Response of the larger protozooplankton to an iron-induced phytoplankton bloom in the Polar Frontal Zone of the Southern Ocean (EisenEx)

Joachim Henjes*, Philipp Assmy, Christine Klaas, Victor Smetacek

Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany

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Abstract

The responses of larger (> 50 μm in diameter) protozooplankton groups to a phytoplankton bloom induced by in situ iron fertilization (EisenEx) in the Polar Frontal Zone (PFZ) of the Southern Ocean in austral spring are presented. During the 21 days of the experiment, samples were collected from seven discrete depths in the upper 150 m inside and outside the fertilized patch for the enumeration of acantharia, foraminifera, radiolaria, heliozoa, tintinnid ciliates and aplastidic thecate dinoflagellates. Inside the patch, acantharian numbers increased twofold, but only negligibly in surrounding waters. This finding is of major interest, since acantharia are suggested to be involved in the formation of barite (BaSO₄), a palaeoindicator of both ancient and modern high-productivity regimes. Foraminifera increased significantly in abundance inside and outside the fertilized patch. However, the marked increase of juveniles after a full-moon event suggests a lunar periodicity in the reproduction cycle of some foraminiferan species rather than a reproductive response to enhanced food availability. In contrast, adult radiolaria showed no clear trend during the experiment, but juveniles increased threefold, indicating elevated reproduction. Aplastidic thecate dinoflagellates almost doubled in numbers and biomass but also increased outside the patch. Tintinnid numbers decreased twofold, although biomass remained constant because of a shift in the size spectrum. Empty tintinnid loricae, however, increased by a factor of two, indicating that grazing pressure on this group mainly by copepods, intensified during EisenEx. The results show that iron-fertilization experiments can shed light on the biology and the role of these larger protists in pelagic ecosystem, which will improve their use as proxies in paleoceanography.

Keywords: Iron fertilization; Protozooplankton; Acantharia; Barite; Polar Front; Southern Ocean

1. Introduction

Despite the extensive use of their mineral skeletons as proxies for palaeoceanographic recon-
structions, studies of the diversity and the function of larger protozooplankton (> 50 μm) in pelagic food webs in the Southern Ocean are fairly recent (Gowing and Garrison, 1991; Nöthig and Gowing, 1991; Gowing and Garrison, 1992; Gowing et al., 2001; Klaas, 2001). This size class of the protistan plankton tends to be neglected in standard pelagic studies because larger protozoa are not adequately
represented in water samples examined for phytoplankton nor in net samples for zooplankton. Yet their standing stocks in terms of biomass, albeit generally lower than that of smaller protozooplankton (<50µm), can attain the same range as that of metazooplankton: >0.5 g C m⁻². Hence, larger protozooplankton (>50µm) can be expected to play a significant role in pelagic food webs (Alder and Boltovskoy, 1993).

The phylogenetically heterogeneous taxonomic groups making up this size class differ widely in their ecology and their impact on biogeochemical cycles. Large ciliates and dinoflagellates are abundant herbivores, and the carbonate and siliceous skeletons of foraminifera and radiolaria, respectively, contribute significantly to the underlying sediments (reviewed by Caron and Swanberg, 1990; Garrison and Gowing, 1993). Due to their barium (Ba)-enriched celestite (Ba/Sr,SO₄) skeletons, acantharia play a unique role in the Ba and strontium (Sr) cycles (Bernstein et al., 1987, 1992, 1998), and it has thus been suggested that these organisms influence Ba deposition in the sediments. The degree of barite (BaSO₄) deposition in the sediments is used as a proxy for productivity of the overlying water, although the mechanisms leading to its formation are under debate (Dehairs et al., 1991, 1992, 1997; Dymond et al., 1992; Francois et al., 1995; Dymond and Collier, 1996; Esser and Volpe, 2002; Bernstein and Byrne 2004).

Field observations of foraminiferan and radiolarian abundances, vertical distribution patterns and food web interactions in the Southern Ocean have been carried out in the Weddell Gyre and Weddell–Scotia Confluence (WSC) during austral autumn (Abelmann and Gowing, 1996, 1997) and austral winter (Gowing and Garrison, 1991; Nöthig and Gowing, 1991; Gowing and Garrison, 1992). Results from these studies indicate high variability of abundance, biomass and assemblage composition depending mainly on season and region. Klaas (2001) followed the temporal development of abundances, vertical zonation and community composition of all important taxa during the austral spring along a meridional transect across the Polar Frontal Zone (PFZ) of the Southern Ocean. Her results suggest highest abundances in the Polar Front (PFr) concurrent with phytoplankton blooms and that spring distribution patterns of most groups follow productivity in the water column.

Iron-fertilization experiments provide an ideal context to study the responses of the different protozoan groups to an increase in food supply under in situ conditions. In this study, we followed the responses of larger (>50µm) sarcodinid protozoa (i.e., acantharia, foraminifera, radiolaria and heliozoa), tintinnid ciliates and aplastidic thecate dinoflagellates to a phytoplankton bloom induced during an iron-fertilization experiment in the PFZ of the Southern Ocean (EisenEx). Our aims were to investigate the role of these organisms as a trophic link between smaller protozooplankton and larger metazooplankton (Gowing, 1989) and to study a size fraction and group of taxa of which some are important for paleoceanographic studies (Boltovskoy and Alder, 1992; Boltovskoy et al., 1996; Abelmann and Gowing, 1996, 1997).

2. Material and methods

The mesoscale in situ iron-fertilization experiment EisenEx was conducted in the Atlantic Sector of the Southern Ocean (47°S, 21°E) in austral spring (8–29 November 2000) during the cruise ANT XVIII/2 of the R/V Polarstern. A cyclonic eddy (approximately 120 km wide) shed by the Antarctic PFr was chosen as the “container” for the experiment and its center marked with a drifting buoy. An area of about 40 km² around the buoy was fertilized with four tons of iron sulfate added as acidified solution (Fe(II)SO₄) on three occasions at 8-day intervals (Cisewski et al., 2005). Sulfur hexafluoride (SF₆) was added as an inert tracer at the first iron infusion in order to mark the iron fertilized “patch” (Watson et al., 2001). Inside and outside stations were chosen according to SF₆ concentrations measured along surface surveys. The “in-stations” were situated at the highest observed SF₆ concentrations, whereas “out-stations” were located in adjacent waters with background SF₆ concentrations. The day of the first fertilization (day 0) was referred to as the reference station. A detailed description of the temporal evolution of water column properties during Eisen-Ex is given in the discussion section below.

