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# Selective feeding by benthic foraminifera on phytodetritus on the western Antarctic Peninsula shelf: evidence from fatty acid biomarker analysis

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ABSTRACT: This study presents the first direct evidence, based on biochemical analysis of fresh material, that certain benthic foraminifera feed selectively on specific components of seasonally deposited phytodetritus in their natural environment. Three abundant species of benthic foraminifera, the calcareous species *Globocassidulina subglobosa* and *Quinqueloculina seminula* and the agglutinated species *Thurammina albicans*, collected after the deposition of phytoplankton bloom material at a shelf site (560 m water depth) west of the Antarctic Peninsula in March 2001, showed significant differences in their fatty acid profiles compared to the surrounding phytodetritus. Furthermore, the 2 calcareous species contained significantly higher amounts of polyunsaturated fatty acids (PUFAs) than were found in their presumptive phytodetrital food source, indicating that the foraminifera discriminate between, and selectively feed on, the different components of the deposited material. Possible implications for the benthic food web are discussed.

KEY WORDS: Foraminifera · Selective feeding · Polyunsaturated fatty acids · Benthic food web · Antarctic Peninsula shelf



## INTRODUCTION

Antarctic marine environments are characterised by intense seasonality. High nutrient concentrations in seasonally ice-covered Antarctic coastal and shelf areas lead to a massive phytoplankton bloom following the melting of the ice sheet in spring and early summer. A major part of this particulate organic material can be deposited on the seafloor (e.g. Gutt et al. 1998, C. R. Smith et al. 2002) where it is available as food for the benthic community. The seasonality of nutrient input is probably the most significant ecological feature of Antarctic shelf environments (Clarke 1988, Arntz et al. 1994), where foraminifera, similar to deep-sea (Tietjen 1971, Paul & Menzies 1974, Coull et al. 1977, Thiel 1983, Snider et al. 1984, Gooday 1986, K. L. Smith et al. 2002) and other polar environments (Basov 1974, Basov & Khusid 1983), often represent a substantial proportion of the abundance and biomass of benthic communities. Experimental studies indicate that deep-sea species can rapidly ingest a substantial proportion of fresh organic matter after depositional events (Altenbach 1992, Levin et al. 1999, Moodley et al. 2002), leading to increases in population sizes (Heinz et al. 2001, 2002). The potential importance of foraminifera in the cycling of organic matter is also suggested by the high respiration rates of some common species of intertidal benthic foraminifera, which may be 10 times higher than those of naked amoebae of a comparable size (Hannah et al. 1994). In environments where they are abundant, foraminifera may contribute significantly to the benthic carbon cycle (Gooday et al. 1992, Moodley et al. 2000). For example, it is possible that foraminifera, together with bacteria, are responsible for the decomposition of a major part of the labile organic matter deposited on the deep-sea floor (Moodley et al. 2002).

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Selective feeding by a number of foraminiferal species has previously been demonstrated under laboratory conditions (e.g. Bradshaw 1955, Murray 1963, Lee 1966, 1980, Muller 1975, Lee et al. 1988, Kitazato & Ohga 1995), and has been suggested based on field observations or implicated by isotope tracer studies (e.g. Levin et al. 1999, Moodley et al. 2000). In contrast to the previously mentioned studies, this study is the first to directly demonstrate, by analysing full fatty-acid profiles, the selective feeding by certain benthic foraminifera in their natural environment after a natural depositional event.

Fatty acids, in the form of different types of lipids, are essential cellular components of all organisms. They occur as phospholipids in cell membranes and serve, for example, as energy-storage materials in the form of triacylglycerols and wax esters. Certain fatty acids can be used as biomarkers for marine microorganisms such as microphytoplankton (e.g. Sargent & Henderson 1995), or to trace the origin of particulate organic matter on the seafloor (e.g. Boon & Duineveld 1996, Wakeham et al. 1997, Fileman et al. 1998). By identifying individual components in a studied organism, fatty acid biomarker analyses allow conclusions to be drawn regarding its food source, and thus facilitate the direct observation of selective feeding on available organic matter. Researchers studying fatty acid compositions of benthic organisms in the Arctic (Falk-Petersen & Sargent 1982, Graeve et al. 1997, Falk-Petersen et al. 2001) and the deep NE Atlantic (Bühring & Christiansen 2001) were able to identify their respective planktonic food sources and thus demonstrate bentho-pelagic coupling. In this context, (n-3) polyunsaturated fatty acids (PUFAs) such as 20:5(n-3) (Eicosapentaenoic acid: EPA), 20:4(n-6) (Arachidonic acid: AA) and 22:6(n-3) (Docosahexaenoic acid: DHA) are of particular interest. Polyunsaturated fatty acids are produced in large quantities by marine phytoplankton organisms such as diatoms and flagellates, for which some PUFAs can serve as biomarkers (e.g. EPA for diatoms, DHA for flagellates) (Sargent et al. 1987, 1995). Some Antarctic and deep-sea bacteria may also produce PUFAs, but no information is presently available about their relative abundances, biomass and potential contribution to the PUFA pool (Nichols & McMeekin 2002).

