



Trophic modes of large Antarctic Foraminifera: roles of carnivory, omnivory, and detritivory

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ABSTRACT: *Astrammmina rara*, *Crithionina delacai*, and *Notodendrodes hyalinosphaira* are 3 of the largest and most abundant members of the foraminiferal assemblage at a shallow-water (28 to 32 m) site in Explorers Cove, Antarctica. This study summarizes observations from 2 decades of research, during which we employed laboratory-based feeding experiments and fatty acid biomarker analysis to characterize trophic dynamics and ecological roles of the 3 species. In feeding experiments, *A. rara* consumed a variety of co-occurring metazoans (several Crustacea, Mollusca, Echinodermata, and a *Nephtys* species). *C. delacai*, *N. hyalinosphaira*, and a number of other foraminiferal species from Explorers Cove successfully trapped *Artemia* sp. nauplius prey in a setup designed to examine the efficiency of prey capture. Fatty acid analyses on samples from early (November 7, 2001) and late (January 31, 2002) austral summer revealed that the 3 species contained substantial amounts (33 to 45.5%) of polyunsaturated fatty acids (PUFAs), which are produced by microalgae, indicating the downwards transfer of carbon from sea-ice associated primary production. In the case of *A. rara*, this may be due to the ingestion of herbivorous metazoa, rather than direct uptake of microalgal material. *A. rara* contained significantly ($p < 0.05$) higher amounts of the zooplankton biomarkers 20:1(n–9) and 22:1(n–11), and *C. delacai* contained more PUFAs early, compared to late, in the season. Two morphotypes of *N. hyalinosphaira* had different fatty acid profiles, indicating distinct trophotypes. Our results illustrate specific adaptations to different trophic resources in these protists, and they demonstrate the potential impact that large carnivorous species of Foraminifera may have on the structure of benthic communities where they are abundant.

KEY WORDS: Foraminifera · Trophic ecology · Benthic · Food web · Carnivory · Antarctic · Explorers Cove · Community structure

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INTRODUCTION

Foraminiferans are arguably the most diverse and abundant protists in the marine realm. Calcareous and agglutinated species often constitute a substantial proportion and biomass of benthic communities in deep-sea and polar environments (Basov 1974, DeLaca

et al. 1981, Thiel 1983, Smith et al. 2002). Recently, the abundance and diversity of previously overlooked, soft-shelled species, which can account for 10 to 20% of Foraminifera in deep-sea sediments, have become evident (Gooday 2002). An increasing number of studies is revealing the ecological significance of this group of protists (Gooday et al. 1992, Moodley et al. 2002,

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Suhr et al. 2003, Suhr & Pond 2006). Given that Foraminifera are a major component of marine meio- and macrofaunal communities and have a very long geological history, their trophic mechanisms are of considerable importance in understanding modern and ancient benthic food webs (Lipps & Valentine 1970, Lipps 1983, Goldstein 1999). The present study focuses on the large agglutinated species *Astrammmina rara*, *Crithionina delacai* and *Notodendrodes hyalinosphaira*, which are accessible to SCUBA divers at 28 to 32 m depth under sea ice at a site in Explorers Cove, Antarctica. At this site, densities of large Foraminifera (airlift samples of 0 to 1 cm surface sediment layer, total population >500 μm) can reach up to 6810 ind. m^{-2} (Gooday et al. 1996). Specimens of *A. rara* can grow up to a diameter of 4.5 mm, with an average diameter of 2.1 mm. *C. delacai* may reach up to 6.5 mm in diameter and abundances of up to 2527 ind. m^{-2} in airlift samples, which include specimens larger than 1000 μm (Gooday et al. 1995). Finally, the agglutinated species *N. hyalinosphaira* occurs as 2 different morphotypes. The primary test is a shallow infaunal, unilocular sphere consisting of a single layer of sand grains, mainly quartz, which can either be covered with a thick layer of fine detrital material or else have 1 (rarely 2) 'daisy-shaped' appendage that protrudes vertically into the water column. In the latter 'tree-morph' form, specimens of *N. hyalinosphaira* attain a maximum length of up to 2.7 cm (DeLaca et al. 2002). Most specimens of *N. hyalinosphaira* are found as 'quartz balls' (Gooday et al. 1996).