2.1. Abundance

For quantitative assessment of acantharia, radiolaria, foraminifera, heliozoa, tintinnid ciliates and aplastidic thecate dinoflagellates >50µm, water samples were taken from seven discrete depths (10, 20, 40, 60, 80, 100 and 150 m) at 11 in- and 5 out-patch stations with 12 L Niskin bottles mounted on
a CTD rosette. The entire content of individual Niskin bottles was gently passed through a 10 µm mesh plankton net and concentrated to a volume of 50 ml.

The 50 ml concentrated samples were preserved with hexamine buffered formalin solution to a final concentration of 0.5% and stored at 4 °C in the dark for subsequent counting in the home laboratory. Since the concentration method is inappropriate for quantitative abundance estimates of skeletonless or athecate protozooplankton that can squeeze through or be destroyed by the use of nets (Nöthig and Gowing, 1991), only tintinnids and thecate species were counted within the ciliates and dinoflagellates, respectively.

In the case of the acantharia, organisms were mostly counted directly on board. Although Sr sulfate was not added to the samples to preserve the celestite skeletons of acantharia (Beers and Stewart, 1970; Michaels, 1988), they were recognizable by their myonemes and their soft parts even after partial dissolution of the skeleton.

Organisms were identified and enumerated by inverted light and epifluorescence microscopy (Axiovert 25, Axiovert 135; Zeiss, Oberkochen, Germany) according to the method of Utermöhl (1958). For the wind mixed layer samples (10–80 m), organisms were counted in the volume of a whole chamber (~3 ml), and for the other two depths (100 and 150 m) samples were settled in a 10 ml cylinder (HydroBios, Kiel, Germany) and again the whole chamber was counted. Prior to counting 35 µl of stock solution of the nuclear fluorochrome 4′, 6-diamidino-2-phenylindole (Porter and Feig, 1980) was added to the samples to stain the nucleus. Cells with stained nuclei were considered alive at the time of capture. The nucleus of foraminifera was difficult to see because of their tests. As long as the tests were not translucent (containing no organic matter), individuals were considered alive (Nöthig and Gowing, 1991). All samples were counted at a magnification of 200 ×. A minimum of 30 cells of the abundant taxa was counted with an average of about 70 live cells counted per sample (about twice as many if one includes empty tintinnid loricae). This implies, on average, a 95% confidence interval of approximately ±25% for total live larger protozoan abundances (Lund et al., 1958).

Aplastidic thecate dinoflagellates, tintinnid ciliates, heliozoa, foraminifera and phaeodarian radiolarians, distictively characterized by their central capsular membrane, as well as by a mass of pigmented spherules, the phaeodium, were identified to genus or species according to Haeckel (1887), Schröder (1913), Kofoid and Campbell (1939), Loeblich and Tappan (1984) and Tomas (1996); polycystine radiolarians were grouped according to taxonomy into nasellaria with a non-spherical cell body plan and skeletons varying from simple spicules to complex helmet-shaped structures and spumellaria with a spherical cell body plan, although the skeletons may have very different symmetries, and identified to genus or species after Haeckel (1887); acantharia were not identified further. Juvenile individuals were identified only on the level of class or order. Some of the juvenile foraminifera and radiolarians were smaller than 50 µm and are therefore discussed separately.

Findings by Beers et al. (1982), Bishop et al. (1977, 1978, 1980), Gowing and Garrison (1991, 1992), Michaels (1988, 1991, 1995) and Klaas (2001) showed that larger protozooplankton have pronounced vertical distribution features. Therefore, partial correlation analyses between standing stocks of the different protozoan taxa in relation to biological and physico-chemical parameters in the water column were carried out by comparing discrete depth values from each station sampled.

2.2. Volume measurements and biomass conversion

Biovolumes of larger protozoa were estimated from size measurements and appropriate geometrical shape of at least 30 randomly chosen individuals of each taxon for the tintinnids, dinoflagellates and heliozoa. The biovolumes of foraminifera were determined by assuming a spherical shape and using the longest dimension across the calcite test as the diameter (Bé et al., 1982). Biovolumes of acantharia were calculated assuming a sphere, or a spheroid shape (Michaels et al., 1995). For adult radiolarians, biovolume was measured as the diameter of the spherical central capsule (Michaels et al., 1995).

Cell volume was converted to cellular carbon content through recommended carbon conversion equations using the following carbon-to-volume relationships: for dinoflagellates, \( C = 0.444 \times V^{0.864} \) and for tintinnid ciliates, \( C = 0.679 \times V^{0.841} \), with \( V \) representing total cell volume (µm\(^3\)) and \( C \) describing cellular carbon content (pg carbon cell\(^{-1}\); Menden-Deuer and Lessard, 2000). Although tintinnid ciliates contain carbon in their loricae as well as in their cytoplasm, we did not include carbon from tintinnid
loricae in our calculations, as carbon content of the loricae is unknown. In addition, completely intact loricae inside copepod fecal pellets were common in our samples. Similar observations have been reported by Gowing and Garrison (1992). It is, therefore, likely that carbon from tintinnid loricae is not readily available for higher trophic levels.

For larger protozoa other than ciliates and dinoflagellates, biovolumes were converted to biomass (carbon) using measured carbon:volume ratio estimates from Michaels et al. (1995) (0.08 pg mm$^{-3}$ for acantharia, 0.089 pg mm$^{-3}$ for foraminifera and 0.01 pg mm$^{-3}$ for radiolaria and heliozoa). The carbon estimates should be conservative, as protozoan cytoplasm tends to shrink during fixation (Gowing and Garrison, 1991, 1992; Michaels et al., 1995).

For each station, depth-integrated abundances (individuals m$^{-2}$) and biomasses (mg C m$^{-2}$) were calculated from the discrete depth profiles by trapezoidal integration between adjacent depths of the different groups. For tintinnid ciliates, empty tintinnid loricae, aplastidic thecate dinoflagellates, acantharia and foraminifera integrated values were calculated using data from five adjacent depths between 80 m depth and the surface since a significant decline in abundance below the pycnocline was found at all stations. Total larger protozoa, radiolaria, radiolarian skeletons and heliozoa showed no decline in their vertical distribution; therefore, the data from seven adjacent depths between 150 m depth and the surface were used to calculate integrated biomass and abundance.

3. Results

3.1. Composition of the larger protozooplankton assemblage

Total abundance of larger protozooplankton (> 50 μm) ranged between 113 × 10$^5$ and 316 × 10$^5$ ind. m$^{-2}$ (Fig. 1A). No significant temporal trend in total abundance of larger protozooplankton was observed inside or outside the Fe-enriched patch during EisenEx (Fig. 1A).

