann and Gowing, 1996).

During this study, larger radiolaria (> 300 µm) which dominated the assemblage biomass below 200 m depth, did not follow changes in productivity, phytoplankton and heterotrophic standing stocks and sinking fluxes (Bathmann et al., 1997; Detmer and Bathmann, 1997; Fransz and González; 1997; Lochte et al., 1997; Rutgers van der Loeff et al., 1997; Veth et al., 1997). Also, in terms of biomass, the deep net protozoan assemblage did not show any relationship to biological parameters in the water column. In

terms of abundance significant changes in assemblage composition were observed between stations along transect 11, below 200 m depth. Smaller (< 300 μm) phaeodaria always contributed significantly to total assemblage, as for other net protozoan groups their contribution followed more or less the same pattern as in the upper layers sampled (0 to 200 m). In the upper layers (0 to 200 m) the changes in productivity, phytoplankton and heterotrophic standing stocks (Bathmann et al., 1997; Detmer and Bathmann, 1997; Fransz and González; 1997; Lochte et al., 1997; Veth et al., 1997) seem to have primarily favoured the foraminifera, tintinnids and *Protoperidinium* spp. in the southern ACC and foraminifera and radiolaria in the PFr. The increase in importance of tintinnids and *Protoperidinium* spp. in the open water of the southern ACC is easily understood considering the differences in their generation times as compared to sarcodines. Generation times of radiolaria and foraminifera are thought to be in the order of months (Anderson, 1983; Hemleben et al., 1989) whereas tintinnids and *Protoperidinium* spp. should have generation times of about a week (see Results section 3.3). Also, the importance of foraminifera in the southern ACC and foraminifera and radiolaria in the PFr is quite intriguing. Furthermore, in the PFr, the blooms developed from chlorophyll a levels of 0.7 μg. l^{-1} in mid-October to > 2.0 μg. l^{-1} over a period of 34 days (Bathmann et al., 1997). This is a rather short period compared to the generation time of radiolaria and foraminifera. Therefore, the changes in composition between stations in the southern ACC and PFr would logically tend to boost dinoflagellate and tintinnid contributions to net phytoplankton but not those of foraminifera and radiolaria. Also it is likely that the composition of the larger protozoan assemblage in the southern ACC and PFr is also influenced by subantarctic water as evidenced by the northward gradient in spinose foraminifera abundance, and possibly grazing by large zooplankton.

4.3 Experimental results on growth and grazing rates of *P. cf. pellucidum* and field estimates of microprotozoan grazing rates

The maximum specific growth rates of *P. cf. pellucidum* , assuming a Q_{10} of 2, are 0.54 and 0.34 d^{-1} at 20°C, for experiment 1 and 2, respectively. These rates are somewhat lower than the estimates of Buskey et al. (1994) for *P. huberi*, of similar volume, but similar to the growth rates found by Hansen (1992) for the slightly smaller *Gyrodinium spirale*. Archer et al. (1996b) found similar growth rates for different dinoflagellate species near Davis station in

Antarctica during conditions of very high phytoplankton stocks and productivity. Thus, the growth and grazing rates of *P. cf. pellucidum* found during this study should be representative for Antarctic microdinoflagellates. However, both food quality (Strom and Buskey, 1993; Buskey et al., 1994) and experimental conditions (this study) have an important influence on growth rate estimates. Since the experiments with *P. cf. pellucidum* were done using only one diatom species, these results do not represent either minimum or maximum growth capacities for Antarctic dinoflagellates. The results on growth and grazing rates found during this study and by Bjørnsen and Kuparinen (1991) indicate that, like for ciliates (Lee and Fenchel, 1972), the extrapolation using the Q_{10} relationship should give an accurate estimate of dinoflagellate maximal specific growth rates for the cold water of the Southern Ocean. Also, when compared to the study of Bjørnsen and Kuparinen (1991), my results suggest that protozoan metabolic rates at low temperature should be also size dependent (Hansen, 1992; Fenchel and Finlay, 1983; Archer et al., 1996b).

Low temperatures can affect feeding and growth of protozoa by slowing the rates of biochemical processes, decreasing maintenance costs and thus enhancing Gross Growth Efficiency (Choi and Peters, 1992). Higher seawater viscosity at low temperature can affect feeding performance mechanically by decreasing the swimming speed, increasing the costs of motility and decreasing prey detection (Podolsky, 1994). This can change feeding kinetics as a function of food concentration by decreasing maximum clearance rates, increasing threshold levels and the level at which feeding saturates and decreasing the Gross Growth Efficiency (GGE). The GGE calculated for *P. cf. pellucidum* is higher than values found for most flagellate species grown between 12 and 20°C (Fenchel, 1982a; Geider and Leadbeater, 1988; Strom,1991; Hansen, 1992; Nakamura et al., 1992; Strom and Buskey, 1993). The accuracy of the GGE values depends on the estimates of carbon content of food and grazers. In this study, estimates have been done by converting volume (calculated with light microscope measurements) to biomass with conversion factors taken from the literature. Therefore, although it is likely that absolute values are inaccurate, they can still be compared to other studies since the method and conversion factors used are similar to those of most studies of dinoflagellate feeding behaviour.
The GGE found during this study are higher than those found for temperate dinoflagellates (Strom,1991; Hansen, 1992; Nakamura et al., 1992; Strom and Buskey, 1993; Buskey et al., 1994). Positive growth rates were found at

very low food concentrations indicating very low or no threshold concentration. Additionally, when starved, *P. cf. pellucidum* can survive for longer periods than temperate flagellates and ciliate species (Fenchel, 1982b; Hansen, 1992; Montagnes, 1996).

Thus, contrary to the observations of Podolsky (1994), lower temperatures do not seem to significantly affect feeding kinetics. These results are consistent with the findings of Choi and Peters (1992) suggesting that metabolic costs decrease with temperature. Costs of ciliary or flagellar motion in protozoa should be negligible as compared to overall metabolic costs, except in situations of starvation (Fenchel, 1987). Thus, mechanical and metabolic effects of low temperature should affect protozoan energetics mainly under conditions of low food concentration. This study shows that low temperatures increase survival time of *P. cf. pellucidum* under starvation conditions. Therefore, it seems that the gain in gross growth efficiency at low temperatures (Choi and Peters, 1992) seems to largely compensate viscosity effects found by Podolsky (1994), unless higher costs of motility are compensated by changes in behaviour, such as decreasing swimming speed.

Microprotozoan grazing impact

Grazing rates of the whole microprotozoan assemblage on daily primary production (PP) during transect 1 and transect 5, calculated using the functional response found by Bjørnsen and Kuparinen (1991) varied from 6 to 36 % of PP grazed d^{-1}. The grazing rate estimates calculated using the functional response of *P. cf. pellucidum* (this study) were lower, varying from 3 to 12 % of PP grazed d^{-1}. The study of Bjørnsen and Kuparinen (1991) was carried out with a heterotrophic nanodinoflagellate 6-7 μm ESD (Equivalent spherical Diameter). Given the dependence of protozoan growth rates on size (Fenchel and Finlay, 1983; Hansen, 1992, Archer et al., 1996b). It is likely that using the values of Bjørnsen and Kuparinen (1991) leads to an overestimation of microprotozoan grazing rates. The functional response found in this study is from a relatively large dinoflagellate (> 40 μm) and probably underestimates grazing of the smaller size fraction (20 to 40 μm) of microprotozoa.

Both sets of values show the same trend with lowest grazing impact in ice-covered areas, where both phytoplankton and protozoan stocks were lower. In the southern ACC and PFr grazing impact varied significantly between stations but not between these two regions. The higher biomass of copepods in the PFr (Fransz and González, 1997) should lead to increased grazing on

microprotozoa, thus, it is also likely that their grazing rates are higher than the estimates based on their standing stocks in that region.

Microprotozoan grazing on microphytoplankton (diatoms mainly) calculated for transect 5 varied between 7 and 38 % of daily production. These estimates follow the same trend as the grazing impact on total primary production, with lower values in the ice-covered AWB and southern ACC and higher values in the open water of the southern ACC and PFr. Also, higher impact should occur in the PFr due to underestimations related to zooplankton grazing on microprotozoa. The grazing rates on different size classes of phytoplankton also indicates that the smaller fraction (20 to 40 μm) of microphytoplankton is grazed more heavily. These results are consistent with the size composition and distribution pattern of empty diatom frustules (see Results section 3.1.5).

The microprotozoan grazing rates calculated in this study agree with estimates by Archer et al. (1996b) near Davis station in East Antarctica, during summer, but are much lower than measurements from Burkill et al. (1995) in the Bellingshausen Sea. Burkill et al. (1995) used the dilution method (Landry and Hassett, 1982) in order to estimate grazing impact. Also, grazing rates measured by this method correspond to the grazing impact of the whole protozoan community and the smaller metazoa. During ANT X/6 nanoprotozoa grazing impact was, at times, higher than microprotozoa with values varying from 2 to 144 % of primary production grazed daily (Becquevort, 1997). These values added to microprotozoan grazing rates estimated during this study give estimates close to the values found by Burkill et al. (1995).

The functional responses found by Bjørnsen and Kuparinen (1991) and in this study indicate that protozoa in the AWB, southern ACC and PFr are growing and grazing at rates well below their maximum capacities, since saturation food concentrations lie around 300 μg C l^{-1} (Bjørnsen and Kuparinen, 1991; this study). Also, microprotozoan growth and grazing are "food limited". In the open water of the southern ACC and in ice-covered areas, where both phytoplankton and protozoan stocks remain low during the whole growth season (Laubscher et al., 1993), it is unlikely that microprotozoa can control microphytoplankton and thus diatom production. Indeed, for microphytoplankton biomasses in the order of 5 μg C l^{-1}, corresponding to the values found in the open water of the southern ACC (values in ice-covered areas are somewhat lower), microprotozoa should constitute over 80 % of

total microprotist biomass in order to graze all of the microphytoplankton production (assuming a phytoplankton specific growth rate of 0.3 d^{-1}, Fig. 29). This, assuming that microprotozoa only graze microphytoplankton. In the PFr, however, where both phytoplankton and protozoan stocks increased after transect 5 (Bathmann et al., 1997; Detmer and Bathmann, 1997; Scharek, pers. com.), grazing impact of microprotozoa should increase (Fig. 29). Also, microprotozoa could potentially control phytoplankton production in the PFr later in the season.