Initial results from laboratory studies of these 3 conspicuous members of the Explorers Cove foraminiferal assemblage suggested radically different trophic modes. *Astrammmina rara* was previously observed to consume *Artemia* sp. nauplii under laboratory conditions (Bowser et al. 1986, 1992). However, it remained unclear as to whether or not *A. rara* consumes co-occurring metazoan species and whether carnivory occurs *in situ*. Scanning electron microscopic observations revealed diatom spicules in the cell body of *Crithionina delacai* (Gooday et al. 1995). Earlier, radiotracer studies on the related species *Notodendrodes antarcticos* (DeLaca et al. 1981, DeLaca 1982, Rivkin & DeLaca 1990) implicated osmotrophy as a major trophic mechanism in the tree-morph of *N. hyalinosphaira*. DeLaca et al. (2002) suggested that the secondary test features of this species reflect different trophic modes, ranging from the infaunal uptake of dissolved nutrients in the case of the quartz balls to suspension feeding in the tree form. We report the results of additional field and laboratory studies aimed at better describing the trophic habits of these foraminifers, and we discuss the organisms' roles in the benthic community at Explorers Cove and in a wider context.

MATERIALS AND METHODS

Study site and sample collection. The study site and collection methods have been detailed elsewhere (Gooday et al. 1996). Briefly, the silty sand seafloor at Explorers Cove, Antarctica was sampled by SCUBA divers using an airlift apparatus (Pollock & Bowser 1995). Specimens of the tree-morph of *Notodendrodes hyalinosphaira* were recovered by divers using hand-held coring devices.

Feeding experiments. Viability of specimens selected for the experiments was determined by direct microscopic observation of pseudopodial activity. Two types of feeding experiments were conducted according to the methods described by Bowser et al. (1992). To determine the range of possible prey items of *Astrammmina rara*, we kept specimens in Petri dishes at *in situ* temperatures and offered them a range of co-occurring metazoa in austral winter 1986. In a second experiment carried out in November 2006, the prey capture efficiency of a number of foraminiferal species in Explorers Cove was assessed as a function of the number of *Artemia* sp. meta-nauplii (hereafter *Artemia*) trapped by each specimen. In this case, all specimens were kept in Petri dishes, with the exception of the *Notodendrodes hyalinosphaira* tree-morph, which was incubated with nauplii in undisturbed 7.4 cm diameter cores (in an effort to preserve *in situ* conditions). *Artemia* specimens were added at densities up to 1 ml and incubated overnight (i.e. up to 12 h). Prey capture efficiency was described by assigning individuals to 3 different categories: specimens with ≥ 10 attached *Artemia* nauplii were considered to possess high prey capture efficiency, <10 nauplii attached meant lower prey capture efficiency, and specimens without attached nauplii fell into the final category (no prey capture observed). Specimen preparation for electron microscopy was detailed by Bowser & Travis (2000).

Fatty acid biomarker analysis. Samples for fatty acid biomarker analysis of *Astrammmina rara* and *Crithionina delacai* were taken during the early (November 7, 2001) and late (January 31, 2002) austral summer season. After collection, specimens were sorted, snap-frozen in liquid nitrogen, and stored in 1 ml cryovials at -80°C . Five specimens each of *A. rara* and *C. delacai* were analyzed from the early and late sampling occasions. The 2 *Notodendrodes hyalinosphaira* morphotypes were available only from early season samples. From these samples, 5 specimens of the quartz ball and 3 of the tree-morphs were analyzed. In addition, one specimen each of a co-occurring amphipod and a pycnogonid species were analyzed. Fatty acid biomarker analyses were conducted as described previously (Suhr et al. 2003). Biomarker fatty acid contents were converted from mol % to weight %, and univariate sta-

tistical analyses (Kruskal-Wallis ANOVA) were conducted on arcsine transformed data. Multivariate statistical analyses (multidimensional scaling and pairwise comparisons via Analysis of Similarities [ANOSIM]) were carried out on transformed data using the PRIMER version 5.1 software (Carr 2001).