Within the fertilized patch, carbon standing stock of larger protozooplankton increased from 200 to 453 mg C m$^{-2}$ with the highest value on day 16 (Fig. 1B). The biomass of total larger protozoa outside the fertilized patch increased from 192 to 291 mg C m$^{-2}$ (Fig. 1B). There was a significant difference between stations inside and outside the fertilized patch in total larger protozooplankton biomass from day 11 ($P < 0.05$, unpaired $t$-test).

**Turborotalita quinqueloba** was the most abundant foraminiferan species present, contributing 20–88% of adult foraminiferan abundances at all stations. **Globigerina bulloides** was second in abundance and accounted for 0–68% of adult foraminifera. **Sticholone zanclea** was the predominant heliozoan species. However, some individuals may have belonged to the *Sticholone* species described by Takahashi and Ling (1980). **Cycladophora bicornis** was the most abundant nassellarian species (0–60% of nassellarian abundance). **Spongotrochus glacialis** and **Protocystis swirei** were the dominant species of spumellaria and phaeodaria, respectively (16–100%...
and 0–100% of abundances, respectively). *Codonolopsis pusilla* and *Cymatocylis* spp. (including *C. antarctica*, *C. calyciformis* and *C. vanhoffeni*) contributed significantly to tintinnid numbers at all stations (32–83%), followed by *Amphorides* spp. (5–28%), with *C. vanhoeffeni* showing an increase in relative importance in the course of the experiment (Fig. 2A and B). Other abundant tintinnid species/genera found were *Salpingella* spp., *Acanthostomella norvegica* and *Protorhabdonella* spp. contributing up to 56% of total larger tintinnid ciliate abundances.

Aplastidic dinoflagellate assemblages were dominated by *Protoperidinium* spp. and *Dinophysis* spp. (Fig. 2C and D).

### 3.2. Temporal evolution and depth distribution of the large protozooplankton taxa

#### 3.2.1. Acantharia

Inside the fertilized patch, abundances of acantharia increased over the 3 weeks of the experiment, from initially $9 \times 10^5$ to $16 \times 10^5$ ind.$m^{-2}$ on day 21 (Fig. 3A). Outside the fertilized patch no temporal trend was observed (Fig. 3A).

Biomass of acantharia showed the same trends as abundances inside and outside the Fe-enriched patch (Table 1). From day 7 on, the difference between in- and out-patch stations in abundance and biomass was significant ($P<0.05$, unpaired t-test).

Acantharia were more abundant in the upper 80 m of the water column inside and outside the Fe-enriched patch ($P<0.05$, Mann–Whitney U-test), resulting in a negative correlation with depth and positive correlation with temperature (Table 2). In addition, acantharian abundances were positively correlated with biological properties in the water column (Chlorophyll *a* (Chl-*a*), phaeopigments, diatoms and heterotrophs; Table 2).

#### 3.2.2. Foraminifera

Total foraminiferal abundance inside the patch showed a sixfold increase (Table 1). Adult foraminifera...
Fig. 3. Temporal development of larger (>50 μm) protozooplankton abundances inside (full diamonds) and outside (open squares) the fertilized patch. (A) Acantharia; (B) adult foraminifera; (C) juvenile foraminifera; (D) helioza; (E) adult radiolaria; (F) juvenile radiolaria; (G) tintinnid ciliates; (H) thecate dinoflagellates. The thin line represents running averages over three temporally adjacent stations inside the fertilized patch. The arrows in panels (B) and (C) indicate the day of the full-moon event.
showed a constant increase in abundance (Fig. 3B). Abundance of juvenile foraminifera, however, was very low until day 3 (0–3 × 10^5 ind. m\(^{-2}\)), when numbers increased to a maximum of 15 × 10^5 ind. m\(^{-2}\) on day 7. By day 21, juvenile foraminiferan abundances had decreased to 5 × 10^5 ind. m\(^{-2}\) (Table 1, Fig. 3C). Inside the fertilized patch, adult (mature) individuals made up 89% of total foraminifera abundances before fertilization and 78% of total abundance on day 21. Outside the fertilized patch adult and juvenile foraminiferan abundances were not significantly different from in-patch values (Fig. 3B and C). The number of empty foraminiferan tests found in course of the experiment was negligible.

Adult foraminifera were more abundant in the upper 80 m of the water column inside and outside the Fe-enriched patch (P < 0.05, Mann–Whitney U-test), resulting in a negative correlation with depth and positive correlation with temperature (Table 2). Juvenile foraminifera showed no significant difference in abundances below and above 80 m depth inside and outside the patch. As in the case of acantharia, foraminfera abundances were positively correlated with biological properties in the water column (Chl-a, phaeopigments, diatoms and heterotrophs; Table 2).

Total foraminiferan biomass increased from 7 to 79 mg C m\(^{-2}\) inside the patch over the 21 days of the experiment. Overall out-patch stations showed no significant difference as compared to the fertilized patch, although highest biomass (39 mg C m\(^{-2}\) on day 21) was lower than inside the fertilized patch. Adult foraminifera clearly dominated foraminiferan biomass, accounting for 60–100% of total foraminiferan carbon inside and outside the Fe-enriched patch.

### 3.2.3. Radiolaria

Total adult radiolarian abundances ranged between 2 × 10^5 and 17 × 10^5 ind. m\(^{-2}\). No temporal trend was observed inside the fertilized patch (Fig. 3E). Consequently, no significant correlations between radiolarian abundances and environmental conditions (with the exception of large dinoflagellates) were found inside the patch (Table 2).

Adult polycystine radolarian abundances ranged from 1 to 10 × 10^5 ind. m\(^{-2}\) with no significant differences between in- and out-patch stations. Adult living phaeodarian abundances showed the same range as the nassellaria (0–3 × 10^5 ind. m\(^{-2}\)) but not at the same stations. Inside the patch no trend was observed, and the phaeodarian species distribution was very patchy. Numbers of living phaeodaria were significantly different between in- and out-patch stations until day 16 because of the high abundances outside the fertilized patch.

Juvenile radiolarian abundances increased from initially 5 × 10^5 ind. m\(^{-2}\) to a maximum of 17 × 10^5 ind. m\(^{-2}\) on day 16 inside the iron-enriched patch but dropped markedly during the last week (Fig. 3F). Outside the fertilized patch abundances of juvenile radiolaria stayed comparatively constant.