The results also indicate that, during winter, since overall phytoplankton growth rates are lower and microprotozoa can constitute up to 90 % of microphytoplankton biomass (Scharek et al., 1994), microprotozoa could graze all of the primary production due to the diatoms.

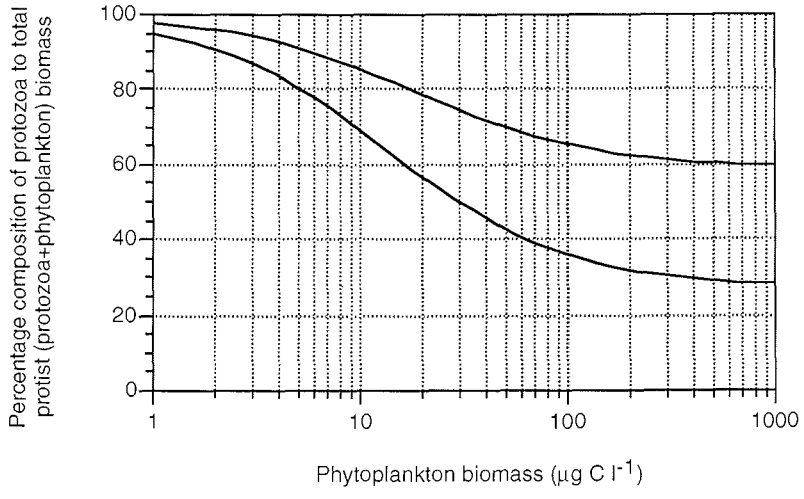

Figure 29. Relative abundance of protozoa, in % of phytoplankton + protozoan biomass as a function of phytoplankton biomass, necessary to graze 100 % of primary production assuming a phytoplankton specific growth rate of 0.3 d^{-1}. Upper curve was calculated using the functional response of *P. cf. pellucidum* found in this study. Lower curve was calculated using the functional response of Bjørnsen and Kuparinen (1991) for a small *Gymnodinium* species.

Grazing impact by nanoprotozoa measured by Becquevort (1997) during transect 5 give values below 50 % of the primary production grazed d^{-1}. These results, combined to the microprotozoan grazing rates calculated during this study, indicate that, although protozoa are major grazers in the ice-covered AWB and southern ACC as well as in open water of the southern ACC, other loss terms such as zooplankton grazing (Dubischar and

Bathmann, 1997) or sedimentation are necessary to account for the constant phytoplankton biomasses found both in the ice-covered areas of the Weddell Gyre, AWB and southern ACC as well as in open water of the Southern ACC.

The grazing rates of microprotozoa on the different groups and size fractions of the protist assemblage indicate that, given no selective feeding behaviour, microprotozoa should have a significant grazing impact both on diatoms and possibly on the heterotrophic assemblage too. Grazing estimates were calculated assuming that food items were eaten proportionally to their contribution to total biomass, however, most of the abundant diatoms in the PFr were chain forming species. This factor was not taken into consideration in the size classification since chains were badly preserved. Although several dinoflagellates have been reported to feed also on diatom chains (Jacobson and Anderson, 1986; Strom and Strom, 1996), some protozoa (especially the choreotrich ciliates which preferentially feed on particle smaller than their oral diameter) might not feed at all on those chains. Additionally, selective feeding behaviour seems to be a rule for most microprotozoa (Stoecker et al., 1981; Verity et al., 1986; Verity, 1991). Thus, factors such as selectivity might be significant in determining grazing impact of microprotozoa on diatom production. Therefore, microprotozoan feeding behaviour, microprotozoan and phytoplankton assemblage composition are important factors determining grazing impact of microprotozoa on the diatom assemblage. It should be also noted that Schnepf et al. (1990) and Kühn (1995) showed that nanoplanktonic flagellates and dinoflagellates can also feed on large diatoms. With our present knowledge on protozoan feeding behaviour, it is impossible to conclude whether the grazing impact of microprotozoa on diatom production calculated for transect 5 is under- or overestimated. However, the results found in this study indicate that the overall importance of protozoan grazing on diatoms has possibly been underestimated in conceptual models of marine food webs to date.

4.4 Particle production by protozoa (> 20 µm) during ANT X/6

Faecal pellets

The olive green pellets observed in the samples were generally small and contained a matrix of amorphous material often mixed with very small debris of diatom frustules. Such pellets have been commonly seen in phaeodaria radiolaria by several authors and during this study (Gowing and Silver, 1985;

Riemann, 1989; Nöthig and Gowing, 1991; González, 1992) but could also be produced by dinoflagellates (Elbrächter, 1991b). The presence of diatom debris indicates that they originate from re ingestion of larger pellets produced by metazoa capable of crushing diatom frustules (mainly copepods and krill). These observations indicate that during spring, phaeodaria and probably dinoflagellates too are trophic generalists and may have an important role in the repackaging of detritus (Gowing and Silver, 1985; Riemann, 1989; Nöthig and Gowing, 1991; González, 1992). The other pellet type seen in the samples resembles the unarmoured dinoflagellate pellets described by Buck *et al.* (1990) and Buck and Newton (1995). Pellets containing intact *Corethron criophilum* cells described in González (1992) were also common.

During this study, faecal pellet standing stocks showed high variability between stations and a significant trend or relationship with biological parameters in the water column could not be found. Faecal pellet volume distribution showed a more coherent distribution pattern with higher pellet volume in the open water of the southern ACC and the PFr. Pellet volume was significantly related to microphytoplankton and only marginally to microprotozoan stocks. This situation is however not surprising since feeding rates are dependent on food concentration (see Results section 3.3), additionally, the correlation analysis does not take larger protozoa such as phaeodarian radiolaria and the composition of microprotozoan assemblage into consideration. Tintinnids and aloricate ciliates seem to produce faecal aggregates that disintegrate rapidly (Stoecker, 1984; Antia, 1991). Dinoflagellates and other flagellates have quite diverse feeding modes (Jacobson & Anderson, 1986; Suttle et al., 1986; Drebes, 1988; Drebes and Schnepf, 1988; Schnepf et al., 1990; Hansen, 1991a; Kühn et al., 1995) and should, therefore, produce different types of faecal material. Thus, the composition of microprotozoan assemblages should have a determining influence on pellet stock and composition in the water column.

In the southeastern Weddell Sea, Bathmann et al. (1991) found protozoan faecal pellet sedimentation rates of about 0.5 to 15 10^3 pellets m^{-2} d^{-1} at 250 m depth. During sedimentation peaks, krill faeces dominated. Protozoan pellets constituted a background sedimentation flux with less variability but contributing an important fraction of total fluxes during the periods of lower sedimentation. Nöthig and von Bodungen (1989) recorded protozoan pellet concentrations from 0 to 214 10^3 pellets m^3 in the suface water of the eastern Weddell Sea. An average of 28.5 % sedimented out per day (Nöthig and von

Bodungen, 1989) leading to protozoan pellet sedimentation rates similar to those found by Bathmann et al. (1991). Protozoan pellets constituted 6 to 85 % of the total volume of pellet flux (Nöthig and von Bodungen, 1989). During this study, in the ice-covered areas of the southern ACC and AWB, abundances of faecal pellets was comparable to those found by Nöthig and von Bodungen (1989). In the open water of the southern ACC and PFr, concentrations were one order of magnitude higher. Similar observations were made by González (1992) around the WSC. Differences in pellet stocks between Transect 11 and those found by González (1992) and Nöthig and von Bodungen (1989) might be due to the different size range of pellets counted (>10 μm, >5 μm and > 30 μm, respectively). In the present study pellets in the same size group as those counted by Nöthig and von Bodungen (1989, 20 to 40 μm) accounted for 20 to 100 % of total pellet abundance (average 70 %). These results indicate that the pellet stocks found in the southern ACC and PFr are indeed higher than values found by Nöthig and von Bodungen (1989) in the eastern Weddell Sea. Also, the vertical flux of protozoan faecal pellet sedimenting out of the water column should be at least as high in ice-covered areas than values found by Nöthig and von Bodungen (1989) and Bathmann et al. (1991) and possibly even higher in open water of the southern ACC and PFr.

In the study of Nöthig and von Bodungen (1989) protozoan pellets contributed significantly to fluxes out of the suface layers, but their numbers decreased rapidly below 100 m depth. Sometimes a second peak between 300 and 500 m depth was observed. Nöthig and von Bodungen (1989) suggest that the deep peaks might be due to local production. Nothing is known about the fate of protozoan pellets at depth but, given their smaller size, it is assumed that they are degraded faster than large pellets (Gowing and Silver, 1985). High abundance of protozoan faecal pellets at depth is generally attributed to local production and transport mechanisms associated with fast sinking marine aggregates (Gowing and Silver, 1985; Nöthig and von Bodungen, 1989; Riemann, 1989). Also it seems that although protozoan pellets contribute significantly to vertical fluxes out of the euphotic zone they are probably rapidly degraded before reaching the sediments. This seems to be confirmed by sediment trap studies in the Southern Ocean.
The sediment trap studies of Nöthig and von Bodungen (1989) and Bathmann et al. (1991) in the southeastern Weddell Sea are the only ones mentioning the importance protozoan faecal pellet contribution to vertical fluxes in the southern Ocean. Descriptions of the "transparent" faecal pellets

found in sediment trap studies by Sasaki and Hoshiai (1986) in the Kitano-seto Strait correspond well with faecal pellets produced by unarmoured dinoflagellates, containing intact, empty diatom frustules surrounded by a membrane. The term "transparent pellets" (Sasaki and Hoshiai, 1986) describes fairly well the appearance of those pellets under the light microscope. Some of the pellets described by Gersonde and Wefer (1987) in the Powell Basin also correspond to protozoan type faecal pellets. Thus, the few works mentioning a significant contribution of protozoan pellets in sediment trap collections were all done with shallow sediment traps or in shallow coastal areas except for the Powell Basin which showed very low sedimentation rates (Gersonde and Wefer, 1987). Thus, it likely that most protozoan faecal pellets are rapidly degraded below the euphotic zone and do not reach the sea floor except in shallow areas (Sasaki and Hoshiai, 1986; Buck and Newton, 1995).