RESULTS

Feeding experiments

Feeding experiments showed that *Astrammmina rara* ingests a wide range of co-occurring metazoan prey (Table 1), including small (<1 cm) crustaceans, mollusks, annelids, and juvenile echinoderms. Only the mollusk *Margarella* sp. and larvae of the ciliated asteroid *Acodontaster* sp. were not captured, even after prolonged (>1 wk) incubation with the viable foraminifer. In no case was *A. rara* consumed by the metazoans. Results from the prey capture efficiency study (Table 2) show that *Astrammmina triangularis*, *Notoden-*

Table 1. *Astrammmina rara*. Metazoan prey captured and killed in the laboratory in austral summer 1986. Foraminiferal and metazoan specimens were collected from Explorers Cove and near McMurdo station ('sp. 1, sp. 2, sp. 3, sp. 4' distinguish species that were not further identified)

Species	Number of specimens offered	Number of specimens consumed
Crustacea		
<i>Eudorella splendida</i>	36	31
Cumacean sp. 2	10	6
<i>Austrosignum grandis</i>	12	9
<i>Echinozone</i> cf. <i>magnifica</i>	4	4
<i>Muna</i> sp. 3	8	5
Isopod sp. 4	4	1
<i>Nototanais dimorphus</i> (♀ & ♂)	9	7
Amphipod sp. 1	7	3
Amphipod sp. 2	5	1
Ostracod sp. 1	5	5
Ostracod sp. 2	1	1
Mollusca		
<i>Cuspidaria</i> sp.	5	5
Bivalve sp. 2	8	8
<i>Limatula hodgsoni</i>	2	2
<i>Margarella</i> sp.	3	0
Gastropod sp. 2	4	3
Echinodermata		
<i>Abatus</i> sp.	3	3
<i>Sterechinus neumayeri</i> juvenile	2	2
<i>S. neumayeri</i> larvae	2	2
<i>Odontaster validus</i> juvenile	1	1
<i>O. validus</i> larvae	2	1
<i>Acodontaster</i> larvae	4	0
Annelida		
<i>Nephtys</i> sp. juveniles	1	1

droides antarctikos, *Notodendrodes hyalinospaera*, *Pilulina* sp., and the calcareous foraminifers *Pyrgo peruviana* and *Cornuspira antarctica* were highly efficient in trapping the metazoa offered, whereas *Crithionina delacai* and *Gloiogullmia* sp. had lower efficiencies in prey capture. In some cases, *Artemia* sp. nauplii were clearly ensnared within pseudopodial networks extending from the test, as shown previously for *A. rara* (Bowser et al. 1992). *A. rara* readily captured nauplii of all sizes and swimming ability and to such an extent that all offered prey were ultimately captured (see also Bowser et al. 1992). In other species (e.g. *Notodendrodes* spp.), prey were seen clustered around certain portions of the test, while other areas were devoid of prey (Fig. 1A). Closer inspection via scanning electron microscopy (SEM) confirmed that pseudopodial networks were restricted to certain areas of the test surface, consistent with the qualitative observations of prey attachment patterns from light microscopy (Fig. 1B). Nauplii were not seen to be trapped by 2 dead specimens of *Pilulina* sp., nor by *Gromia* sp., a related rhizarian protist.

Fatty acid biomarker analysis

Astrammmina rara, *Crithionina delacai* and *Notodendrodes hyalinospaera* (both morphotypes) contained substantial amounts (33 to 45.5%) of polyunsaturated fatty acids (PUFAs) (Tables 3 & 4). PUFAs are produced in large amounts by microplanktonic organisms such as diatoms and flagellates, and can serve as bioindica-

Table 2. *Astrammmina rara*. Results of feeding experiments with *Artemia* sp. nauplii. Total no. of foram specimens: number of specimens of each foraminifer species that fell into each of the defined prey capture efficiency categories. (+++) Heavily labeled Foraminifera, ≥10 *Artemia* attached, high prey capture efficiency; (+) <10 *Artemia* attached, lower prey capture efficiency; (-) not labelled, no *Artemia* attached