### Table 1

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Abundance (×10^5 ind. m(^{-2}))</th>
<th>Biomass (mg C m(^{-2}))</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Day 0</td>
<td>Day 21 in patch</td>
</tr>
<tr>
<td>Acantharia</td>
<td>8.5</td>
<td>16.4</td>
</tr>
<tr>
<td>Adult foraminifera</td>
<td>2.5</td>
<td>16.5</td>
</tr>
<tr>
<td>Juvenile foraminifera</td>
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<td>4.6</td>
</tr>
<tr>
<td>Total foraminifera</td>
<td>3.4</td>
<td>21.1</td>
</tr>
<tr>
<td>Nassellaria</td>
<td>6.4</td>
<td>8.7</td>
</tr>
<tr>
<td>Spumellaria</td>
<td>2.6</td>
<td>2.6</td>
</tr>
<tr>
<td>Phaeodaria</td>
<td>2.0</td>
<td>2.3</td>
</tr>
<tr>
<td>Total adult radiolaria</td>
<td>11.0</td>
<td>13.6</td>
</tr>
<tr>
<td>Juvenile radiolaria</td>
<td>5.1</td>
<td>7.3</td>
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<tr>
<td>Heliozoa</td>
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<td>Tintinnid ciliates</td>
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<td>90.8</td>
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<td>Large thecate dinoflagellates</td>
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<td>Total larger protozooplankton</td>
<td>231.1</td>
<td>306.0</td>
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Table 2
Partial correlation analysis for larger protozooplankton abundances

<table>
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<tr>
<th>Parameter</th>
<th>Protozooplankton group</th>
<th>Tintinnid ciliates</th>
<th>Thecate dinoflagellates</th>
<th>Acantharia</th>
<th>Foraminifera</th>
<th>Radiolaria</th>
<th>Heliozoa</th>
</tr>
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<tr>
<td></td>
<td></td>
<td>In-patch</td>
<td>Out-patch</td>
<td>In-patch</td>
<td>Out-patch</td>
<td>In-patch</td>
<td>Out-patch</td>
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<tr>
<td>Depth</td>
<td></td>
<td>−0.612</td>
<td>−0.527</td>
<td>−0.713</td>
<td>−0.661</td>
<td>−0.437</td>
<td>−0.524</td>
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<td>Temp.(^a)</td>
<td></td>
<td>−0.208</td>
<td>−0.432</td>
<td>0.290</td>
<td>0.332</td>
<td>0.503</td>
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<tr>
<td>Chl-(^b)</td>
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<td>NS</td>
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<td>NS</td>
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<tr>
<td>PP(^c)</td>
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<td>NS</td>
<td>−0.370</td>
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<tr>
<td>Phaeopigments(^d)</td>
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<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>0.282</td>
<td>NS</td>
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<tr>
<td>Diatoms(^e)</td>
<td></td>
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<td>NS</td>
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<td>NS</td>
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<tr>
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<td>NS</td>
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<tr>
<td>Small copepods (&lt;1.5 mm)(^f)</td>
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<td>0.388</td>
<td>NS</td>
<td>0.313</td>
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<tr>
<td>Other ciliates(^f)</td>
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<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>0.210</td>
<td>NS</td>
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<tr>
<td>Dinoflagellates &lt;50 μm(^f)</td>
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<td>−0.258</td>
<td>0.392</td>
<td>−</td>
<td>−</td>
<td>0.269</td>
<td>NS</td>
</tr>
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</table>

Values of correlation coefficients for significant correlations are shown. (NS) = not significant ($P > 0.05$); $N = 96$ (in patch); $N = 42$ (out-patch). Comparison was done using abundance data from discrete samples of all stations and depth sampled and the following parameters: depth (m); Chl-\(^a\) (chlorophyll \(a\) in μg chl-\(a\) l\(^{-1}\)); PP (primary production in μg Cl\(^{-1}\) d\(^{-1}\)); diatom abundance (cells l\(^{-1}\)); small copepod (<1.5 mm), other ciliate and dinoflagellate <50 μm abundance (ind. m\(^{-3}\)); bacterial abundance (cells ml\(^{-1}\));

\(^a\)Cisewski et al. (2005).
\(^b\)Gervais et al. (2002).
\(^c\)I. Peeken (unpubl. data).
\(^d\)Assmy et al. (2007).
\(^e\)Arietta et al. (2004).
\(^f\)Henjes et al. (2007).
Adult radiolaria showed no significant difference in abundances below and above 80 m depth in the fertilized patch. At out-patch stations, nassellaria were more abundant from 80 to 150 m depth than in the upper 80 m ($P<0.05$, Mann–Whitney $U$-test). Juvenile radiolaria were more abundant between 80 and 150 m depth as compared to the upper 80 m, but only within the iron fertilized patch ($P<0.05$, Mann–Whitney $U$-test).

Biomass of adult radiolaria ranged between 1.2 and 9.5 mg C m$^{-2}$ and also showed no temporal trend. Inside the fertilized patch juvenile radiolarian biomass went up from initially 0.2 to 0.5 mg C m$^{-2}$ after 3 weeks. Biomass outside the fertilized patch remained stable (Table 1).

Integrated abundance of radiolarian skeletons ranged between $2 \times 10^5$ and $4 \times 10^5$ ind. m$^{-2}$ and constituted on average 18% of dead+live radiolarian abundances. At individual depths, abundances ranged from 0 to $6 \times 10^4$ empty radiolarian skeletons m$^{-3}$. The radiolarian skeleton assemblage consisted mainly of juvenile nassellaria and spumellaria which could not be further identified. Skeletons of adult individuals belonged to the species *Antarctissa strelkovi* and *Spongrotrochus glacialis*.

3.2.4 Heliozoa

Abundances of heliozoa showed high variability ranging from 0 to $10 \times 10^5$ ind. m$^{-2}$ (Fig. 3D). No temporal trend in heliozoan abundances could be observed, and no significant difference between in- and out-patch stations was found. Heliozoa were more abundant between 80 and 150 m depth at both in- and out-patch stations ($P<0.05$, Mann–Whitney $U$-test). Consequently, heliozoan distribution was positively correlated with depth and negatively correlated with temperature. Overall no significant relationship was found between heliozoan abundances and biological parameters in the water column inside the patch. However, at out-patch stations heliozoa were negatively correlated with bacteria (Table 2).

Heliozoan carbon standing stocks inside and outside the fertilized patch showed the same pattern as abundances, ranging from 0 to 5.6 mg C m$^{-2}$. Biomass of heliozoa was also not significantly different in fertilized and non-fertilized waters (Table 1).

3.2.5 Tintinnid ciliates

Abundances of tintinnid ciliates inside the fertilized patch declined slightly from initially 111 to 91 $\times 10^4$ ind. m$^{-2}$ after 21 days (Fig. 3G). Out-patch stations also showed a decrease, with the lowest value ($20 \times 10^3$ ind. m$^{-2}$) on day 21. No significant difference between stations in and out of the Fe-enriched patch was found. Tintinnid abundances did not correlate with environmental or biological variables inside the fertilized patch. A positive correlation with dinoflagellates <$50$ μm was found for the out-patch stations (Table 2).