Overall fluxes in oceanic areas of the Southern Ocean are dominated by faecal pellets produced by large zooplankton (Gersonde and Wefer, 1987; von Bodungen et al., 1987; von Bodungen et al., 1988; Fischer et al., 1988, Bathmann et al., 1991). Protozoan faecal pellets seem to contribute significantly to overall vertical fluxes out of the water column in areas where larger zooplankton (mainly euphausiids) stocks are low and so also vertical fluxes (Nöthig and von Bodungen, 1989; Bathmann et al., 1991; Bathmann, 1996).
Results on zooplankton distribution during this study (Dubischar and Bathmann, 1997s; Fransz and González, 1997) showed that large euphausiid stocks were low during the whole cruise. Additionally, cyclopoid copepods (*Oithona similis* and *Oncea curvata*), which are report to efficiently recycle zooplankton faecal pellets in the surface layers (González and Smetacek, 1994; González et al., 1994), were dominant both in the AWB and southern ACC as well as in the PFr (Fransz and González, 1997). These results indicate that protozoan pellets sedimenting out of the surface layers in the study area, between the Weddell Gyre and PFr, are likely to contribute significantly to overall vertical fluxes. Although no measurement exists on carbon content of protozoan faecal pellets, their appearance in the light microscope suggest that their carbon content should be relatively low when compared with zooplankton pellets (Buck and Newton, 1995). Thus it seems that although a significant number of protozoan pellets should sink out of surface layer during ANT X/6 they would carry very little carbon. However, their impact could be important for opal fluxes by protecting diatom frustules

from dissolution in surface water and thus redistributing silica from the surface to deeper layers (Nöthig and von Bodungen, 1989; Buck and Newton, 1995).

Empty diatom frustules

Empty diatom frustules might originate from disaggregation of metazoan and protozoan faecal material, as direct waste products of protozoan and salp feeding, production of gametangia (Crawford, 1995), and mortality due to abiotic conditions (Peters, 1996). In the area of study, the fractions of empty diatoms (> 20 µm) in ice-covered areas and in the open water of the southern ACC were similar. Significantly lower values were found in the PFr. Moisan and Fryxell (1993) and Kang and Fryxell (1993) found significantly higher proportions of empty diatoms under ice-covered areas than in open water. Despite higher abundance of empty diatom frustules in ice-covered areas Moisan and Fryxell (1993) reject the hypothesis that release of empty frustules due to ice melting has a significant influence on empty diatom distribution, since at the ice edge, abundance of empty frustules was similar throughout the water column sampled. My results do not permit firm conclusions for the entire diatom community since the first depth sampled was 20 m and concern only diatoms > 20 µm. Although algal mortality seems to be important in the ice (Mc Minn, 1996), release through ice melting does not seem to have an important effect on larger empty diatom stocks (> 20 µm) since percentage of empty frustules was similar in ice-covered and open ocean areas. This also indicates that light might not be an important factor determining mortality of diatom assemblages although very long exposure to total darkness might have species-specific effects (Peters and Thomas, 1996a).

Since the early beginning of biological oceanography, nutrients have been considered as having a major influence on productivity and phytoplankton biomass accumulation. To my knowledge only the work of Peters and Thomas (1996b) has demonstrated that prolonged nutrient deficiency (in this case nitrate) can be lethal to diatoms. Iron is thought to be responsible for the low primary production rates and dominance of nanoplankton in the Weddell Gyre and southern ACC (de Baar et al., 1995). In the PFr, Quéguiner et al. (1997) also suggests that silica might be limiting to diatom growth. Although iron, in the AWB and southern ACC, and silica in the PFr, might have been limiting phytoplankton growth (Quéguiner et al., 1997; de Baar et al., 1995) none of these nutrients were actually exhausted. Thus, mortality due to nutrient deficiency should not have been significant. Given the scarcity of studies in

this respect a nutrient deficiency effect on diatom mortality in the whole study area cannot, however, be ruled out.

Sexual events are also a source of empty frustules. In fact, this has been observed for the larger centric diatom species: *Corethron criophilum* (Crawford, 1995) and several *Rhizosolenia* species during this study (personal observation). It is also revealing that empty frustule stocks of larger (> 60 µm) diatoms are not correlated with grazer and live diatom stocks. However, for the dominant diatom species in the area studied (mainly pennate diatoms), sexual events have rarely if ever been recorded.

Although "natural " causes of mortality can not be ruled out, it is likely that grazing by metazoa and protozoa are the main causes for the release of empty diatom frustules in the water column, especially for diatoms < 60 µm. That empty diatom frustules are significantly correlated with live diatom stocks does not contradict this hypothesis since feeding rates in protozoa and metazoa are directly related to food concentrations. The size structure and calculated grazing rates of the microprotozoan population on larger phytoplankton is consistent with the abundance of empty diatom frustules between the regions investigated as well as the differences in mortality of the different size classes of diatoms.

With sinking rates of 0.5 to 3 m d^{-1} (Johnson and Smith, 1985) diatom frustules would have a residence time of 67 to 400 days in the upper 200 m of the water column (corresponding to the Antarctic Surface Water). Nelson and Gordon (1982) measured specific biogenic silica dissolution rates of 7.2 10^{-3} to 4.3 10^{-2} d^{-1} in the Antarctic Circumpolar Current. This would mean that 0.5 to 100 % of the biogenic silica stock can be dissolved in the upper 200 m of the water column. Measurement of silica dissolution in the open water of the southern ACC showed dissolution rates of 18 to 58 % of silica production in surface water. Two thirds of the remaining silica production dissolved before reaching the sediments (Nelson and Gordon, 1982). These results indicate that, although most of the empty diatom frustules stocks probably dissolves in surface layers the few percent reaching deeper layers have a significant impact on the silica enrichment of the CDW (Nelson and Gordon, 1982). The fact that empty diatom frustules produced by protozoan feeding are possibly an important vehicle of silica transport into deeper water masses rather than to the sediments is also confirmed by sediment trap studies. As in the case of protozoan faecal pellets, fluxes of intact empty diatom frustules constituted a

significant proportion of the sedimenting material in shallow sediment trap studies (Bathmann et al., 1991), in shallow areas (Sasaki and Hoshiai, 1986) or in areas of low overall fluxes and krill stocks (Gersonde and Wefer, 1987; Nöthig and von Bodungen, 1989; Bathmann et al., 1991). Thus, it is likely that intact empty frustules constitute, like protozoan pellets, an important portion of silica fluxes below surface layers in the area studied, with most of it dissolving before reaching the sediments. The magnitude of silica transported out of the surface layers will strongly depend on dissolution and sinking rates of the empty diatom frustules and thus on size and thickness of the frustules. Also one can speculate that in the area investigated, vertical flux of empty frustules decreased in importance southwards, from the PFr to the ice-covered areas, due to the gradient in abundance of empty diatom frustules as well as the importance of highly silicified diatoms in the former region.

Empty skeleton and lorica release

The abundances of empty tintinnid loricas found during this study were correlated with stocks of live organisms and were higher than the abundance of empty radiolarian skeletons. However, empty tintinnid lorica abundances might have been overestimated by the use of nets for sampling (see Discussion section 4.1). Little to nothing is known about sinking rates and the fate of tintinnid loricas. Vertical fluxes of empty tintinnid loricas have never been described in the Southern Ocean. The studies of Boltovskoy et al. (1993), Antia (1991) and Bathmann et al., (1990), in other oceanic areas, indicate that tintinnid loricas can contribute significantly to vertical fluxes. None of those studies investigated the relationship between sinking fluxes and tintinnid abundances in the water column. The results of Boltovskoy et al. (1993), in the equatorial Atlantic, indicate that only 0.1 % of tintinnid loricas reach depths of 853 m intact. The differences in abundance of protozoan faecal pellets, and empty diatom frustules and tintinnid loricas indicate that, between the Weddell Gyre and PFr, the contribution of empty tintinnid loricas to vertical fluxes should be negligible.

The contribution of empty polycystine and smaller (< 300 µm) phaeodaria skeletons to total polycystine and smaller (< 300 µm) phaeodarian abundances found during this study are comparable to those found in the Weddell Sea, during winter, by Nöthig and Gowing (1991),in the Southern ACC and PFr (Abelmann and Gowing, 1996) as well as to the surface values found in winter and autumn at the WSC (Gowing, 1989; Gowing and Garrison, 1992). It seems, therefore, that the contribution of dead radiolarian skeletons

to total radiolarian abundances is not dependent on season. All studies showed a marked relation between the proportion of empty skeletons and depth, with increasing contributions of empty radiolarian skeletons to total radiolarian abundances from the surface to deeper layers. The higher proportion of empty skeletons at depth can be explained by increased in situ mortality plus the contribution of empty skeletons sinking from surface layers. During this study, abundance of empty radiolarian skeleton increased from the Weddell Gyre to the PFr. However, the ratio of empty radiolarian skeletons to total radiolarian abundances was lower in the PFr than at southernmost stations for the spumellaria and the smaller (< 300 µm) phaeodaria, showing a negative correlation with food stocks. The contribution of nassellarian skeletons to total nassellarian stocks showed the opposite trend with higher values in the PFr and a significant correlation to zooplankton stocks. Also, total standing stocks of living radiolaria and empty radiolarian skeletons were not significantly correlated. Therefore, during spring, vertical fluxes of radiolarian skeletons should be higher in the PFr, followed by the open water of the southern ACC, with lowest values in the Weddell Gyre and AWB. However, the magnitude of empty radiolarian skeleton vertical fluxes, should not be directly related to radiolarian abundances in the water column. During this study, the composition of empty radiolarian skeleton assemblage was similar to the living assemblage in the Weddell Gyre and AWB but not in the southern ACC and PFr, where both spumellaria and the smaller (< 300 µm) phaeodaria were underrepresented in the empty skeleton assemblage. Also, the assemblage composition of radiolarian skeletons sinking out of the surface layers is not representative of living surface water assemblages either.

Radiolaria skeleton fluxes in the Southern Ocean are four to five orders of magnitude lower than diatom valve fluxes (Abelmann and Gersonde, 1991) and do not significantly contribute to vertical fluxes in the southern Ocean (Gersonde and Wefer, 1987). These values are consistent with the differences in abundance of full and empty frustules, live radiolaria and empty radiolarian skeletons in the water column found during this study.