Species	Total no. of foram specimens	Prey capture efficiency		
		(+++)	(+)	(-)
<i>Notodendrodes hyalinospaera</i> ^a	8	8	0	0
<i>Crithionina delacai</i> ^a	30	5	11	14
<i>Astrammmina triangularis</i>	17	17	0	0
<i>Notodendrodes antarctikos</i>	4	4	0	0
<i>Pilulina</i> sp.	8	6	0	2 ^b
<i>Gloiogullmia</i> sp.	18	0	6	12
<i>Pyrgo peruviana</i>	7	7	0	0
<i>Cornuspira antarctica</i>	5	5	0	0
<i>Gromia</i> sp.	120	0	0	120

^aFatty acid data presented in Tables 3 & 4
^bSpecimens were dead during experiment

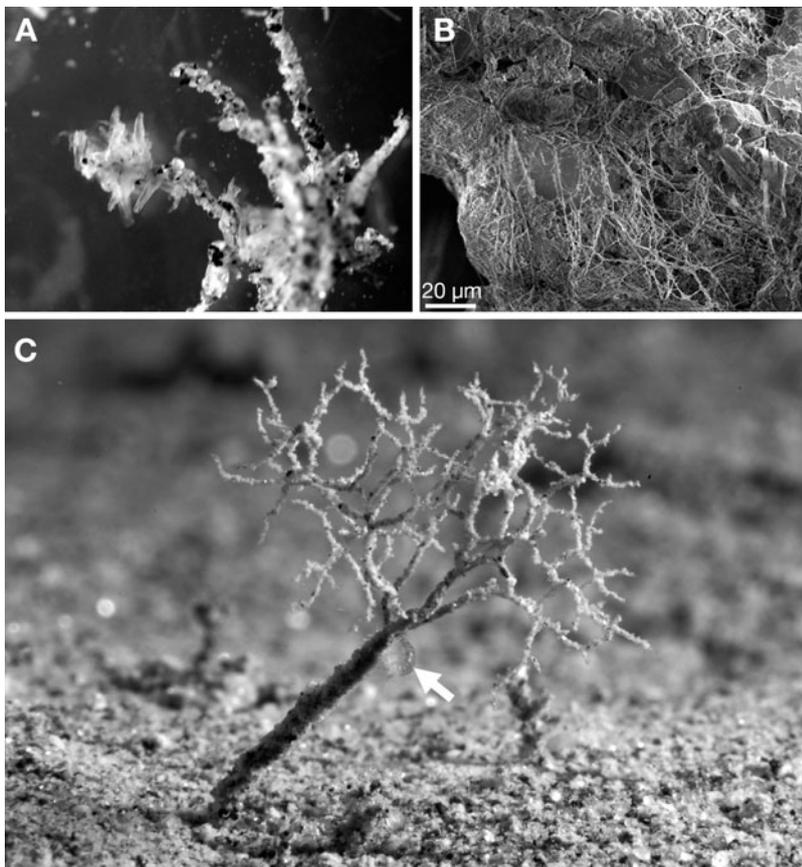


Fig. 1. *Notodendrodes hyalinosphaira* and *N. antarctikos*. (A) Light micrograph of *Artemia salina* nauplii captured on the above-surface 'tree' portion of *N. hyalinosphaira*. (B) Scanning electron micrograph of branch-like structures of *N. hyalinosphaira* showing a dense net of pseudopodia, often arranged like trip wires. (C) *In situ* macro photograph of *N. antarctikos* with attached copepod (arrow). Size of *N. hyalinosphaira* specimen shown >2 cm

tors of the quality and freshness of organic matter of phytoplankton origin (Wakeham et al. 1997, Fileman et al. 1998).

Multivariate statistical analyses based on the full fatty acid profiles of *Astrammia rara* and *Crithionina delacai* revealed a distinct difference in the overall fatty acid composition between the 2 species (Fig. 2). The multidimensional scaling (MDS) plot shows a clear separation between *A. rara* and *C. delacai* into 2 distinct groups, which clearly indicates different feeding patterns of the 2 species.