In this study, we used fatty acid biomarkers to evaluate the role that some common foraminiferal species, at a 560 m deep site on the Antarctic shelf, may play in the processing of fresh phytoplankton-derived material that is deposited on the seafloor. We specifically addressed the fate of the 'high quality' component of this organic matter, the PUFAs, during the early stages of processing by the benthic community. This study is part of the FOODBANCS project, which addresses the impact and fate of biogenic particles derived from the highly seasonal primary production on the seafloor, at 3 sites situated on the shelf off the western Antarctic Peninsula (C. R. Smith et al. 2002).

## MATERIALS AND METHODS

**Study site.** FOODBANCS site A (65° 10′ S, 64° 46′ W) is located at a water depth of 560 m on the western Antarctic Peninsula shelf, south-west of Anvers Island (Fig. 1). Within the study area, the main pulse of phytodetritus deposition takes place between January and

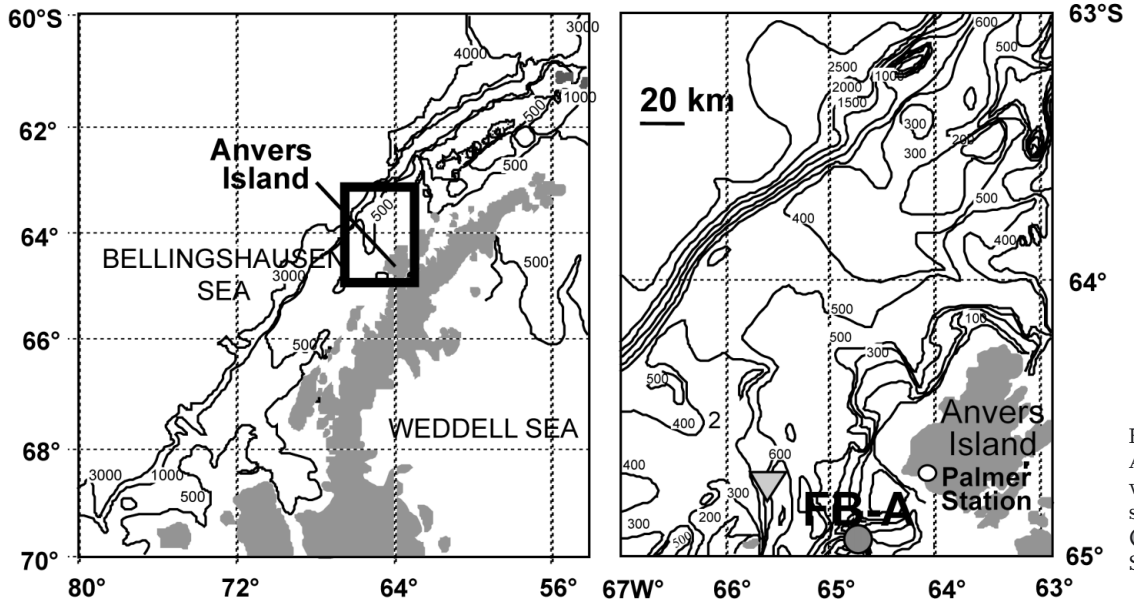


Fig. 1. Northern Antarctic Peninsula with FOODBANCS study area (inlay). ○ = FOODBANCS Site A, ▽ = sediment trap

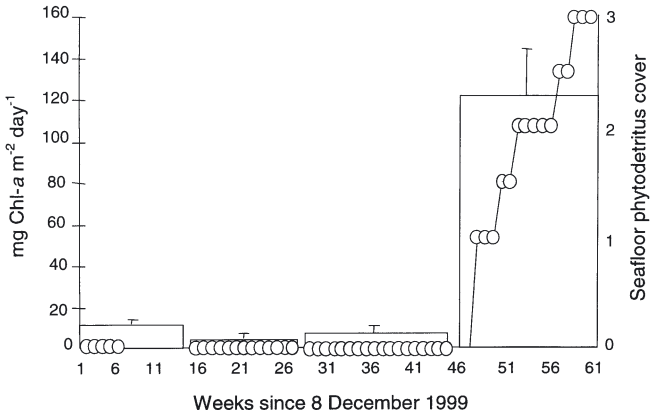


Fig. 2. Chl *a* flux into sediment trap at FOODBANCS Site B (150 m above bottom, *y*1), vs seafloor phytodetritus score (*y*2, histogram, 0 = no phytodetritus, 3 = full phytodetritus cover). Error bars = 95% CI