Overall polycystine radiolarian abundances in the Southern Ocean do not seem to reach higher values than a few thousand individuals m^{-3}, with maximum values during spring and summer (Morley and Stepien, 1984; Morley and Stepien, 1985; Gowing, 1989; Gowing and Garrison, 1991; Nöthig and Gowing, 1991; Boltovskoy and Alder, 1992b, Gowing and Garrison, 1992; Abelmann and Gowing, 1996). Smaller (< 300 µm) phaeodarian abundances are generally higher and more variable on a regional basis than those of

polycystine radiolaria, with maximum abundance reaching 2 10^4 individuals m^{-3} in the open water of the southern ACC during summer (see Discussion section 4.1; Abelmann and Gowing, 1996). Thus, polycystine radiolaria should also contribute little to overall biogenic silica production in surface water between the PFr and the Antarctic continent. Smaller (< 300 μm) phaeodaria might contribute significantly to biogenic silica production in the open water of the southern ACC during summer (Abelmann and Gowing, 1996) and in the WSC and Weddell Sea during winter (Nöthig and Gowing, 1991; Gowing and Garrison, 1992). However, smaller (< 300 μm) phaeodarian contribution to overall radiolarian fluxes in the Southern Ocean is very low (Boltovskoy et al., 1993). Takahashi (1983 and 1987) suggested that because of the higher dissolution rates of phaeodarian skeletons, these organisms are likely to significantly influence silica biogeochemical cycles by transporting silica to deeper layers of both the Subarctic Pacific and tropical oceans and thus redistributing silica in the world's ocean. Given the importance of phaeodarian radiolaria in the biogenic silica production in the southern ACC during summer and in the Weddell Sea and WSC during winter, it is likely that also in the Southern Ocean they contribute to the transfer of silica to deeper water layers.

The importance of radiolarian contribution to vertical fluxes the Southern Ocean is quite different from most of the world's oceans and especially the two HNLC areas which also show high rates of silica accumulation in the sediments: the subarctic and equatorial Pacific (DeMaster, 1981; Tréguer et al., 1995). In the subarctic Pacific radiolaria contribute significantly to silica vertical fluxes with values two to three orders of magnitude higher than those found in the Southern Ocean (1 10^4 to 8 10^4 skeletons m^{-2} day^{-1}; Abelmann and Gersonde, 1991; Takahashi, 1987 and 1991). Radiolaria also contribute significantly to vertical fluxes in the equatorial Pacific, with values similar to fluxes in the subarctic Pacific (Bolstovkoy et al., 1993; Milliman and Takahashi, in press).

4.5 Role of micro and net protozoa in Southern Ocean carbon and silica fluxes, and concluding remarks.

During this study microprotozoa, composed mainly of dinoflagellates and choreotrich ciliates, constituted an important fraction of microprotist biomass both in ice-covered and open-ocean areas. The data on protozoan distribution

of previous studies indicates that this is the case all year round in the Southern Ocean. Thus, microprotozoa are also likely to be an important food source for larger zooplankton all year round. Grazing impact estimates indicate that although microprotozoa graze an important fraction of phytoplankton production (including the diatoms) during spring, they do not control overall primary production.

Net (> 64 µm) protozoan stocks constituted a negligible fraction of the plankton in the euphotic zone. In deeper layers (below the euphotic zone) their biomass, dominated by larger (> 300µm) phaeodaria, was significant. Although very little is known on sarcodine feeding and growth rates, it is likely that larger (> 300 µm) phaeodaria contribute significantly to retaining and repackaging material sinking out of the euphotic layer. Larger phaeodaria (> 300 µm) seem to be equally important in surface layers of the Weddell Sea during winter (Nöthig and Gowing, 1991) and smaller (< 300 µm) phaedodaria in the open water of the southern ACC during summer (Abelmann and Gowing, 1996). Too few studies exist on net protozoa in the Southern Ocean to give an overall picture of their distribution and importance.

The estimates of microprotozoan grazing rates on diatoms and the study of empty frustule distribution indicates that microprotozoa are likely to be majors agents in the release of empty frustules in surface water. Distribution of faecal pellets and empty diatom frustules showed that they should significantly contribute to vertical fluxes at the ice edge as well as in open water between the Weddell Sea and PFr, where large euphausiids are rare. Particles of protozoan origin should carry little carbon out of the surface layers but might be significant for the silica budget in the Southern Ocean between the Weddell Sea and the PFr. The same might be true for smaller (< 300 µm) phaeodarian skeletons in the southern ACC during summer (Abelmann and Gowing, 1996). Protozoan faecal pellets, empty diatom frustules and smaller (< 300 µm) phaeodarian skeletons do not seem to efficiently transport high quantities of silica to the sediments but might be important agents in the redistribution of silica to deeper water layers.

The role of protozoa in the Southern Ocean can be visualised as a "differential pump" retaining both new and regenerated carbon production (in combination with nitrogen and phosphate; Holm-Hansen, 1985; Goeyens et al., 1991) in surface layers, and transferring it to higher trophic levels while transferring silica to deeper water layers. The decoupling of carbon, nitrogen and

phosphate from silica vertical fluxes, through protozoan grazing, combined with the northward circulation pattern of the Antarctic Surface Water (AASW), might be a key factor in explaining the northward decrease in silica concentrations in the AASW between the Weddell Gyre and the PFr (Bakker et al., 1994). The fact that faecal pellets and empty diatom frustules released by protozoa seem to degrade and dissolve respectively before reaching the sediments, might also explain the characteristic enrichment of dissolved silica in deeper layers of the southern ACC (Nelson and Gordon, 1982) as well as the high ratios of biogenic silica to carbon in the sediments (Nelson and Gordon, 1982; DeMaster et al., 1991).

During this study, both the microprotozoan and net (> 64 μm) protozoan assemblage showed distinct differences in terms of biomass and composition related to changes in biological parameters of the water column as well as ice cover and water mass. Given the diversity in protozoan feeding behaviour, differences in assemblage composition should have a significant influence on protozoan grazing rates on the different compartments of pelagic assemblages and thus on carbon and silica budgets in the Southern Ocean.

Overall the results of this study show that improved knowledge of the feeding behaviour of protozoan assemblages and of the fate of particles of protozoan origin might be a key to understanding biogeochemical cycles in the Southern Ocean as well as in other HNLC areas.

5 REFERENCES

Abelmann A. and R. Gersonde (1991) Biosiliceous particle flux in the Southern Ocean. Marine Chemistry, 35, 503-536.

Abelmann A. and M. Gowing (1996) Horizontal and vertical distribution pattern of living radiolarians along a transect from the Southern Ocean to the South Atlantic Subtropical region. Deep-Sea Research, 43, 361-382.

Abelmann A. and M. Gowing (1997) Spatial distribution pattern of living polycystine radiolaria taxa - Baseline study for paleoenvironmental reconstructions in the Southern Ocean (Atlantic sector). Marine Micropaleontology, 30, 3-28.

Alder V. A. and D. Boltovskoy (1991) Microplanktonic distributionnal patterns west of the Antarctic peninsula, with special emphasis on the tintinnids. Polar Biology, 11, 103-112.

Alder V. A. and D. Boltovskoy (1993) The ecology of larger microzooplankton in the Weddell-Scotia Confluence area: horizontal and vertical distribution patterns. Journal of Marine Research, 51, 323-344.

Anderson R. O. (1983) Radiolaria. Springer-Verlag, New York, Berlin, Heidelberg, Tokyo, pp. 1-109.

Antia A. N. (1991) Microzooplankton in the pelagic food web of the East Greenland Sea and its role in sedimentation processes. Bericht der Sonderforschungsbereich 313, Universität Kiel, 33, 1-109.

Antia A. N., E. Bauerfeind, B. von Bodungen and U. Zeller (1993) Abundance, encystment and sedimentation of acantharia during Autumn 1990 in the East Greenland Sea. Journal of Plankton Research, 15, 99-114.

Archer S. D., R. J. G. Leakey, P. H. Burkill, M. A. Sleigh and C. J. Appleby (1996a) Microbial ecology of sea ice at a coastal Antarctic site: community composition, biomass and temporal changes. Marine Ecology Progress Series, 135, 179-195.

Archer S. D., R. J. G. Leakey, P. H. Burkill and M. A. Sleigh (1996b) Microbial dynamics in coastal waters of East Antarctica: herbivory by heterotrophic dinoflagellates. Marine Ecology Progress Serie, 139, 239-255.

Atkinson A. (1996) Subantarctic copepods in an oceanic, low chlorophyll environment: ciliate predation, food selectivity and impact on prey populations. Marine Ecology Progress Series, 130, 85-96.

Azam F., T. Fenchel, J. G. Field, J. S. Gray, L. A. Meyer-Reil and F. Thingstad (1983) The ecological role of water-column microbes in the sea. Marine Ecology Progress Series, 10, 257-263.

Baar de H. J. W., J. T. M. de Jong, D. C. E. Bakker, B. M. Löscher, C. Veth, U. Bathmann and V. Smetacek (1995) Importance of iron for plankton blooms and carbon dioxide drawdown in the Southern Ocean. Nature, 373, 412-415.

Bakker K., P. Fritsche and J. Poncin (1994) Nutrients. In: The expeditions Antarktis X/6-8 of the Research Vessel "Polarstern" in 1992/93, U. Bathmann, V. Smetacek, H. de Baar, E. Farbach and G. Krause, editors, Reports on Polar Research, 135, 38-41.

Banse K. (1992) Grazing, temporal changes of phytoplankton concentrations, and the microbial loop in the open sea. In: Primary productivity and Biogeochemical cycles in the sea, P. G. Falkowsky and A. D. Woodhead, editors, Plenum Press, New York, pp. 409-440.

Bathmann U. V. (1996) Abiotic and Biotic forcing on vertical particle flux in the Southern Ocean. In: Particle flux in the ocean, V. Ittekot, P. Schäfer, S. Honjo and P. J. Depetris, John Wiley and Sons Ltd., pp. 243-250.

Bathmann U. V., R. Peinert, T. T. Noji B. von Bodungen (1990) Pelagic origin and fate of sedimenting particles in the Norwegian Sea. Progress in Oceanography, 24, 117-125.