A significant ($p < 0.05$) difference existed between the quantities of the zooplankton marker fatty acids 20:1 (n-9) and 22:1(n-11) found in *Astrammia rara* early (4.8%) compared to late (2.8%) in the season (Table 3). These fatty acids occur in large amounts in storage substances (wax esters) of calanoid copepods (Albers et al. 1996), and are also abundant in deep-sea seastars (Howell et al. 2003). They are synthesized de novo by metazoans (Graeve et al. 2005), and neither has

been found in phytoplankton to date. These characteristics make 20:1(n-9) and 22:1(n-11) useful biomarkers for metazoan organisms (Falk-Petersen et al. 2000, Auel et al. 2002), and the presence primarily of 20:1(n-9) in *A. rara* supports earlier observations of carnivorous feeding by this species (Bowser et al. 1992). In an attempt to explain the high amounts of PUFAs also found in *A. rara*, we analyzed 2 co-occurring metazoans from Explorers Cove: an amphipod and a pycnogonid species. The metazoans were found to contain similarly high amounts of PUFAs: 45% of all fatty acids in the amphipod and 35.5% in the pycnogonid. The combination of the high amount of PUFAs and the elevated amount of zooplankton biomarker found in *A. rara* in early November suggests that the PUFAs contained in this species may originate from recently ingested herbivorous metazoans, which in turn were feeding on fresh microalgal material, rather than *A. rara* feeding on microalgal material directly. This is similar to observations by Cripps & Atkinson (2000) and Auel et al. (2002), who found high amounts of PUFAs from their food source in zooplankton feeding on herbivorous metazoans.

The relative PUFA content of *Astrammia rara* and the 2 *Notodendrodes hyalinosphaira* morphotypes was not significantly different between sam-

pling occasions (early and late in the season). *Crithionina delacai* was the only one of 3 Explorers Cove species that had a significantly higher relative amount of PUFAs early in the season (45.5%, on November 7) compared to later (34.2%, on January 31) (Table 3).

Crithionina delacai displayed an increase in variability within its fatty acid profile on the late season sampling occasion at the end of January, which is indicated by the greater standard deviations (Table 3). This suggests a more variable or unselective food intake at that time of year. The amounts of the diatom markers 16:1(n-7) and 20:5(n-3) in *Astrammia rara* and *C. delacai* were high and even increased slightly over the austral summer between early November and late January (from 18.9 to 21.8% in *A. rara* and from 21.6 to 22.7% in *C. delacai*), which indicates the ongoing availability of diatoms throughout the season. It may be problematic to consider 16:1(n-7) as a diatom marker in sedimentary systems, because some bacteria contain large amounts of this fatty acid. However,

Table 3. *Astrammmina rara* and *Crithionina delacai*. Seasonal comparison (early summer vs. late summer) of fatty acid profiles (weight % \pm SD). PUFAs: polyunsaturated fatty acids; C20 (I) and C20 (II): 20C-fatty acids not further identified; n = 4 (except *C. delacai* late season, when n = 3). nd: not detected