March, and the estimated mean annual primary production in this region is 143 g C $m^{-2}$ $yr^{-1}$ (Smith et al. 1998a), although the amount of phytoplankton biomass in the Antarctic Peninsula area is variable (Moline & Prézelin 1996, Smith et al. 1998b). The bottom-water temperature is fairly constant at ca. 1.1°C, and oxygen concentrations are ~2 ml $l^{-1}$. Sediments are muddy, with approximately 1% organic carbon content, and current velocities are low. No evidence of sediment resuspension was observed on the 5 cruises to the site over 15 months. A strong seasonal pulse of phytoplankton primary production was recorded in a sediment trap which was deployed further out on the shelf throughout the duration of the project (Fig. 2).

**Sampling procedure.** Three replicate sediment cores were taken at FOODBANCS Site A in October 2000 and 4 in March 2001, in each case from a single megacorer drop (Megacorer Mark II-400, Bowers and Connelly). In October, the 0 to 0.5 cm surface sediment layer of the cores (10 $cm^2$ diameter = 78.6 $cm^2$ surface area) was removed and sieved over a 150 µm screen using chilled and filtered (45 µm) seawater, and the residue was frozen at –80°C. The cores taken in March 2001 had a 2 cm thick layer of loose, recently deposited phytodetritus on top of the sediment surface. In this case, the phytodetritus layer on top of the cores was homogenised by gentle stirring before a 1 ml subsample of the phytodetritus was taken using a cut-off syringe. The remaining phytodetritus was then sieved, and the residues and phytodetritus subsamples were frozen at –80°C.

In the laboratory, the most abundant species present in the 2 sets of samples were established, and as many specimens as possible were picked out of the residues using a Wild dissecting microscope. Actual numbers were: 29 to 36 specimens of *Globocassidulina subglobosa* (150 to 200 µm) in 2 replicate cores, and 4 to 5 specimens of *Quinqueloculina seminula* (>250 µm) in 3 replicate cores (October 2000); 23 to 94 small specimens (150 to 200 µm) of *G. subglobosa*, 4 to 15 of *Thurammina albicans* (>250 µm) and 8 to 13 of *Q. seminula* (>250 µm) in 4 replicate cores each (March 2001). During the sorting procedure, the samples were kept chilled in a small glass Petri dish, which was placed in a larger Petri dish filled with ice and water. Only specimens that were assumed to have been alive (and feeding) at the time of sampling were picked out. Criteria for selection were the presence of distinctly green- or brown-coloured protoplasm and/or detrital material around the aperture. The specimens were transferred into different 1 ml glass vials containing chloroform and methanol in a ratio of 2:1 (v:v). Phytodetritus subsamples were transferred into 10 ml glass vials containing proportionally higher amounts of solvents (1 ml sample + 9 ml solvent mix). Separate quantitative faunal analyses were carried out on 4 (October 2000) or 5 (March 2001) replicate cores from each sampling occasion.

**Fatty acid analysis.** Since only relatively small numbers of specimens were available, a highly sensitive method adapted from Guezennec et al. (1996) and Sonesson et al. (1987) was used, in which free fatty acids are derivatized as Pentafluorobenzyl (PFB) esters and analysed using a gas chromatograph coupled to an electron capture detector (GC-ECD). Derivatisation of the samples was followed by purification through high-performance thin-layer chromatography (HPTLC). A volume of 1 µl of the sample was then injected into the gas chromatograph (Carlo-Erba Trace 2000 series) fitted with a ZBWAX fused silica capillary column (30 m × 0.32 mm internal diameter). Nitrogen, at a flow rate of 35 ml $min^{-1}$, was used as make-up and hydrogen at 2 ml $min^{-1}$ as carrier gas. The following temperature programme was run: initial temperature 80°C, increasing to 190°C at a rate of 40°C $min^{-1}$, then increasing to 230°C at 4°C $min^{-1}$. The temperature remained at 230°C for 47 min, followed by a cooling period of ca. 3 min back to 80°C. Individual fatty acids were identified using fatty acid standards (Marinol and Sigma 37 FAME Standard, derivatised as PFB esters).

All glassware used during extraction, saponification and derivatization of the samples was first thoroughly soaked and washed with industrial detergent (Decon), rinsed with hot tap water and subsequently soaked overnight in distilled water. The glassware was then heated overnight at 550°C in a muffle furnace. Directly before use, every vial, including their tops, was rinsed with solvent (chloroform:methanol, 2:1 v:v) before adding any reagent or sample. The vials were closed with open-top screw caps with Teflon-coated septa. New septa were used at every step in the procedure.