Bathmann U. V., G. Fischer, P. J. Müller and D. Gerdes (1991) Short-term variations in particulate matter sedimentation off Kapp Norvegia, Weddell Sea, Antarctica: relation to water mass advection, ice cover, plankton biomass and feeding activity. Polar Biology, 11, 185-195.

Bathmann U. V., R. Scharek C. Klaas, C. D. Dubischar and V Smetacek (1997) Spring development of phytoplankton biomass and composition in major water masses of the Atlantic sector of the Southern Ocean. Deep-Sea Research, 44, 51-67.

Baumann M. (1990) Untersuchung zur Primärproduktion und Verteilung des Phytoplanktons der Grönlandsee mit Kulturexperimenten zum Einfluß des Lichtes und der Temperatur auf Wachstums und Photosyntheseleistung arktischer Diatomeen. PhD thesis, Rheinisch-Westfälischen Technischen Hochschule Aachen, pp. 1-129.

Bé A. W. H. (1967) Foraminifera. Families: Globigerinidae and Globorotaliidae. Fiches d'identification du zooplankton, conseil permanent international pour l'exploration de la mer, 108, 1-10.

Becquevort S. (1997) Nanoprotozooplankton of the Atlantic sector of the Southern Ocean in early spring: biomass and feeding activities. Deep-Sea Research, 44, 355-373.

Becquevort S., S. Mathot and C. Lancelot (1992) Interactions of the microbial community of the marginal ice zone of the northwestern Weddell Sea through size distribution analysis. Polar Biology, 12, 211-218.

Beers J. R. and G. L. Stewart (1967) Micro-zooplankton in the euphotic zone at five locations across the California Current. Journal of the Fisheries Reasearch Board of Canada, 24, 2053-2068.

Beers J. R. and G. L. Stewart (1969) Microzooplankton and its abundance relative to the larger zooplankton and other seston components. Marine Biology, 4, 182-189.

Beers J. R. and G. L. Stewart (1970) Numerical abundance and estimated biomass of microzooplankton. In: The ecology of the plankton off La Jolla, California in the period April through September, 1967, J. D. H. Strickland, editor, Bulletin of the Scripps Institute of Oceanography, 17, 67-87.

Beers J. R., F. M. H. Reid and G. L. Stewart (1982) Seasonal abundance of the microplankton population in the North Pacific central gyre. Deep-Sea Research, 29, 277-245.

Berberich D. (1996) The planktonic foraminifera Neogloboquadrina Pachyderma (Ehrenberg) in the Weddell Sea, Antarctica. Repports on Polar Research, 195, 1-193.

Bernstein R. E., P. R. Betzer and K. Takahashi (1990) Radiolarians from the western North Pacific Ocean: a latitudinal study of their distributions and fluxes. Deep-Sea Research, 37, 1677-1696.

Bjørnsen P. K. and J. Kuparinen (1991) Growth and herbivory by heterotrophic dinoflagellates in the Southern Ocean, studied by microcosm experiments. Polar Biology, 109, 397-405.

von Bodungen B., G. Fischer, E.-M. Nöthig and G. Wefer (1987) Sedimentation of krill faeces during spring development of phytoplankton in Bransfield Strait, Antarctica. Mitt. Geol. Paläont. Inst. Univ. Hamburg., 62, 243-257.

von Bodungen B., E.-M. Nöthig and Q. Sui (1988) New production and sedimentation during summer 1985 in the south eastern Weddell Sea. J. comp. Biochem. Physiol., 90, 475-487.

Boltovskoy D., V. A. Alder and F. Spinelli (1989) Summer Weddell Sea microplankton: Assemblage structure, distribution and abundance, with special emphasis on the tintinnina. Polar Biology, 9, 447-456.

Boltovskoy D. and V. A. Alder (1992a) Microzooplankton and tintinnid species-specific assemblage structures: patterns of distribution and year-to-year variations in the Weddell Sea (Antarctica). Journal of Plankton Research, 14, 1405-1423.

Boltovskoy D. and V. A. Alder (1992b) Paleoecological implications of radiolarian distribution and standing stocks versus accumulation rates in the Weddell Sea. Antarctic Research Series, 56, 377-384.

Boltovskoy D., V. A. Alder and A. Abelmann (1993) Annual flux of radiolaria and other shelled plankters in the eastern equatorial Atlantic at 853 m: seasonal variations and polycystine species-specific responses. Deep-Sea Research , 40, 1863-1895.

Booth B. C., J. Lewin and J. R. Postel (1993) Temporal variations in the structure of autotrophic and heterotrophic communities in the Subarctic Pacific. Progress in Oceanography, 32, 57-99.

Bröckel von K. (1981) The importance of nanoplankton within the pelagic antarctic ecosystem. Kieler Meeresforschungen, Sonderheft, 5, 61-67.

Bröckel von K. (1985) Primary production data from the south-eastern Weddell Sea. Polar Biology, 4, 75-80.

Buck, K. R., P. A. Bolt and D. L. Garrison (1990) Phagotrophy and fecal pellet production by an athecate dinoflagellate in antarctic sea ice. Marine Ecology Progress Series, 60, 75-84.

Buck, K. R. and J. Newton (1995) Fecal pellet flux in Dabob Bay during a diatom bloom: contribution of microzooplankton. Limnology and Oceanography, 40, 306-315.

Buma A. G. J., H. J. W. de Baar, R. F. Noltig and A. J. van Bennekom (1991) Metal enrichment experiments in the Weddell-Scotia Seas: Effects of iron and manganese on various plankton communities. Limnology and Oceanography, 36, 1865-1878.

Burkill P. H., E. S. Edwards, A. W. G. John and M. A. Sleigh (1993) Microzooplankton and their herbivorous activity in the northeast Atlantic Ocean. Deep-Sea Research , 40, 479-493.

Burkill P. H., E. S. Edwards and M. A. Sleigh (1995) Microzooplankton and their role in controlling phytoplankton growth in the marginal ice zone of the Bellingshausen Sea. Deep-Sea Research, 42, 1277-1290.

Buskey E. J., C. J. Coulters and S. L. Brown (1994) Feeding, growth and bioluminescence of the heterotrophic dinoflagellate Protoperidinium Huberi. Marine Biology, 121, 373-380.

Capriulo G. M., E. B. Sherr and B. F. Sherr (1991) Trophic behaviour and related community feeding activities of heterotrophic marine protists. In: Protozoa and their role in marine processes, P. C. Reid, C. M. Turley, P. H. Burkill, editors, NATO ASI Series, Vol. G25, Springer-Verlag, Berlin, pp. 219-265.

Caron D. A. and B. J. Finlay (1994) Protozoan links in food webs. In: Progress in Protistology, Proceedings of the IX International Congress of Protistology Berlin 25-31 July 1993, K. Hausamann and N. Hülsmann, editors, Gustav Fischer Verlag, Stuttgart, Jena, New York, pp. 125-130.

Choi J. W. and F. Peters (1992) Effect of temperature on two psychrophilic ecotypes of a heterotrophic nanoflagellate, Paraphysomonas imperforata. Applied and Environmental Microbiology, 58, 593-599.

Choi J. W. and D. K. Stoecker (1989) Effects of fixation on cell volume of marine planktonic protozoa. Applied and Environmental Microbiology, 55, 1761-1765.

Crawford R. (1995) The role of sex in the sedimentation of a marine diatom bloom. Limnology and Oceanography, 40, 200-204.

Davis P. G. and J. M. Sieburth (1982) Differentiation of phototrophic and heterotrophic nanoplankton populations in marine waters by epifluorescence microscopy. Annales de l' Institut Océanographique de Paris, 58, 249-260.

DeMaster D. J. (1981). The supply and accumulation of silica in the marine environment. Geochimica et Cosmochimica Acta, 45, 1715-1732.

DeMaster D. J., T. M. Nelson, S. L. Harden C. A. Nittrouer (1991) The cycling and accumulation of biogenic silica and organic carbon in Antarctic deep-sea and continental margin environments. Marine Chemitry, 35, 489-502.

Detmer A. E. and U. V. Bathmann (1997) Distribution patterns of autotrophic pico- and nanoplankton and their relative contribution to algal biomass during spring in the Atlantic sector of the Southern Ocean. Deep-Sea Research, 44, 299-320.

Dieckmann G. S., M. Spindler, M. A. Lange, S. F. Ackley and H. Eicken (1991) Antarctic sea ice: a habitat for the foraminifer Neogloboquadrina pachyderma. Journal of Foraminiferal Research, 21, 182-189.

Dodge J. D. (1982) Marine dinoflagellates of the British Isles. Her Majesty's Stationery Office, London, pp. 1-303

Dodge J. D. and J. Priddle (1987) Species composition and ecology of dinoflagellates from the Southern Ocean near South Georgia. Journal of Plankton Research, 9, 685-697.

Dowd J. E. and D. S. Riggs (1965) A comparison of estimates of Michaelis-Menten kinetics constants from various linear transformations. The Journal of Biological Chemistry, 240, 863-869.

Drebes G. (1988) Syltodinium listii gen. et spec. nov., a marine ectoparasitic dinoflagellate on eggs of copepods and rotifers. Helgoländer Meeresuntersuchungen, 42, 583-591.

Drebes G. and E. Schnepf (1988) Paulsenella Chatton (Dynophyta), ectoparasites of marine diatoms: development and taxonomy. Helgoländer Meeresuntersuchungen, 42, 563-581.

Dubischar C. D. and U. V. Bathmann (1997) Grazing impact of copepods and salps on phytoplankton in the Atlantic sector of the Southern Ocean. Deep-Sea Research, 44, 415-433.

Ducklow H. W., D. A. Purdie, P. J. le B. Williams and J. M. Davies (1986) Bacterioplankton: a sink for carbon in a coastal marine plankton community. Science, 232, 865-867.

Ducklow H. W. and A. H. Taylor (1991) Modelling - Session summary. In: Protozoa and their role in marine processes, P. C. Reid, C. M. Turley, P. H. Burkill, editors, NATO ASI Series, Vol. G25, Springer-Verlag, Berlin, pp. 431-442.

Dugdale R. C. and Wilkerson (1991) Low specific nitrate uptake: A common feature of high-nutrient, low-chlorophyll marine ecosystems. Limnology and Oceanography, 36, 1678-1688.