Fatty acid	— <i>Astrammmina rara</i> —		— <i>Crithionina delacai</i> —	
	Early season	Late season	Early season	Late season
14:0	3.7 \pm 1.1	7.4 \pm 1.8	3.3 \pm 0.1	5.7 \pm 1.1
15:0	0.7 \pm 0.2	0.7 \pm 0.2	1 \pm 0.1	2.4 \pm 2.4
16:0	10.7 \pm 3	12.1 \pm 2.2	8.7 \pm 1.2	12.6 \pm 7.9
16:1(n-9)	0.5 \pm 0.2	0.3 \pm 0.1	0.9 \pm 0	0.6 \pm 0.4
16:1(n-7)	11.8 \pm 3.3	13.7 \pm 3.4	9.3 \pm 1.6	12.7 \pm 8.1
16:1(n-5)	1.8 \pm 1.3	1.1 \pm 0.2	1 \pm 0	1.2 \pm 1.1
17:0	1.2 \pm 0.2	1.6 \pm 0.5	0.6 \pm 0.1	1.7 \pm 0.7
17:1	0.9 \pm 0.4	1 \pm 0.2	1 \pm 0.3	1 \pm 0.5
16:4(n-1)	2.6 \pm 0.6	3.4 \pm 0.7	2.4 \pm 0.2	2.5 \pm 0.6
18:0	5.1 \pm 0.2	4.8 \pm 0.4	3.9 \pm 0.2	3.9 \pm 0.4
18:1(n-9)	11.1 \pm 1.6	12.2 \pm 1.2	9.1 \pm 1	9.3 \pm 1.6
18:1(n-7)	2.2 \pm 0.1	1.2 \pm 0.5	0.7 \pm 0.1	0.7 \pm 0.4
18:2(n-6)	2.2 \pm 0.3	1.7 \pm 0.4	2 \pm 0.2	1.5 \pm 0.4
18:3(n-6)	1.9 \pm 0.5	1.1 \pm 0.4	2.2 \pm 0.1	1.5 \pm 0.4
18:3(n-3)	1 \pm 0.2	0.5 \pm 0.3	1.2 \pm 0.1	0.5 \pm 0.3
18:4(n-3)	2.2 \pm 0.3	2 \pm 0.4	2.5 \pm 0.2	1.7 \pm 0.8
20:0	0.8 \pm 0.3	0.4 \pm 0.2	1.4 \pm 0.4	0.7 \pm 0.4
20:1(n-9)	4.7 \pm 0.8	2.8 \pm 2	1 \pm 0.2	1.1 \pm 0.6
20:1(n-7)	1.5 \pm 0.2	0.6 \pm 0.2	2.4 \pm 0.4	2.3 \pm 1.1
C20 (I)	1.3 \pm 0.4	0.8 \pm 0.4	7.5 \pm 0.7	7.3 \pm 2.2
20:4(n-6)	10 \pm 2.7	7.7 \pm 2.2	10.3 \pm 0.4	7.1 \pm 1.7
C20 (II)	0.4 \pm 0.1	0.3 \pm 0.1	0.7 \pm 0	0.4 \pm 0.2
20:4(n-3)	0.5 \pm 0.1	0.3 \pm 0.1	0.9 \pm 0.1	0.7 \pm 0.5
20:5(n-3)	7.1 \pm 1	8.1 \pm 0.6	12.3 \pm 0.7	10 \pm 4.4
22:0	5 \pm 1	4.8 \pm 1.9	0.7 \pm 0.3	0.7 \pm 1
22:1(n-11)	0.1 \pm 0	nd	0.1 \pm 0.1	nd
21:5(n-3)	0.3 \pm 0.1	0.3 \pm 0.2	2.9 \pm 0.5	2.5 \pm 1.7
22:5(n-3)	0.3 \pm 0.1	0.3 \pm 0.1	0.5 \pm 0.1	0.4 \pm 0.4
22:6(n-3)	6.6 \pm 2.3	7.6 \pm 1.9	8.3 \pm 1.2	5.8 \pm 3.3
PUFAs	34.7 \pm 8.2	33.0 \pm 7.3	45.5 \pm 3.8	34.2 \pm 14.5

levels of the bacterial marker 18:1(n-7) were very low in all 3 species, suggesting that bacteria are not an important part of their diets and that the 16:1(n-7) observed was most likely of diatom origin.

The amounts of PUFAs and the combined bacterial biomarkers 15:0, 17:0 and 18:1(n-7) were relatively similar between the *Notodendrodes hyalinosphaira* morphotypes (PUFAs: 34.6 and 37.1%; bacterial markers: 3.1 and 2.5% in the 2 morphotypes). Both morphotypes contained high relative amounts of the diatom marker fatty acids 16:1(n-7) and 20:5(n-3), with 28.6% in quartz balls and 22.4% in tree-morphs (Table 4). Only the relative content of metazoan biomarkers differed between the two with 20:1(n-9) accounting for only 0.2% of total fatty acids in the tree-morph and 5.3% in the quartz ball, while 22:1(n-11) made up only 0.4% in the quartz ball, and the tree-morph had none of this fatty acid (Table 4). The 2 morphs differed substantially in their relative amounts of arachidonic acid, 20:4(n-6), with tree-morphs containing 11.2% and quartz balls only 1.1%.