Table 1. Fatty acid compositon (in weight %) of common species (>150 µm) and phytodetritus at FOODBANCS Site A in October 2000 and March 2001. C20 (I) and C20 (II) = unidentified fatty acids of *Globocassidulina subglobosa*, *Quinqueloculina seminula* and *Thurammina albicans*

| | October 2000 | | | | March 2001 | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *G. subglobosa* | | *Q. seminula* | | Phytodetritus | | *G. subglobosa* | | *T. albicans* | | *Q. seminula* | |
| | Weight (%) | SD | Weight (%) | SD | Weight (%) | SD | Weight (%) | SD | Weight (%) | SD | Weight (%) | SD |
| 14:0 | 11.6 | 2.3 | 4.5 | 0.9 | 8.8 | 0.7 | 4.4 | 3.0 | 12.1 | 5.1 | 7.3 | 0.9 |
| 15:0 | 4.4 | 1.8 | 3.5 | 0.7 | 3.0 | 0.3 | 2.0 | 0.6 | 6.4 | 2.8 | 3.8 | 1.7 |
| 16:0 | 6.9 | 15.8 | 12.1 | 3.0 | 19.3 | 3.8 | 11.4 | 2.3 | 33.8 | 10.2 | 20.0 | 2.9 |
| 16:1(n-9) | 2.5 | 2.1 | 2.9 | 1.9 | 4.1 | 3.6 | 1.8 | 0.3 | 3.6 | 2.2 | 1.6 | 0.6 |
| 16:1 (n-7) | 2.7 | 1.8 | 2.6 | 1.4 | 15.3 | 6.8 | 5.9 | 1.0 | 4.4 | 3.1 | 5.5 | 3.2 |
| 16:1 (n-5) | 1.4 | 0.6 | 2.3 | 0.6 | 5.7 | 2.9 | 4.5 | 1.0 | 2.0 | 1.0 | 4.3 | 0.7 |
| 16:4 (n-1) | – | – | – | – | – | – | 0.6 | 0.1 | 0.2 | 0.1 | – | – |
| 17:0 | 2.9 | 0.5 | 2.2 | 1.4 | 2.7 | 0.2 | 1.4 | 1.2 | 2.0 | 1.5 | 2.6 | 1.0 |
| 17:1 | 4.1 | 2.5 | 2.0 | 0.2 | 1.9 | 1.6 | 1.6 | 0.2 | 0.6 | 0.4 | 1.4 | 1.8 |
| 18:0 | 28.1 | 9.5 | 11.6 | 2.3 | 6.9 | 2.9 | 4.2 | 0.5 | 14.8 | 13.6 | 4.3 | 1.6 |
| 18:1 (n-9) | 13.6 | 5.9 | 5.5 | 2.1 | 5.7 | 1.1 | 8.9 | 1.4 | 6.7 | 1.8 | 9.0 | 3.8 |
| 18:1 (n-7) | 4.1 | 0.9 | 16.7 | 2.7 | 8.8 | 1.6 | 8.0 | 1.0 | 2.7 | 2.3 | 16.1 | 2.0 |
| 18:2 (n-6) | 2.1 | 0.9 | 1.0 | 0.4 | 1.5 | 1.2 | 2.9 | 0.4 | 1.2 | 0.5 | 2.5 | 2.2 |
| 18:3 (n-6) | 1.0 | 0.1 | 0.8 | 0.1 | 0.5 | 0.4 | 0.5 | 0.6 | 1.0 | 0.2 | 3.2 | 3.7 |
| 18:3 (n-3) | 0.3 | 0.4 | 1.6 | 1.7 | 0.4 | 0.5 | 0.6 | 0.6 | 0.3 | 0.3 | 0.3 | 0.1 |
| 18:4 (n-3) | 0.0 | 0.1 | 0.1 | 0.1 | 0.2 | 0.2 | 1.2 | 0.8 | 1.4 | 1.6 | 0.7 | 0.4 |
| 20:0 | 3.2 | 1.2 | 1.1 | – | 1.5 | 1.3 | 0.6 | 0.5 | 0.5 | 0.6 | 0.1 | 0.3 |
| 20:1 (n-9) | 1.2 | 0.6 | 1.1 | 0.6 | 0.6 | 0.1 | 0.7 | 0.1 | 0.3 | 0.3 | 0.7 | 0.5 |
| 20:1 (n-7) | – | 0.1 | 0.4 | – | 0.8 | 0.2 | 0.6 | 0.1 | 0.2 | 0.2 | 1.9 | 2.9 |
| C20 (I) | 1.1 | 0.1 | 9.2 | 5.7 | 0.4 | 0.3 | 6.5 | 3.8 | 0.4 | 0.6 | 12.1 | 8.7 |
| 20:4 (n-6) | 0.8 | 0.2 | 9.4 | – | 0.9 | 0.8 | 6.4 | 3.7 | 0.8 | 1.0 | 3.6 | 1.8 |
| C20 (II) | 0.6 | 0.2 | 0.2 | 0.3 | 0.2 | 0.2 | 4.3 | 2.4 | 0.1 | 0.2 | 0.7 | 0.6 |
| 20:4 (n-3) | – | – | – | – | 0.1 | 0.1 | 1.4 | 0.2 | 0.3 | 0.4 | 0.2 | – |
| 20:5 (n-3) | 0.9 | 0.3 | 3.8 | 1.3 | 0.3 | 0.3 | 12.4 | 1.4 | 0.3 | 0.5 | 0.5 | 0.4 |
| 22:0 | 2.3 | 0.9 | 1.2 | 0.1 | 5.2 | 2.7 | 3.4 | 0.6 | 2.9 | 2.0 | 0.7 | 0.2 |
| 22:1 (n-11) | 1.4 | 0.3 | 1.2 | 1.5 | 3.1 | 3.1 | 0.6 | 0.4 | – | – | 0.1 | 0.1 |
| 21:5 (n-3) | 0.2 | 0.3 | 1.6 | 0.3 | – | – | 1.0 | 0.1 | – | – | 0.1 | 0.2 |
| 22:5 (n-3) | – | – | – | – | – | – | 0.7 | 0.1 | – | – | – | 0.1 |
| 22:6 (n-3) | 2.6 | 0.9 | 1.6 | 0.1 | 2.0 | 3.0 | 5.1 | 1.0 | 1.1 | 0.7 | 1.3 | 1.4 |
| PUFAs | 5.7 | 2.3 | 18.9 | 3.6 | 4.5 | 5.3 | 30.0 | 8.7 | 5.4 | 4.7 | 10.0 | 8.0 |