Biomass of tintinnid ciliates inside the Fe-enriched patch followed the same trend as abundances, with an initial value of 40 mg C m$^{-2}$ and a final value 31 mg C m$^{-2}$ after 21 days (Table 1). Outside the fertilized patch, biomass of larger tintinnids decreased markedly down to a value of 8 mg C m$^{-2}$ on day 21 (Table 1), resulting in a significant difference between in- and out-patch stations after day 11 ($P<0.05$, unpaired $t$-test).

Tintinnid ciliates were more abundant in the upper 80 m of the water column than between 80 m and 150 m depth both inside- and outside the Fe-enriched patch ($P<0.05$, Mann–Whitney $U$-test).

Integrated abundances of empty tintinnid loricae increased from initially $400 \times 10^3$ to $698 \times 10^5$ ind. m$^{-2}$ (day 21) inside the Fe-enriched patch. Outside the fertilized patch empty loricae first increased in abundance but declined from day 9 to $274 \times 10^5$ ind. m$^{-2}$ after 3 weeks (Fig. 4A). A significant difference between in- and out-patch stations from day 7 ($P<0.05$; unpaired $t$-test) was found. *Acanthostomella norvegica* and *Cymatocylis* spp. accounted numerically for 67% of empty loricae after 3 weeks inside the Fe-enriched patch (73% outside the fertilized patch). Empty *Cymatocylis* spp. loricae declined in relative abundance after day 7 (Fig. 4B and C). Abundances of empty tintinnid loricae from individual depths were significantly correlated with abundances of live tintinnids (partial correlation coefficient = 0.304; $P<0.01$), small copepods (<1.5 mm) (partial correlation coefficient = 0.239; $P<0.05$) (Henjes et al., 2007) and total sarcodines (partial correlation coefficient = 0.371; $P<0.001$) inside the patch. Vertical distribution of empty loricae showed a distinct trend in the course of the experiment, with abundance maxima in the upper 20–40 m of the mixed layer before day 11 and a homogeneous vertical distribution throughout the mixed layer after that. Empty loricae were significantly more abundant in the upper 80 m of the water column inside- and outside the Fe-enriched patch ($P<0.05$, Mann–Whitney $U$-test).
3.2.6. Aplastidic thecate dinoflagellates

Thecate dinoflagellates almost doubled in numbers from initially 47 to $97 \times 10^5$ ind. m$^{-2}$ on day 21 (Fig. 3(H)). Carbon standing stock of aplastidic thecate dinoflagellates also increased in the course of the experiment starting at 51 mg C m$^{-2}$ on day 0 and ending at 102 mg C m$^{-2}$ 3 weeks later (Table 1). No significant differences between in- and out-patch stations were found. Aplastidic thecate dinoflagellates were always more abundant in the upper 80 m of the water column ($P<0.05$, Mann–Whitney U-test).

4. Discussion

The depth of the mixing layer varied considerably over the course of the EisenEx experiment. At the beginning of the experiment the wind-mixed layer depth of 10–50 m was relatively shallow for spring both inside and outside the patch providing favorable light conditions for phytoplankton growth (Cisewski et al., 2005). On day 5 and on two occasions in the second half of the experiment, wind speeds exceeding 20 m s$^{-1}$ (gale force winds) deepened the wind-mixed layer down to 80 m depth and occasionally more. Surface temperatures increased from initially 3.5 to 4.0 °C by day 21 (Gervais et al., 2002). Surface salinity stayed more or less stable at 33.8% (Cisewski et al., 2005). Horizontal dispersion of the patch doubled its size every 4–5 days from initially 40 to 950 km$^2$ by day 21 (Watson et al., 2001). Concentrations of all major nutrients decreased during the experiment but were still high by day 21 inside the patch (>21 μM nitrate, >1.5 μM phosphate, >10 μM silicic acid; averaged over 80 m depth; Gervais et al., 2002).

Out-patch Chl-$a$ concentrations and rates of primary production (range between 128 and 218 mg C m$^{-2}$ d$^{-1}$) remained at similar levels during the 3 weeks of the experiment, indicating that
phytoplankton growth was balanced by mortality. In striking contrast Chl-a concentrations and rates of primary production within the fertilized patch rose steadily during the 3 weeks to 2.5 mg Chl a m\(^{-3}\) and 790 mg C m\(^{-2}\) d\(^{-1}\) on day 19 and 16, respectively (Gervais et al., 2002). The peak-integrated chlorophyll stock in the 80 m mixed layer (231 mg Chl a m\(^{-2}\)) recorded on day 21 is one of the highest reported from any of the iron fertilization experiments carried out so far.

The increase in Chl-a was mostly due to a fivefold increase in diatom abundances dominated by a long, needle-shaped diatom species of the genus *Pseudo-nitzschia* (in particular *Pseudo-nitzschia lineola*) that contributed 30% of total plankton biomass in the surface layer at the end of the experiment (Assmy et al., 2007). Other important species were *Fragilariopsis kerguelensis* (3% of biomass), *Corethron pennatum* (11% of biomass), *Haslea trompeii* (5% of biomass), *Dactyliosolen antarcticus* (5% of biomass), *Proboscia alata* (5% of biomass). Small copepods (<1.5 mm), copepod nauplii and protozooplankton contributed, respectively, 11% (0.7 g C m\(^{-2}\)), 9% (0.5 g C m\(^{-2}\)) and 19% (1.1 g C m\(^{-2}\)) of grazer biomass at the end of the experiment. Aloricate ciliates >20 \(\mu\)m showed an increase in abundance as well as in biomass. Aplastidic thecate (<50 \(\mu\)m) and athecate dinoflagellates initially showed a strong increase until the middle of the experiment and declined to about double the initial values by the end of the experiment (Henjes et al., 2007). Medium (<2 mm) and large-sized (>2 mm) suspension-feeding copepods contributed 55% (3.2 g C m\(^{-2}\)) of the biomass of grazers (Schultes et al., 2006). A twofold increase in copepod fecal pellet carbon during the experiment indicated at least a corresponding increase in copepod grazing pressure inside the patch (Henjes et al., 2007). Bacterial abundance almost doubled inside the patch and remained constant outside with no changes in bacterial community composition (Arrieta et al., 2004).