Edler L. (1979) Recommendations on methods for marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll. Baltic Marine Biologists Publication, 5, 1-38.

Ehrenberg C. G. (1838) Die Infusionsthierchen als vollkommene Organismen. Leipzig, pp.1-548.

Elbrächter M. (1991a) Faeces production by dinoflagellates and other small flagellates. Marine Microbial Food Webs, 5, 189-204.

Elbrächter M. (1991b) Food uptake mechanisms in phagotrophic dinoflagellates and classification. In: The Biology of Free-Living Heterotrophic Flagellates. D. J. Patterson and J. Larsen, editors, Clarendon Press, Oxford, pp. 303-312.

Eppley R. W., J. N. Rogers and J. J. McCarthy (1969) Half saturation constants for the uptake of nitrate and ammonium by marine phytoplankton. Limnology and Oceanography, 14, 912-920.

Fenchel T. (1982a) Ecology of heterotrophic microflagellates. II. Bioenergetics and growth. Marine Ecology Progress Series, 8, 225-231.

Fenchel T. (1982b) Ecology of heterotrophic microflagellates. III. Adaptations to heterogeneous environments. Marine Ecology Progress Series, 9, 25-33.

Fenchel T. (1986) Protozan filter feeding. In: Progress in protistology, volume I, J. O. Corliss and D. J. Patterson, editors, Biopress, Bristol, pp. 65-113.

Fenchel T. (1987) Ecology of protozoa: the biology of free living phagotrophic protists. Science Tech Publishers, Madison Wisconsin/Springer-Verlag, Berlin, Heidelberg, New York London, Paris, Tokyo, pp 1-193.

Fenchel T. (1988) Marine plankton food chains. Annual Revue of Ecological Systematics, 19, 19-38.

Fenchel T. and C. C. Lee (1972) Studies on ciliates associated with sea ice from Antarctica I. The nature of the fauna. Archiv für Protistenkunde, 114, 231-236.

Fenchel T. and B. J. Finlay (1983) Respiration rates in heterotrophic, free-living protoza. Microbial Ecology, 9, 99-122.

Fessenden L. and T. J. Cowles (1994) Copepod predation on phagotrophic ciliates in Oregon coastal waters. Marine Ecology Progress Series, 107, 103-111.

Field J. G., K. R. Clarke and R. M. Warwick (1982) A practical strategy for analysing multispecies distribution patterns. Marine Ecology Progress Series, 8, 37-52.

Fischer G., D. Fütterer, R. Gersonde, S. Honjo, D. Ostermann and G. Wefer (1988) Seasonal variability of particle flux in the Weddell Sea and its relation to ice cover. Nature, 335, 426-428.

Franeker van J. A. (1994) Sea-ice cover and icebergs. In: The expeditions Antarktis X/6-8 of the Research Vessel "Polarstern" in 1992/93, U. Bathmann, V. Smetacek, H. de Baar, E. Farbach and G. Krause, editors, Reports on Polar Research, 135, 17-22.

Fransz G. and S. González (1997) Latitudinal metazoan plankton zones in the Antarctic Circumpolar Current of the Atlantic along 6°W during austral spring 1992. Deep-Sea Research, 44, 395-414.

Froneman P. W. and R. Perissinotto (1996) Structure and grazing of the microzooplankton communities of the Subtropical Convergence and a warm-core eddy in the Atlantic sector of the Southern Ocean. Marine Ecology Progress Series, 135, 237-245.

Frost B. W. (1991) The role of grazing in nutrient-rich areas of the open ocean. Limnology and Oceanography, 36, 1616-1630.

Garrison D. L. (1991) An overview of the abundance and role of protozooplankton in Antarctic waters. Journal of Marine Systems, 2, 317-331.

Garrison D. L. and K. R. Buck (1989) Protozooplankton in the Weddell Sea, Antarctica: abundance and distribution in the ice-edge zone. Polar Biology, 9, 341-351.

Garrison D. L., K. R. Buck and M. M. Gowing (1993) Winter plankton assemblage in the ice edge zone of the Weddell and Scotia Seas: composition, biomass and spatial distributions. Deep-Sea Research , 40, 311-338.

Garrison D. L.and A. R. Close (1993) Winter ecology of the sea ice biota in Weddell Sea pack ice. Marine Ecology Progress Series, 96, 17-31.

Geider R. J. and B. S. C. Leadbeater (1988) Kinetics and energetics of growth of the marine choanoflagellate Stephanoeca diplocostata. Marine Ecology Progress Series, 47, 169-177.

Gersonde R. and G. Wefer (1987) Sedimentation of biogenic siliceous particles in antarctic waters from the Atlantic sector. Marine Micropaleonthology, 11, 311-332.

Goeyens L., P. Téguer, C. Lancelot, S. Mathot, S. Becquevort, J. Morvan, J. Dehairs W. Baeyens (1991) Ammonia regeneration in the Scotia-Weddell Confluence area during spring 1988. Marine Ecology Progress Series, 78, 241-252.

González H. E. (1992) Distribution and abundance of minipellets around the Antarctic peninsula. Implications for protistan feeding behaviour. Marine Ecology Progress Series, 90, 223-236.

González H. E. and V. Smetacek (1994) The possible role of the cyclopoid copepod Oithona in retarding vertical flux of zooplankton faecal material. Marine Ecology Progress Series, 113, 233-246.

González H. E., F. Kurbjeweit and U. V. Bathmann (1994) Occurrence of cyclopoid copepods and faecal material in the Halley Bay region, Antarctica, during January-February 1991. Polar Biology, 14, 331-342.

Gowing M. M. (1989) Abundance and feeding ecology of Antarctic phaeodarian radiolarians. Mar. Biol., 103, 107-118.

Gowing M. M. and D. L. Garrison (1991) Austral winter distribution of large tintinnid and sarcodinid protozooplankton in the ice-edge zone of the Weddell/Scotia Seas. Journal of Marine Systems, 2, 131-141.

Gowing M. M. and D. L. Garrison (1992) Abundance and feeding ecology of larger protozooplankton in the ice edge zone of the Weddell and Scotia Seas during the austral winter. Deep-Sea Research, 39, 893-919.

Gowing M. M. and M. W. Silver (1985) Minipellets: A new and abundant size class of marine fecal pellets. Journal of Marine Research, 43, 395-418.

Haeckel E. (1887) Report on the Radiolaria collected by H.M.S. Challenger during the year 1873-1876. Repports on the scientific Results of H.M.S. Challenger, Zoology, 18, 1-1803.

Hansen P. J. (1991a) Dinophysis - a planktonic dinoflagellate genus which can act both as prey and a predator of a ciliate. Marine Ecology Progress Series, 69, 201-204.

Hansen P. J. (1991b) Quantitative importance and trophic role of heterotrophic dinoflagellates in a coastal pelagial food web. Marine Ecology Progress Series, 73, 253-261.

Hansen P. J. (1992) Prey size selection, feeding rates and growth dynamics of heterotrophic dinoflagellates with special emphasis on Gyrodinium spirale. Marine Biology, 114, 327-334.

Hansen B., P. K. Bjørnsen and P. J. Hansen (1994) The size ratio between planktonic predators and their prey. Limnology and Oceanography, 39, 395-403.

Harvey H. W. (1928) Biological chemistry and physics of seawater. Cambridge University Press, Cambridge, pp. 1-194.

Harvey H. W., L. H. N. Cooper, M. V. Lebour and F. S. Russell (1935) Plankton production and its control. Journal of the Marine Biological Association of the United Kingdom, 20, 407-441.

Heinbokel J. F. (1978a) Studies on the functionnal role of tintinnids in the southern California bight. I. Grazing and growth rates in laboratory cultures. Marine Biology, 47, 177-189.

Heinbokel J. F. (1978b) Studies of the functional role of tintinnids in the southern California Bight. 2. Grazing rates of field populations. Marine Biology, 17, 191-197.

Heinbokel J. F. and J. R. Beers (1979) Studies on the functionnal role of tintinnids in the southern California bight. I. Grazing impact of natural assemblages. Marine Biology, 52, 23-32.

Hemleben, C., Spindler, M., Anderson, R. O. 1989. Modern planktonic foraminifera. Springer-Verlag, New York, pp. 1-355

Hewes C. D., O. Holm-Hansen and E. Sakshaug (1985) Alternate carbon pathways at lower trophic levels in the antarctic food web. In: Antarctic nutrient cycles and food webs, W. R. Siegfried, P. R. Condy and R. M. Laws, editors, Springer Verlag, Berlin, pp. 277-283.

Holm-Hansen O. (1985) Nutrient cycles in antarctic ecosystems. In: Antarctic nutrient cycles and food webs, W. R. Siegfried, P. R. Condy, R. M. Laws, editors, Springer Verlag, Berlin, Heidelberg, New York, pp. 6-10.

Honjo S. (1990) Ocean particles and fluxes of material to the interior of the Deep Ocean: the azoic theory 120 years later. In: Facets of modern biogeochemistry, V. Ittekkot, S. Kempe, W. Michaelis and A. Spitzy, editors, Springer Verlag, Berlin, Heidelberg, New York, London, Paris, Tokyo, Hong Kong, pp. 62-73.

Jacobson D. M. and R. A. Andersen (1994) The discovery of mixotrophy in photosynthetic species of Dinophysis (Dinophyceae): light and electron microscopical observations of food vacuoles in Dinophysis acuminata, D. norvegica and two heterotrophic dinophysoid dinoflagellates. Phycologia, 33, 97-110.

Jacobson D. M. and J. M. Anderson (1986) Thecate heterotrophic dinoflagellates feeding behaviour and mechanisms. Journal of Phycology, 22, 249-258.

Jacques G. (1991) Is the concept of new production - regenerated production valid for the Southern Ocean? Marine Chemistry, 35, 273-286.

Jeong H. J. (1994a) Predation by the heterotrophic dinoflagellate Protoperidinium cf. divergens on copepod eggs and earlier naupliar stages. Marine Ecology Progress Series, 114, 203-208.

Jeong H. J. (1994b) Predation effects of the calanoid copepod Acartia tonsa on a population of the heterotrophic dinoflagellate Protoperidinium cf. divergens in the presence of co-occuring red-tide dinoflagellate prey. Marine Ecology Progress Series, 111, 87-97.