The amounts of biomarker fatty acids in the samples were converted from mol % to weight %. All percentages of fatty acids are given in weight %. Univariate statistical analyses (Kruskal-Wallis ANOVA) were carried out on arcsine-transformed data. Multivariate statistics (multidimensional scaling and pairwise comparisons, ANOSIM) were performed on untransformed data using the software PRIMER (Version 5.1) (Clarke & Warwick 1994, Carr 2001).

## RESULTS AND DISCUSSION

Of the 3 species selected for this study[1], *Globocassidulina subglobosa* was the most abundant, representing on average 19% of the foraminiferal community >150 µm in the 0 to 1 cm layer of the pre-bloom assemblage (October 2000), and 21% in the post-bloom samples from March 2001. The average size of post-bloom specimens of *G. subglobosa* was 185 µm (n = 50). Both *Quinqueloculina seminula* and *Thurammina albicans* were less common, but considerably larger in size (*Q. seminula:* 6.6% of the population in October 2000, 0.3% in March 2001; *Thurammina albicans*: 1.7% in October 2000 and 0.7% in March 2001). On average, both species (*Q. seminula* and *T. albicans*) measured between 250 and 300 µm. Thus, while *G. subglobosa* obviously dominated the assemblage in terms of abundance, the other 2 species were assumed to be important in terms of biomass.

Following a late-summer phytoplankton bloom, a significant amount of organic material was deposited

[1]**Taxonomic notes.** *Globocassidulina subglobosa* Brady, 1884 (=*Cassidulina subglobosa* Brady, 1881). Brady (1884), Plate 54, Fig. 17a–c; Loeblich & Tappan (1988), Plate 557, Figs. 18–23; Mackensen et al. (1993), Plate II, Fig. 9. As *Cassidulina subglobosa* in Echols (1971), Plate 12, Fig. 2; Herb (1971), Plate 4, Fig. 12.

*Quinqueloculina seminula* Brady, 1881 (=*Quinqueloculina seminulum* Linné, 1758). Brady (1884), Plate 5, Fig. 6; Loeblich & Tappan (1988), Plate 344, Figs. 8–13.

*Thurammina albicans* Brady, 1884. Plate 37, Figs. 2–7

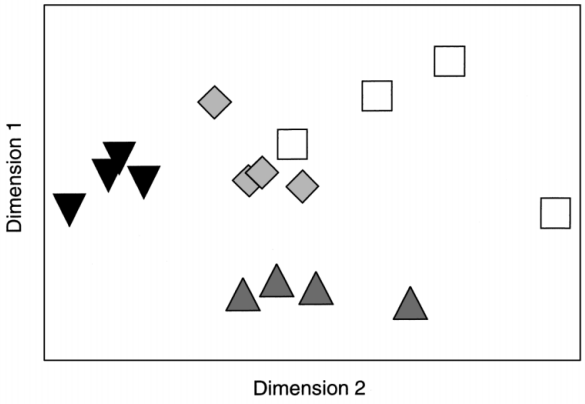


Fig. 3. March 2001. Multidimensional scaling of complete fatty acid profiles of 4 replicate samples for each species and phytodetritus (stress = 0.09). ▼ = phytodetritus, ▲ = *Quinqueloculina seminula*, ◆ = *Globocassidulina subglobosa*, □ = *Thurammina albicans*