### 4.1. Larger protozooplankton abundances and biomass

Larger protozooplankton are a common component of the micro- and mesozooplankton in many marine environments (Beers et al., 1975, 1982; Bishop et al., 1977, 1978, 1980). However, their abundance and biomass have generally been underestimated because of methodological constraint. Understanding patterns of larger protozoan abundance is a necessary initial step in determining the ecological role of these organisms and interpreting the paleoceanographic record.

Large (>50 \(\mu\)m) protozoan assemblages were numerically dominated by tintinnids and aplastidic thecate dinoflagellates. In terms of biomass, however, acantharia, foraminifera and polycystine radiolaria were equally important. In contrast to previous studies (Gowing and Garrison, 1992; Abelmann and Gowing, 1996; Klaas, 2001), small phaeodaria were a minor component of large protozoan assemblages, whereas the relative contribution of tintinnids and aplastid thecate dinoflagellates to biomass was higher. Maximum initial values of abundance and biomass of larger protozooplankton found during EisenEx (286181 ind. m\(^{-3}\) and 2261 \(\mu\)g C m\(^{-3}\) respectively, at 40 m depth) are significantly higher than spring values found during a similar study in the PFr region: Klaas (2001) found maximum values from 10930 ind. m\(^{-3}\) (452 \(\mu\)g C m\(^{-3}\)) of larger (>64 \(\mu\)m) protozoa in the upper 100 m in the PFr region during austral spring. The significantly higher abundances found in the present study may be partly due to the use of Niskin bottles for sample collection, the gentle concentration method and the use of smaller mesh sizes (10 \(\mu\)m instead of 64 \(\mu\)m) for concentrating the samples. The methodological differences in sampling can cause these organisms to be underestimated by plankton nets by an order of magnitude compared to densities calculated from Niskin bottle samples (Michaels, 1988). Results of this study support the assumption that larger protozooplankton can be seasonally and spatially abundant and thus might have a larger impact on biological and geochemical processes in the upper layers of the Southern Ocean than previously thought.

### 4.2. Response of the large protozooplankton assemblage

#### 4.2.1. Acantharia

The maximum initial abundances of acantharia (16812 ind. m\(^{-3}\) in 10 m depth) found during this study were among the highest ever observed in Southern Ocean waters. The maximum fall abundance in the Weddell Sea was 2758 m\(^{-3}\) (Gowing, 1989), and winter abundances did not exceed 342 m\(^{-3}\) in the upper 85 m (Gowing and Garrison,
1992). In the southeastern Atlantic, Bishop et al. (1978) observed a maximum concentration of ~33000 ind. m\(^{-3}\) in the surface layer during summer. Generally, acantharia abundances in the upper 200 m in lower latitude waters range from <1 to 30000 m\(^{-3}\) (reviewed by Caron and Swanberg, 1990).

Inside the fertilized patch, acantharia increased in abundance in the upper 80 m of the water column, with net accumulation rate of 0.07 d\(^{-1}\), similar to the rates shown by many phytoplankton species inside the Fe-enriched patch (Assmy et al., 2007). Acantharia responded to favorable food concentrations by increasing population size indicating that they were actively feeding. Studies by Trégouboff (1957) and Strass et al. (1991) showed that acantharia feed predominantly on tintinnids and other ciliates, but also on bacteria, diatoms, dinoflagellates and even small metazoans in lower latitudes. Also, the positive correlations between acantharian abundances and various possible food sources (Table 2) is a further indication of active feeding.

In addition, unidentified symbiotic algae were observed in several specimens examined by epifluorescence microscopy. This is a commonly observed phenomenon in many acantharian species in lower-latitude oligotrophic regions (Michaels, 1988; Michaels, 1991; Caron et al., 1995) as well as in the Southern Ocean (Gowing and Garrison, 1992). In a seasonal study in the North Pacific, Michaels (1991) found that these symbionts could meet 50–100% of their host’s respiratory requirements based on symbiont primary production measurements; furthermore, the energy substrate provided by the symbiont might allow the host to use prey biomass more efficiently (Michaels, 1988). A combination of active feeding and stimulation of symbiont photosynthesis by iron fertilization could also have led to the population growth of acantharia in the fertilized patch.

Data on grazing impact of larger metazoan predators on the acantharian community are lacking from the EisenEx experiment; however, estimates of grazing rates and feeding selectivity of dominant copepods suggests that in spite of changes in food selectivity, copepod ingestion rates increased for all food types in the Fe-enriched patch (Schultes et al., 2006). Hence, if anything, grazer-mediated mortality of acantharia should have increased in the Fe-enriched patch.

The life cycle of acantharia is far from being completely understood, but nutrition appears to affect growth rates in many sarcodines (Bé et al., 1982; Bjorklund and Swanberg, 1987). Still, our study indicates that acantharia are able to respond to iron fertilization and increased productivity on very short time scales. This might have important consequences for present productivity and Sr and Ba cycling (Bernstein et al., 1987, 1992, 1998).

Estimates of the carbon fixation ability of acantharian symbionts show that they are able to account for up to 41% (102 µg C m\(^{-3}\) h\(^{-1}\)) of the total carbon fixed in the upper euphotic zone of lower-latitude oligotrophic waters when acantharian abundances are high (30000 m\(^{-3}\); Michaels, 1988). During EisenEx, acantharia were very abundant (up to 43000 m\(^{-3}\) on day 19, 10 m) suggesting that the symbionts of these organisms could significantly contribute, at least locally, to total primary productivity. Acantharian abundances peaked in the upper 20 m of the water column at most of the stations. Deeper maxima (60 m) were found only after storm events, supporting the findings of Michaels (1988) that the need for light of symbionts might control their position in the water column and imply a preference for surface waters during calmer weather conditions.

4.2.2. Foraminifera

Maximum initial abundances of foraminifera during this study (8406 ind. m\(^{-3}\) in 10 m depth) are comparable to values found by Klaas (2001) during austral spring in the same area (maximum 6118 ind. m\(^{-3}\) in 50–100 m depth interval). T. quinqueloba, which was the most abundant species during EisenEx, is known to have highest abundances during spring bloom conditions north of the PFr (Kemle-von Mücke and Hemleben, 1999). Significantly higher densities of foraminifera in the same size range as considered in this study were observed in the upper 100 m of the southeast Atlantic Ocean during summer (44000 ind. m\(^{-3}\); Bishop et al., 1978).