Jochem F. J., S. Mathot B. Quéguiner (1995) Size-fractionated primary production in the open Southern Ocean in austral spring. Polar Biology, 15, 381-392.

Johannes R. E. (1965) Influence of marine protozoa on nutrient regeneration. Limnology and Oceanography, 10, 434-442.

Johnson T. O. and W. O. Smith Jr. (1985) Sinking rates of natural phytoplankton populations in the western Weddell Sea. Antarctic Journal of the United States, 20, 139-140.

Jonsson P. R. (1986) Particle size selection, feeding rates and growth dynamics of marine planktonic oligotrichous ciliates (Ciliophora, Oligotrichina). Marine Ecology Progress Series, 33, 265-277.

Kang S.-H. and G. A. Fryxell (1993) Phytoplankton in the Weddell Sea, Antarctica: composition abundance and distribution in water-column assemblages of the marginal ice-edge zone during austral autumn. Marine Biology, 116, 335-348.

Kivi K. and H. Kuosa (1994) Late winter microbial communities in the western Weddell Sea (Antarctica). Polar Biology, 14, 389-399.

Kivi K. and O. Setälä (1995) Simultaneous measurement of food particle selection and clearance rates of planktonic oligotrich ciliates (Ciliophora: Oligotrichina). Marine Ecology Progress Series, 119, 125-137.

Kleppel G. S., D. V. Holliday and R. E. Pieper (1991) Trophic interactions between copepods and microplankton: A question about the role of diatoms. Limnology and Oceanography, 36, 172-178.

Knox F. and M. B. McElroy (1984) Changes in atmospheric CO2: influence of the marine biota at high latitudes. Journal of Geophysical Research, 89, 4629-4637.

Kühn S. F. (1995) Infection of marine diatoms by parasitoid protists.PhD thesis, University of Bremen, pp. 1-150.

Kühn S. F., G. Drebes and E. Schnepf (1995) Five new species of the nanoflagellate Pirsonia in the German Bight, North Sea, feeding on planktic diatoms. Helgoländer Meeresuntersuchungen, 50, 205-222.

Laackmann H. (1909) Die tintinnodeen der Deutsche Südpolar-Expedition 1901-1903. Deutsche Südpolar expedition, 2, 341-496.

Landry M. R. and R. P. Hassett (1982) Estimating the grazing impact of marine microzooplankton. Marine Biology, 67, 283-288.

Laubscher R. K., R. Perissinotto and C. D. McQuaid (1993) Phytoplankton production and biomass at frontal zones in the Atlantic sector of the Southern Ocean. Polar Biology, 13, 471-481.

Leakey R. G. J., P. H. Burkill and M. A. Sleigh (1994) A comparison of fixatives for the estimation of abundance and biovolume of marine planktonic ciliate populations. Journal of Plankton Research, 16, 375-389.

Leakey R. G. J., N. Fenton and A. Clarke (1994) The annual cycle of planktonic ciliates in nearshore waters at Signy Island, Antarctica. Journal of Plankton Research, 16, 841-856.

Lee C. C. and T. Fenchel (1972) Studies on ciliates associated with sea ice from Antarctica. II. Temperature responses and tolerances in ciliates from antarctic, temperate and tropical habitats. Archiv für Protistenkunde, 114, 237-244.

Lochte K., P. K. Bjørnsen, H. Giesenhagen and A. Weber (1997) Bacterial standing stock and production and their relation to phytoplankton in the Southern Ocean. Deep-Sea Research, 44, 321-340.

Lohmann H. (1908) Untersuchungen zur Feststellung des vollständigen Gehaltes des Meeres an Plankton. Wissenschaftliche Meeresuntersuchungen, Abteilung Kiel, Neue Folge, 10, 1129-370.

Lohmann H. (1911) Über das Nannopalnkton und die Zentrifugierung kleinster Wasserproben zur Gewinnung desselben in Lebendem Zustand. Internationale Revue der gesamte Hydrobiologie und Hydrographie, 4, 1-38.

Marin V. (1988) Qualitative models of the life cycles of Calanoides acutus, Calanus propinquus, and Rhincalanus gigas. Polar Biology, 8, 439-446.

Martin J. H., M. R. Gordon and S. E. Fitzwater (1991) The case for iron. Limnology and Oceanography, 36, 1793-1802.

McKenzie C. H. and E. R. Cox (1991) Spatial and seasonal changes in the species composition of armoured dinoflagellates in the southwestern Atlantic Ocean. Polar Biology, 11, 139-144.

McMinn A. (1996) Preliminary investigation of the contribution of fast-ice algae to the spring phytoplankton bloom in Ellis Fjord, eastern Antarctica. Polar Biology, 16, 301-307.

Miller C. B. (1993) Pelagic production processes in the subarctic Pacific. Progress in Oceanography, 32, 1-15.

Meyer K. (1934) Die geographische Verbreitung der tripyleen Radiolarien des Südatlantischen Ozeans. Deutschen Atlantischen Expedition METEOR 1925-1927. Wissenschaftliche Ergebnisse,12, 122-198.

Mills E. L. (1989) Biological Oceanography. An early history, 1870-1960. Cornell University Press, pp.1-378.

Milliman J. D. and K. Takahashi (in press) Carbonate and opal production and accumulation in the Ocean. In: Global surficial geofluxes: modern to glacial, T. M. Usselman, W. Hay and M. Meybeck, editors, National Academy Press.

Moisan T. A. and G. A. Fryxell (11993) The distribution of antarctic diatoms in the Weddell Sea during austral winter. Botanica Marina, 36, 489-497.

Moloney C.L. and J. G. Field (1991) Modelling carbon and nitrogen flows in a microbial plankton community. In: Protozoa and their role in marine processes, P. C. Reid, C. M. Turley, P. H. Burkill, editors, NATO ASI Series, Vol. G25, Springer-Verlag, Berlin, pp. 387-415.

Montagnes D. J. S. (1996) Growth responses of planktonic ciliates in the genera Strobilidium and Strombidium. Marine Ecology Progress Series,130, 241-254.

Morley J. J. and J. C. Stepien (1985) Antarctic radiolaria in late winter/early spring Weddell Sea waters. Micropaleontology, 31, 365-371.

Morley J. J. and J. C. Stepien (1984) Siliceous microfauna in waters beneath Antarctic sea ice. Marine Ecology Progress Series, 19, 207-210.

Nakamura Y., Y. Yamazaki and J. Hiromi (1992) Growth and grazing of a heterotrophic dinoflagellate, Gyrodinium dominans, feeding on a red tide flagellate, Chattonella antiqua. Marine Ecology Progress Series, 82, 275-279.

Nelson D. M. and L. I. Gordon (1982) Production and pelagic dissolution of biogenic silica in the Southern Ocean. Geochimica et Cosmochimica Acta, 46, 491-501.

Nelson D. M., W. O. Smith Jr., L. I. Gordon and B. A. Huber (1987) Spring distribution of density, nutrients and phytoplankton in the ice edge zone of the Weddell-Scotia Sea. Journal of Geophysical Research, 92, 7181-7190.

Nöthig E.-M. (1988) On the ecology of the phytoplankton in the southeastern Weddell Sea (Antarctica) in January/February 1985. Reports on Polar Research, 53, 1-118.

Nöthig, E.-M. and B. von Bodungen (1989) Occurence and vertical flux of faecal pellets of probably protozoan origin in the Southeastern Weddell Sea (Antarctica). Marine Ecology Progress Series, 56, 281-289.

Nöthig E.-.M. and M. Gowing (1991) Late winter abundance and distribution of phaeodarian radiolarians, other large protozooplankton and copepod nauplii in the Weddell Sea, Antarctica. Marine Biology, 111, 473-484.

Ohman M. D. and R. A. Snyder (1991) Growth kinetics of the omnivorous oligotrich ciliate Strombidium sp. Limnology and Oceanography, 36, 922-935.

Owens N. J. P., J. Priddle and M. J. Whithouse (1991) Variations in phytoplanktonic nitrogen assimilation around South Georgia and in the Bransfield Strait (Southern Ocean). Marine Chemistry, 35, 287-304.

Peinert, R., von Bodungen, B., Smetacek, V. S. (1989) Food web structure and loss rates. In: Productivty of the ocean: present and past, W. H. Berger, V. S. Smetacek and G. Wefer, editors, John Wiley & Sons Limited, Chichester, New York, Brisbane, Toronto Singapore, pp. 35-48.

Peters E. (1996) Phytoplankton Mortalität unter suboptimale Bedingungen. PhD thesis, University of Bremen, pp. 1-154.

Peters E. and D. N. Thomas (1996a) Prolonged darkness and diatom mortality I: Marine antarctic species. Journal of Experimental Marine Biology and Ecology, 207, 25-41.

Peters E. and D. N. Thomas (1996b) Prolonged nitrate exhaustion and diatom mortality: a comparison of polar and temperate Thalassiosira species. Journal of Plankton Research, 18, 953-968.

Petz W., W. Song and N. Wilbert (1995) Taxonomy and ecology of the ciliate fauna (Protozoa, Ciliophora) in the endopelagial and pelagial of the Weddell Sea, Antarctica. Stapfia, 40, 1-223.

Podolsky R. D. (1994) Temperature and water viscosity: physiological versus mechanical effects on suspension feeding. Science, 265, 100-103.

Pomeroy L. R. (1974) The ocean´s food web, a changing paradigm. BioScience, 24, 499-504.

Pomeroy L. R. (1984) Direct counting of bacteria preserved with lugol's iodine solution. Applied and Environmental Microbiology, 47, 1191-1192.

Porter G. K., M. L. Pace and J. F. Battey (1979) Ciliate protozoans as links in freshwater planktonic food chains. Nature, 277, 563-565.

Porter G. K. and Y. S. Feig (1980). The use of DAPI for identifying and counting aquatic microflora. Limnology and Oceanography, 25, 943-948.

Priddle J., R. Leakey, C. Symon, M. Whitehouse, D. Robins, G. Cripps, E. Murphy and N. Owens (1995) Nutrient cycling by Antarctic marine microbial plankton. Marine Ecology Progress Series, 116, 181-198.