at FOODBANCS Site A in March 2001, which was recorded both in a sediment trap situated in relative proximity to the study site, and in photographic images of the seafloor in the study area (Fig. 2). The fatty acid profiles of all 3 benthic foraminiferal species sampled after this depositional event differed substantially from each other, as well as from the surrounding phytodetritus (Table 1), suggesting differing food preferences of the foraminifera. These differences are significant in all cases ($p < 0.05$ ANOSIM), which is also reflected during multidimensional scaling of the complete fatty-acid profiles of the investigated foraminifera and phytodetritus (Fig. 3). In the MDS plot, the 4 replicates of the 3 foraminiferal species and the phytodetritus form separate distinct groups, while the replicate samples of *Globocassidulina subglobosa* and *Quinqueloculina seminula* are grouped tighter than those of *Thurammina albicans*, indicating greater feeding selectivity of these 2 calcareous species, compared to the agglutinated species.

The different behaviour, observed by multidimensional scaling of the replicate samples, of foraminifera and phytodetritus collected in March 2001 reflects primarily their contrasting polyunsaturated fatty acid content. This is significantly higher in the 2 calcareous species ($p < 0.05$, Kruskal-Wallis ANOVA) compared to the surrounding phytodetritus (PUFAs = 4.5%), almost 7 times higher (30%) in the case of *Globocassidulina subglobosa* and more than twice as high (10%) in *Quinqueloculina seminula* (Table 1). In the case of *G. subglobosa*, this seemed to result mainly from a selective ingestion of diatoms, since the diatom biomarker 20:5(n-3) (e.g. Ackman et al. 1968, Sargent et al. 1987, Viso & Marty 1993, Dunstan et al. 1994) alone made up ca. 41% of the polyunsaturated fatty acids in *G. subglobosa*. In contrast, the amount of PUFAs in *Thurammina albicans* (5.4%) did not differ greatly from that in the surrounding phytodetritus. Instead, *T. albicans* contained a much higher proportion of saturated fatty acids, such as 16:0 and 18:0, both products of degradation of unsaturated and longer-chain fatty acids, than the 2 calcareous species. While the proportion of 16:0 and 18:0 in *T. albicans* was, at 48.6%, almost twice as high as in the phytodetritus (26.2%), it was slightly lower in *Q. seminula* (24.3%) and considerably below the phytodetritus value in *G. subglobosa*, in which these 2 fatty acids made up only 15.7% of the total fatty acids. This indicates that *T. albicans* may have been feeding on degraded material to a greater extent than the other 2 investigated species.

A comparison of the fatty acid contents of a small number of replicate samples of the 2 calcareous species, collected previously in October 2000 (before the summer bloom), with samples from March 2001 (after the summer bloom) shows significantly higher ($p < 0.05$) amounts of polyunsaturated fatty acids in the post-bloom samples of *Globocassidulina subglobosa*. The opposite is the case with *Quinqueloculina seminula*, in which the amount of PUFAs is higher in the pre-bloom than in the post-bloom samples (Table 1), although the difference is not statistically significant in this case. Multidimensional scaling of the pre- and post-bloom samples of *Q. seminula* and *G. subglobosa* (Fig. 4) reveals that the fatty acid composition of *G. subglobosa* in October 2000 (no phytoplankton-derived matter) differed significantly (ANOSIM $p < 0.05$) from that in March 2001 (phytoplankton-derived matter present on top of the sediment), while that of *Q. seminula* is relatively similar on both occasions.

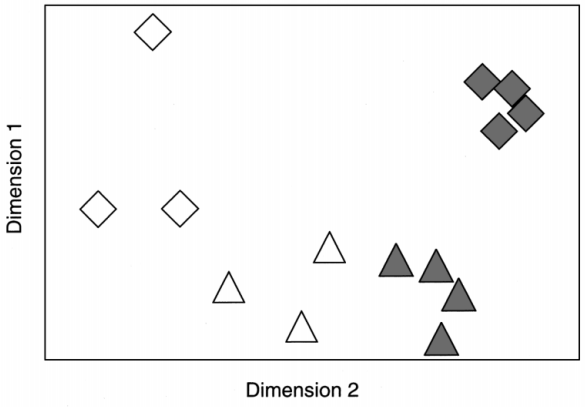


Fig. 4. Multidimensional scaling of fatty acid profiles of *Globocassidulina subglobosa* and *Quinqueloculina seminula* in October 2000 (pre-bloom) and March 2001 (post-bloom) in comparison (stress = 0.1). ◇ = *G. subglobosa*, pre-bloom; ◆ = *G. subglobosa*, post-bloom; △ = *Q. seminula*, pre-bloom; ▲ = *Q. seminula*, post-bloom