Adult foraminiferan abundances and biomass increased significantly inside the fertilized patch but showed also an increase in the surrounding water (Fig. 3B) and were positively correlated with phytoplankton, bacteria and small dinoflagellates. Studies by Gowing (1989) and Gowing and Garrison (1992) during austral winter and fall in the Weddell Sea show that foraminifera tend to feed predominantly on diatoms and other algal cells, but particularly spinose species are known to consume mainly heterotrophic prey (Hemleben et al., 1989). Foraminifera were also positively correlated with
phaeopigments (an indicator of algal detritus), suggesting that they could be feeding on sinking detritus with associated plankton cells. During EisenEx, foraminifera were significantly more abundant above 80 m depth than below inside the patch and showed clear peak abundances in the chlorophyll maximum (60 m depth) in the course of the experiment. Thus, results during this study support the findings from lower latitude waters where foraminifera tend to concentrate in the chlorophyll maximum developed mostly at the bottom of the euphotic zone. However, abundances and standing stocks of foraminifera also showed an increase outside the patch, although no marked increase in phytoplankton was found. In the first week of the experiment, we found indications that the abundance of some species of foraminifera might be influenced by the phase of the moon. To analyze the trends of the juvenile fraction, residuals were calculated as recommended by Bijma et al. (1990). We found that about 3–5 days after the full moon (on day 3 after fertilization) inside and outside the fertilized patch, a significant increase in juveniles occurred with maximum abundances on the fourth day after the full-moon event, but decreased in numbers thereafter to less than half of peak values (Fig. 3C). Moreover, abundances of adult (mature) foraminifera showed a clear maximum in deeper waters (100 m) in the station after full moon. Previous observations of several authors have clearly demonstrated that at least some species have a synodic lunar periodicity in their reproduction cycle with gametogenesis occurring mainly within a time span of 3–7 days after full moon deeper (>60 m) in the water column (Spindler et al., 1979; Hemleben et al., 1989; Bijma et al., 1990). From the species present during EisenEx, one (G. bulloides) has been shown to reproduce following a lunar cycle (Schiebel et al., 1997) or even reproduce twice a month (Marchant, 1995). Our study indicates that mass reproduction around full moon explains the concurrent increase in foraminifera abundance inside and outside the fertilized patch. However, since juveniles could not be identified to species level, it is not possible to say which species went into reproduction phase.

4.2.3. Radiolaria

High variability in radiolarian abundances and biomass were found with no significant difference between in- and out-patch stations. Nevertheless the maximum initial abundances (11882 ind. m\(^{-3}\) in 80 m depth) of adult radiolaria are higher than those reported in studies from the Southern Ocean. In winter, Gowing and Garrison (1992) reported maximal values of 2663 ind. m\(^{-3}\) in the Weddell and Scotia Sea. At the PFr in spring, Klaas (2001) found maximum abundances of 3803 m\(^{-3}\) in the 50–100 m depth range, and in austral fall Gowing (1989) observed maximum densities of 4647 m\(^{-3}\) at 150 m depth. In the coastal upwelling regions in the southeastern Atlantic, however, abundances of radiolaria can reach values of >10000 m\(^{-3}\) during summer (Bishop et al., 1978). Furthermore, an increase in abundances of juvenile individuals inside the patch was observed which is an indication that reproduction was possibly enhanced. Hence, although radiolarians did not respond within the time span of our experiment due to higher grazer-mediated mortality or to lower intrinsic growth rate compared with that of acantharia, one cannot rule out a response to enhanced primary production. Since we have currently no reason to believe that radiolaria are grazed preferentially as compared to other sarcodines, the second explanation is however more likely.

4.2.4. Heliozoa

Species of the heliozoan genus Sticholonche have been investigated in the Southern Ocean. In the western Weddell Sea, in the WSC and west of the Antarctic Peninsulas studies were conducted in autumn (maximum 4215 ind. m\(^{-3}\) at 100 m depth; Gowing, 1989) and winter (maximum 2779 ind. m\(^{-3}\) in the 115–125 m depth range; Gowing and Garrison, 1992) and north of the PFr in spring (maximum 1512 ind. m\(^{-3}\) in the 50–100 m depth interval; Klaas, 2001). The use of larger mesh sizes by Klaas (2001) might, however, have led to an underestimation of abundances. All studies showed that Sticholonche spp. was concentrated below 80 m depth. During this study heliozoan abundances were also significantly higher below the pycnocline and showed a significant correlation with depth inside the patch, confirming previous observations that, in the Southern Ocean, Sticholonche spp. tends to grow at the base of the mixed layer. Abundances found during EisenEx (13151 ind. m\(^{-3}\) in 100 m) were the highest recorded for the Southern Ocean (Gowing, 1989; Gowing and Garrison, 1992; Klaas, 2001), further indicating that abundances of Sticholonche spp. show seasonality with lower values during winter and an increase in abundances from early spring to fall (Klaas, 2001). However, during EisenEx
abundances inside and outside the Fe-enriched patch remained similar in the course of the experiment, suggesting lower intrinsic growth rates than acantharians.

Abundances of *Sticholonche* spp. in lower latitudes (e.g., equatorial Pacific and East China Sea) can be markedly higher and with peak values tightly associated with Chl-α concentrations and at shallower depths (Takahashi and Ling, 1980; Tan et al., 1978). At present it is not clear why circumpolar populations of *Sticholonche* spp. show different distribution patterns as compared to low-latitude heliozoa. One might speculate that Southern Ocean species have a different ecological pattern, feeding on detritus rather than planktonic organisms.

4.2.5. *Tintinnid ciliates*

As a group tintinnid ciliates decreased in abundance over the experiment, but the behavior of individual species was more complex. Tintinnids, in contrast to dinoflagellates, have restrictions imposed by the lorica opening on the size of particles they can ingest. So the noticeable increase in importance of the larger species, predominantly *Cymatocylis vanhoffeni*, during the experiment might have been due to the concomitant increase in phytoplankton size with bloom progression.

Empty tintinnid loricae increased twofold in the course of the experiment, making up to 89% of total (empty + live) tintinnid loricae. The high percentages of empty tintinnid loricae found during this study are comparable with values observed by Nöthig and Gowing (1991) and Klaas (2001) both of whom counted multi-net samples. Klaas (2001) concluded that her high percentage of empty loricae was possibly due to the use of nets for sampling, causing the tintinnids to detach from the loricae because of mechanical disturbance. This assumption was supported by studies of Gowing and Garrison (1992), who found significantly lower percentages of empty loricae in the WSC during winter by counting reverse-filtered water samples (23–85% depending on depth and species). Comparison of the temporal trend of both empty and full loricae during EisenEx from concentrated (this study) and non-concentrated (Henjes et al., 2007) samples showed no significant difference (linear regression analysis, \( P > 0.05, R^2 = 0.921 \)), suggesting that the concentration procedure did not affect the temporal trends of live or empty tintinnid loricae.