Quéguiner B., P. Tréguer, I. Peeken and R. Scharek (1997) Biogeochemical dynamics and this silicon cycle in the Atlantic sector of the Southern Ocean during austral spring 1992. Deep Sea Research, 44,69-89.

Rassoulzadegan F., M. Laval-Peuto and R. W. Sheldon (1988) Partitioning of the food ration of marine ciliates between pico- and nanoplankton. Hydrobiologia, 95, 221-230.

Reid P. C. (1987) Mass encystment of a planktonic oligotrich ciliate. Marine Biology, 95, 221-230.

Reitmeier (1994) Untersuchungen zur Verbreitung, zur Biomasse und zum Grazing des Mikrozooplanktons in polaren Gewässern. Bericht der Sonderforschungsbereich 313, Universität Kiel, 48, 1-114.

Riemann F. (1989) Gelatinous phytoplankton detritus aggregates on the Atlantic deep-sea bed. Structure and mode of formation. Marine Biology, 100, 533-539.

Rutgers van der Loeff M. M., J. Friedrich and U. V. Bathmann (1997) Carbon export during the spring bloom at the Antarctic Polar Front determined with the natural tracer 234Th. Deep-Sea Research, 44, 457-478.

Sakshaug E. and O. Holm-Hansen (1984) Factors governing pelagic production in polar oceans. In: Marine phytoplankton and productivity, Lecture notes on coastal and estuarine studies, Vol. 8, O. Holm-Hansen, L. Bolis and R. Gilles, editors, Springer Verlag, Berlin, pp. 1-18.

Sanders R. W. and K. G. Porter (1988) Phagotrophic phytoflagellates. In: Advances in microbial ecology, Vol. 10, K. C. Marshall, editor, Plenum Press, New York, pp. 167-192.

Sarmiento J. L. and J. R. Toggweiler (1984) A new model for the role of the oceans in determining atmospheric P CO2. Nature, 308, 621-624.

Sasaki H. and T. Hoshiai (1986) Sedimentation of microalgae under the antarctic fast ice in summer. Mem. Natl. Inst. Polar Res., Spec. Issue, 40, 45-55.

Scharek R., V. Smetacek, E. Fahrbach, L. I. Gordon, G. Rohardt and S. Moore (1994) The transition from winter to early spring in the eastern Weddell Sea, Antarctica: Plankton

biomass and composition in relation to hydrography and nutrients. Deep-Sea Research, 41, 1231-1250.

Schnack S. B., V. Smetacek, B. Von Bodungen and P. Stegmann (1985) Utilisation of phytoplankton by copepods in Antarctic waters during spring. In: Marine biology of polar regions and effects of stress on marine organisms, J. S. Gray and M. E. Christiansen, editors, John Wiley & Sons Ltd., Chichester, pp. 65-81.

Schnepf E., G. Drebes and M. Elbrächter (1990) Pirsonia guinardiae, gen. et spec. nov.: A parasitic flagellate on the marine diatom Guinardia flaccida with an unusual mode of food uptake. Helgoländer Meeresuntersuchungen, 44, 275-293.

Schnepf E. and M. Elbrächter (1992) Nutritionnal strategies in dinoflagellates. A review with emphasis on cell biological aspects. European Journal of Protistology, 28, 3-24.

Schütt F. (1892) Analytische Planktonstudien. Lipsius and Tischer, Kiel, Leipzig, pp.1-117.

Sherr B. F., E. B. Sherr and G.-A. Pafenhoffer (1986) Phagotrophic protozoa as food for metazoans: a "missing" trophic link in marine pelagic food webs. Marine Microbial Food Webs, 1, 61-80.

Sherr E. B. and B. F. Sherr (1993) Preservation and storage of samples for enumeration of heterotrophic protists. In: Handbook of methods in aquatic microbial ecology, P. F. Kemp, B. F. Sherr, E. B. Sherr and J. J. Cole, editors, Lewis Publishers, Bocaraton, Florida, pp. 207-212.

Sieburth J. M., V. Smetacek and J. Lenz, (1978) Pelagic ecosystem structure. heterotrophic compartments of the plankton and their relationship to plankton size fractions. Limnology and Oceanography, 23, 1256-1263.

Smetacek V. (1975) Die Sukzession des Phytoplanktons in der westlichen Kieler Bucht. PhD thesis, University of Kiel, pp. 1-151.

Smetacek V. (1981) The annual cycle of protozooplankton in the Kiel Bight. Marine Biology, 63, 1-11.

Smetacek V. (1984a) Growth dynamics of a common Baltic protozooplankter: the ciliate genus Lohmanniella. Limnologica, 15, 371-376.

Smetacek V. (1984b) The supply of food to the benthos. In: Flows of energy and materials in marine ecosystems. Theory and practise, M. J. R. Fasham, editors, Nato conference series, series IV: Marine Sciences, Plenum Press, New York, London, pp. 517-547.

Smetacek V and F. Pollehne (1986) Nutrient cycling in pelagic systems: a reappraisal of the conceptual framework. Ophelia, 26, 401-428.

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

Smith Jr. W. O. and D. M. Nelson (1985) Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. Science, 227, 163-166.

Smith Jr. W. O. and D. M. Nelson (1986) Importance of ice edge phytoplankton production in the Southern Ocean. BioScience, 36, 251-257.

Sorokin Y. I. (1971) Seasonal dynamics of plankton productivity in shore and pelagic areas of Rybinsk reservoir. Byull. Inst. Biol. Vodokhran, 3, 7-10.

Sorokin Y. I. (1977) The heterotrophic phase of plankton succession in the Japan Sea. Marine Biology, 41, 107-117.

Sorokin Y. I., A. I. Kopylov and N. V. Mamaeva (1985) Abundance and dynamics of microplankton in the central tropical Indian Ocean. Marine Ecology Progress Series, 24, 27-41.

Spittler P. (1973) Feeding experiments with tintinnids. Oikos, supplement 15, 128-132.

Stoecker D. K., R. R. L. Guillard and R. M.Kavee (1981) Selective predation by Favella ehrenbergii (Tintinnina) on and among dinoflagellates. Biological Bulletin of the Woods Hole Oceanographic Institution, 160, 136-145.

Stoecker D. K.and G. T. Evans (1985) Effects of protozoan herbivory and carnivory in a microplankton food web. Marine Ecology Progress Series, 25, 159-167.

Stoecker D. K., K. R. Buck and M. Putt (1993) Changes in the sea-ice brine community during the spring-summer transition, McMurdo Sound, Antarctica. II. Phagotrophic protists. Marine Ecology Progress Series, 95, 103-113.

Stosch von H. A. and G. Drebes (1964) Entwicklungsgeschichtliche Untersuchungen an zentrische Diatomeen IV. Die Planktondiatomee Stephanopyxis turris - ihre Behandlung und Entwicklungsgeschichte. Helgoländer Wissenschaftliche Meeresuntersuchungen 11, 209-257.

Strathmann R. R. (1967) Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnology and Oceanography, 12, 411-418.

Strom S. L. (1991) Growth and grazing rates of the herbivorous dinoflagellate Gymnodinium sp. from the open subarctic Pacific Ocean. Marine Ecology Progress Series, 78, 103-113.

Strom S. L. and E. J. Buskey (1993) Feeding, growth, and behaviour of the thecate heterotrophic dinoflag'late Oblea rotunda. Limnology and Oceanography, 38, 965-977.

Strom S. L., J. R. Postel C. Booth (1993) Abundance, variability, and potential grazing impact of plank 'es in the open subarctic Pacific Ocean. Progress in Oceanography

Strom S. L. and M. Microplankton growth, grazing and community structure in the northen G ne Ecology Progress Series, 130, 229-240.

Sullivan C. W., K. F Clain, J. C. Comiso and J. Firestone (1993) Distribution of phytoplanktor uthern Ocean. Science, 262, 1832-1837.

Suttle C. A., A. M. C and P. J. Harrison (1986) Grazing of planktonic diatoms by microflagellate. ıkton Research, 2, 393-398.

Swanberg N. R. and (1991) Patterns of sarcodine feeding in epipelagic oceanic plankton. Journal ɔn Research, 13, 287-312.

Takahashi K. (1983) Phaeodarian skeletons: their role in the silica transport to the deep Sea. Science, 222, 616-618.

Takahashi K. (1987) Radiolarian flux and seasonality: climatic and El Niño response in the subarctic Pacific, 1982-1984. Global Biogeochemical Cycles, 1, 213-231.

Takahashi K. (1991) Mineral flux and biogeochemical cycles of marine planktonic protozoa - Session summary. In: Protozoa and their role in marine processes, P. C. Reid, C. M. Turley, P. H. Burkill, editors, NATO ASI Series, Vol. G25, Springer-Verlag, Berlin, pp. 347-359.

Takahashi K. and H. Y. Ling (1980) Distribution of Sticholonche (Radiolaria) in the upper 800 m of the waters in the Equatorial Pacific. Marine Micropaleontology, 5, 311-319.

Tibbs J. F. and S. D. Tibbs (1986) Further studies on the phaeodaria (Protozoa: Radiolaria) of the antarctic seas. Antarctic Research Series, 41, 167-202.

Tréguer P., D. M. Nelson, A. J. van Bennekom, D. J. DeMaster, A. Leynaert and B. Quéguiner (1995) The silica balance in the world ocean: a reestimate. Science, 268, 375-379.

Utermöhl H. (1958) Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. Mitteilungen des Internationalen Vereins für theoretiche und angewandte Limnologie, 9, 1-38.

Venrick E. L. (1978) How many cells to count. In: Phytoplankton manual, A. Sournia, editor, UNESCO, Paris, pp. 167-180.

Verity P. G. and T. A. Villareal (1986) The relative food value of diatoms, dinoflagellates, flagellates and cyanobacteria for tintinnid ciliates. Archiv für Protistenkunde, 131, 71-84.

Verity P. G. (1991) Feeding in planktonic protoza: evidence for non-random acquisition of prey. Journal of Protozoology, 38, 69-76.

Veth C., I. Peeken and R. Scharek (1997) Physical anatomy of fronts and surface waters in the ACC near the 6° W meridian during austral spring 1992. Deep-Sea Research, 44, 23-49.

Wefer, G., Fischer, G. (1991) Annual primary production and export flux in the Southern Ocean from sediment trap data. Marine Chemistry, 35, 597-613.