It seems that, of the 2 calcareous species, *Globocassidulina subglobosa* shows a more specific response to material derived from the phytoplankton bloom than *Quinqueloculina seminula*, which is in agreement with previous studies. *G. subglobosa* has previously been observed to increase in abundance following seasonal pulses of fresh phytodetritus (Gooday 1988, 1993). It is abundant in other areas of the Antarctic which experience seasonal organic matter input (Ward 1983, Jones & Pudsey 1994, Schmiedl et al. 1997), indicating a specific, significant response to phytodetritus input by this species. Some of the literature for *Q. seminula*, in contrast, indicates a possibly wider range of food preferences, including fresh, phytoplankton-derived matter when it is available, as well as bacteria (e.g. Heeger 1990, Gooday & Rathburn 1999). This is supported by the observation of both substantial amounts of 18:1(n-7), as well as polyunsaturated fatty acids in the post-bloom samples taken at FOODBANCS Site A. 18:1(n-7) is widely distributed in free-living marine bacteria, particulary methanotrophic and thiotrophic species, and is commonly regarded as a bacterial biomarker (e.g. Gillan & Johns 1986, Bowman et al. 1991, Wakeham & Beier 1991, Guezennec & Fiala-Medioni 1996, Pearson et al. 2001).

It has been firmly established that, as well as microphytoplanktonic organisms, some Antarctic marine bacteria, the majority of which are found in sea-ice, may also produce polyunsaturated fatty acids, such as EPA, AA and DHA (Nichols et al. 1993, 1997, Bowmanet al. 1998a,b, Russell & Nichols 1999, Nichols & McMeekin 2002). For this reason, high amounts of any of these fatty acids may not always serve as evidence for the presence of undegraded, phytoplankton-derived organic matter. However, although bacterial densities in sea-ice can be considerable (Palmisano & Sullivan 1983, Grossi et al. 1984, Sullivan & Palmisano 1984, Kottmeier et al. 1987), they may contribute only a small part to overall carbon production (Kottmeier et al. 1987). In contrast, rates of spring phytoplankton primary production on the Western Antarctic Peninsula shelf are high (e.g. Bodungen et al. 1986, Smith et al. 1998b). In addition, no pack ice was observed at FOODBANCS Site A on any of the sampling occasions, although brash-ice streams were present during the 2 spring cruises in December 1999 and October 2000. Thus, it seems reasonable to assume that the major part of polyunsaturated fatty acids in deposited, spring-bloom-derived material may be of phytoplankton origin, and that the high content of PUFAs observed in the 2 calcareous foraminifera after the depositional event reflects a feeding link between the protozoans and the primary production in the overlying water column.

**Implications for the benthic food web**

As a group, foraminifera ingest a wide range of food items and operate at various trophic levels, ranging from unselective deposit feeding, or active selection of certain food items (Lee 1980, Lipps 1983, Goldstein 1999), the uptake of dissolved amino acids (DeLaca et al. 1980, 1981, DeLaca 1982) to carnivory (Buchanan & Hedley 1960, Bowser et al. 1986, 1992, DeLaca 1986). Many species appear to feed at a low trophic level, and it has been widely assumed that they form an important link in the benthic food web between small-sized food items, such as bacteria or microalgae, and larger metazoan species (Lipps & Valentine 1970, Lee & Muller 1973, Brand & Lipps 1982, Gooday et al. 1992). Our study suggests that the overall role of some species of foraminifera in the benthic food web could be more complex than this. The significant difference in the PUFA content of *Globocassidulina subglobosa* between pre- (October 2000) and post-bloom (March 2001) samples indicates that, while this species shows a preference for the PUFA-rich part of phytoplankton-derived organic matter, it only contains high amounts of this component for a short period of time (during and shortly after a depositional event).

PUFAs are thought to be essential for several functions in higher marine organisms (which are generally unable to synthesise them de novo), for example for reproduction efficiency in zooplankton (Gulati & Demott 1997), intracellular signaling in the nervous system of marine mollusks (Piomelli 1991) or the neuronal development of marine fish (Sargent et al. 1999). A number of organisms have been shown to keep high levels of polyunsaturated fatty acids in their cell membranes in order to maintain membrane fluidity at low temperatures or under pressure (e.g. sea-ice and deep-sea bacteria: DeLong & Yayanos 1985, Hamamoto et al. 1994, 1995, Yano et al. 1997, Russell & Nichols 1999). In an ecosystem context, Müller-Navarra et al. (2000) discovered that low transfer-efficiencies between primary and secondary producers in a hyper-eutrophic pelagic ecosystem were very strongly linked to a low content of eicosapentaenoic acid, 20:5(n-3) in the phytoplankton community. Thus, low concentrations or a lack of certain polyunsaturated fatty acids may significantly limit the carbon transfer in aquatic environments.