The presence of abundant empty tintinnid loricae during EisenEx could be also due to preservation. We compared the morphology of naked ciliates in concentrated samples to tintinnids with a lorica and did not see convincing evidence that the naked ciliates in the samples corresponded to tintinnids having shed their lorica. Hence, the preservation of samples, which can provoke detachment of the cell from the lorica, as indicated by Paranaje and Gold (1982), seems to have had a minor influence on abundances during this study. Cell lysis upon fixation could also contribute to the high proportion of empty loricae in our samples. Studies by Leakey et al. (1994) and Karayanni et al. (2004) found no significant differences in abundance of full and empty loricae treated with different fixatives, but the authors pointed out that cell lysis is taxon-specific. We can, therefore, not rule out that some fraction of the empty tintinnid loricae was produced during fixation of samples. During EisenEx, an enhancement in abundance of empty tintinnid loricae could also be due to higher grazing by other heterotrophic protists or crustaceans following release from disintegrating fecal pellets (Henjes et al., 2007). The fact that the smaller *Acanthostomella norvegica* and *Cymatocylis* spp. accounted generally for the highest relative amount of empty tintinnid loricae (Figs. 4B and C) could indicate that they were preferentially grazed because of their optimal size (Henjes et al., 2007).

Tintinnid abundances were significantly higher in the upper 80 m of the water column and negatively correlated with depth. Peak abundances often occurred between 10 and 60 m depth. Below 80 m depth tintinnid concentrations decreased significantly, and only a few individuals m\(^{-3}\) were found at 150 m depth. This distribution pattern is similar to the spring distribution patterns described by Klaas (2001), who found highest abundances of tintinnid ciliates between 50 and 100 m in the PFZ. Our results therefore support the assumption of Klaas (2001) that larger tintinnids (>50 μm) live primarily in the surface-mixed layer with the tendency to accumulate at the base of the euphotic zone. However, their distribution within the mixed layer inside the patch seemed to be dependent mainly on food concentrations, which appeared to be primarily nanophytoplankton but also diatoms, at least in the first half of the experiment (Henjes et al., 2007). These findings are in good agreement with observations of Gowing (1989) and Gowing and Garrison (1992), who found that food vacuoles of autumn and winter tintinnids also contained diatoms. However, size of prey consumed by
tintinnid ciliates does not generally exceed 45% of their lorica diameter (Heinbokel, 1978). Therefore, it is likely that long diatom chains and large diatoms species, which contributed to 80% of total diatom abundance (Assmy et al., 2007), would have been difficult to ingest for these ciliates. Therefore, diatoms probably made up only a small fraction of their diets in the latter half of the experiment.

4.2.6. Aplastidic thecate dinoflagellates

Results from this and previous studies indicate that thecate dinoflagellate abundances show strong seasonality, with low values during winter (maximum 160 m\(^{-3}\), Nöthig and Gowing, 1991) and an increase in abundances from spring (average 40926 m\(^{-3}\), this study) to summer and fall average (109000 m\(^{-3}\), Alder and Boltovskoy, 1991) in Southern Ocean waters.

Aplastidic thecate dinoflagellate abundance and biomass doubled inside the fertilized patch but with a high variability between stations and were significantly correlated with Chl-\(a\), primary productivity and diatom abundance. Apparently these organisms were able to respond to increased productivity and diatom standing stocks during the Fe-induced bloom with population growth which suggests that overall distribution and seasonal patterns are possibly related to productivity and prey concentration. Depth distribution, with significantly higher abundances of thecate dinoflagellates in the upper 80 m, also supports these conclusions. Thecate dinoflagellate assemblages were dominated mainly by species of the genus _Protoperidinium_ (Nöthig and Gowing, 1991; Gowing and Garrison, 1992; Klaas, 2001; this study). This genus can feed on large diatoms and diatom chains (reviewed by Jacobson, 1999) and their generation times are on the order of days (0.06–0.15 d\(^{-1}\); Archer et al., 1996). However, during austral spring, Klaas (2001) found no significant response of aplastidic thecate dinoflagellates to the increase in phytoplankton standing stocks (~2 mg Chl \(a\) m\(^{-3}\)) at the PFr. Klaas (2001) concluded that loss terms, such as grazing pressure by mesozooplankton, might influence heterotrophic dinoflagellate distribution in addition to productivity during spring. Findings by Jeong (1994) and Merrell and Stoecker (1998) indicate that even nauplii and copepodites actively feed on heterotrophic dinoflagellates >40 \(\mu m\). Since very high abundances of metazoa, especially copepod nauplii, copepodites and adults of small species were found during the experiment (average of 40378 ind. m\(^{-3}\)) and were positively correlated with aplastidic thecate dinoflagellate abundances, grazing pressure on aplastidic thecate dinoflagellates during EisenEx should have been significant (Henjes et al., 2007).

5. Conclusions

The temporal evolution of large (>50 \(\mu m\)) protozoan assemblage could be followed during an iron-induced phytoplankton bloom in the PFr region of the Southern Ocean. Overall initial large protozoan abundances and biomass were higher than during similar studies in the Southern Ocean. Abundances were dominated by tintinnids and aplastidic dinoflagellate, but acantharians, foraminifera and polycistine radiolaria were equally important contributors to biomass. In contrast to previous studies, however, we observed a higher contribution of tintinnids and aplastidic thecate dinoflagellates to large protozoan biomass, whereas the contribution of small phaeodaria was relatively minor. During this study only acantharia and aplastidic thecate dinoflagellates showed a response to the increase in productivity within the iron-enriched patch, suggesting that the other sarcodine groups studied have longer generation times than covered by the duration of our study. In particular, the response of the dominant foraminiferal species seemed to be constrained by their lunar reproduction cycle. In the case of tintinnids the lack of response to productivity possibly reflects increased grazing pressure within the fertilized patch (Henjes et al., 2007). Our results shed new light on the ecology of large heterotrophic protists and their potential role in pelagic ecosystems, but there are still many fundamental gaps in our understanding of their function in marine food webs, their life cycles and their response to changes in environmental conditions.

The ability of acantharia to respond to rapid changes in productivity qualifies them as a quantitative indicator of productivity. Barite, a potential proxy for primary production, would be the logical signal from the acantharia, but there are other likely sources, such as diatom aggregates (Esser and Volpe, 2002), that might be distinguishable.

Although foraminiferan biomass is only a fraction of the total phagotrophic protist biomass, their shells contribute a disproportionately large amount to the underlying sediments. A better understanding of the ecology of sarcodines is, therefore, of
particular interest to the investigation and understanding of the paleoceanographic record.

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