Interestingly, the 2 calcareous species *Globocassidulina subglobosa* and *Quinqueloculina seminula* contained significant amounts (6.4 and 3.6%, respectively) of 20:4(n-6) (arachidonic acid) (Table 1). Very high amounts of this polyunsaturated fatty acid (16% of total fatty acids) have previously been found in the large agglutinated foraminiferan *Bathysiphon capillare* from the NE Atlantic (Gooday et al. 2002). Arachidonic acid is a major component of the phospholipids

of marine animals, and has a possible role in maintaining cell membrane integrity in deep-sea organisms and in cold adaptation (Harwood & Vigh 1998). There is also accumulating evidence that it plays a vital role in reproductive processes and development in higher organisms (e.g. Leitz et al. 1994, Koven et al. 2001, Sorbera et al. 2001). The significance of the relatively high amounts of this fatty acid in these 2 foraminiferal species is unclear, but may have implications for its availability within the benthic foodweb.

After depositional events, when they contain high amounts of polyunsaturated fatty acids, species such as *Globocassidulina subglobosa* would represent a valuable nutritional resource for other benthic organisms. *G. subglobosa* is common around the Antarctic at water depths from ca. 240 to 4500 m (e.g. Echols 1971, Ward 1983, Mackensen et al. 1990, Ishman & Domack 1994, Jones & Pudsey 1994, Schmiedl et al. 1997). However, it is unclear how many, and which, benthic species depend on foraminifera as a food source. There is evidence that juvenile gastropod species do not choose calcareous foraminifera as food items for their calorific value, but for the calcium carbonate in their shells, which the predators then utilise for their own shell growth (Hickman & Lipps 1983). Similar conclusions may be drawn from a very detailed study of the feeding behaviour of the predatory opisthobranch gastropod *Retusa obtusa* from the Forth Estuary in Scotland (Berry 1994). Benthic foraminifera made up the largest part of the diet in growing juveniles, while food preferences switched to enhanced uptake of the gastropod *Hydrobia ulva* in reproductive specimens. In addition, while many sediment-feeding organisms, including those living in the deep sea, take up foraminifera together with other food items (e.g. Buzas & Carle 1979, Brand & Lipps 1982, Buzas & Sen Gupta 1982, Buzas et al. 1989, Sokolova 2000), they may not actually be digested by the organism in all cases. For example, foraminifera have been observed to pass the guts of the gastropod *Littorina littorea* relatively unharmed, and may resume normal reticulopodial activity on excretion (Walker 1971). The number of specialised predators of foraminifera which have been reported so far is low. Among these are Gastropoda (Brand & Lipps 1982, Hickman & Lipps 1983), Isopoda (Svavarsson et al. 1993, Gudmundsson et al. 2000) and Scaphopoda (Langer et al. 1995). However, nematodes have also been observed to enter foraminifera through their aperture and feed on their protoplasm in a number of instances (A. Rathburn pers. comm. and S. B. Suhr pers. obs.). Because of their great abundance in benthic ecosystems, they may potentially be important predators. Selective predation by nematodes on *G. subglobosa* or similar species after the deposition of fresh organic matter, when they are rich in essential fatty acids, could have implications not only for the benthic food web and carbon cycle, but also for the foraminiferal fossil record. Such selective predation would significantly affect palaeoceanographic reconstructions, for which *G. subglobosa* is widely used (e.g. Corliss 1979, Ishman & Foley 1996, Loubère 1996, Fariduddin & Loubère 1997, Jian & Wang 1997, Jian et al. 1999).

The extent to which foraminifera serve as a link between lower and higher trophic levels in benthic food webs is a major unresolved question. The fatty acid evidence from this study indicates that the 3 species examined had different diets, and therefore potentially different roles in the transfer of essential fatty acids between different trophic levels. Our findings demonstrate the necessity to consider foraminiferal species individually in food web studies, rather than treating them as a single trophic entity. The proposed selective feeding of dominant species observed at our study site on the western Antarctic Peninsula shelf suggests that, if foraminifera act as a nutritional resource for metazoans, they may do so only for a short period during certain times of the year (due to PUFA enrichment shortly after a phytodetrital pulse). On the other hand, the low number of predators described so far that are specialised on foraminifera potentially means that the selective feeding behaviour displayed by some species of foraminfera may decrease the availability of polyunsaturated fatty acids for other organisms in surface sediments. The relative importance of foraminifera in these opposing roles merits further investigation. In addition, the role of polyunsaturated fatty acids in foraminiferal nutrition should be examined in more detail.

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