DISCUSSION

The remarkably high amounts of PUFAs found in the 3 foraminiferal species examined is an unexpected result, indicating a significant input of carbon from primary production to the benthic community in Explorers Cove. Some Antarctic marine bacteria, the majority of which only occur in sea ice (Nichols & McMeekin 2002), also produce PUFAs such as 20:5(n-3) (eicosapentaenoic acid), 20:4(n-6) (arachidonic acid) and 22:6(n-3) (docosahexaenoic acid) (reviewed by Russell & Nichols 1999, Nichols 2003). However, although bacterial densities within sea ice can be considerable (Palmisano & Sullivan 1983, McGrath Grossi et al. 1984, Sullivan & Palmisano 1984), they may contribute only 9% of total carbon production (Kottmeier et al. 1987). In addition, all 3 of the species examined contained only low amounts of the bacterial biomarkers 15:0, 19:0 and 18:1(n-7), indicating that the contribution of bacteria to their diet is, at most, very modest, and that the primary source of the PUFAs is phytoplankton.

The efficiency of prey capture differed among the 3 species, indicating that prey capture is targeted and that prey items do not 'stick' to extended pseudopodia randomly. The fact that there were no prey attached to dead specimens of *Pilulina* sp. or to specimens of the related protist *Gromia* sp. in the feeding experiments indicates that prey capture is restricted to the presence of functional pseudopodia of live Foraminifera.

New insights into the autecology of the species examined

Notodendrodes hyalinosphaira

The 2 morphotypes of this species have distinctly different fatty acid profiles, which strengthens the premise that they also represent different trophotypes. The observation of higher relative amounts of zooplankton markers in the quartz ball than in the tree-morph of *Notodendrodes hyalinosphaira* suggests that the ingestion of metazoans plays a more important part in the diet of the quartz ball and is negligible in the tree-morph. It may seem surprising at first that the shallow infaunal

Table 4. *Notodendrodes hyalinosphaira*. Comparison of fatty acid profiles (weight %) of tree- and quartz ball morphotypes. nd: not detected

Fatty acid	Tree-morph	Quartz balls
14:0	4.0	2.9
15:0	1.9	0.6
C15	1.2	2.7
16:0	15.5	11.1
16:1(n-9)	5.3	3.8
16:1(n-7)	8.9	5.4
16:1(n-5)	1.5	0.4
17:0	0.2	0.9
17:1	0.2	0.4
16:4(n-1)	2.6	2.6
18:0	3.6	3.8
18:1(n-9)	18.7	16.6
18:1(n-7)	1.0	1.0
18:2(n-6)	0.7	0.8
18:3(n-6)	0.7	1.2
18:3(n-3)	0.1	0.3
18:4(n-3)	1.2	1.0
20:0	0.4	0.5
20:1(n-9)	0.2	5.3
20:(n-7)	1.0	1.8
C20 (I)	1.6	4.6
20:4(n-6)	11.2	1.1
C20 (II)	0.2	0.4
20:4(n-3)	0.1	0.4
20:5(n-3)	13.5	23.2
22:0	nd	0.3
22:1(n-11)	nd	0.4
21:5(n-3)	nd	0.1
22:5(n-3)	0.1	0.4
22:6(n-3)	4.4	6.0
PUFAs	34.6	37.1

quartz ball should be feeding on metazoans; however, it is possible that this morphotype extends pseudopodia onto the sediment surface to trap prey, or alternatively that infaunal metazoans are targeted.

The low levels of zooplankton markers in the tree-morph of *Notodendrodes hyalinosphaira* contrast with the highly efficient prey capture observed. Unfortunately, the quartz ball morphotype was not included in the prey capture assay, since the primary goal was to replicate *in situ*-like conditions, which was only possible by incubating the tree-morph in a sediment core. The 'tree' protrudes above the sediment surface, whereas the quartz ball is infaunal, precluding direct observation. DeLaca et al. (1980) suggested that the related species *N. antarctikos*, which occurs only as a tree-morph, captures small particles from the water column during summer and directly absorbs dissolved organic carbon (DOC) during the less productive times of the year, when less particulate material is present. Even during summer, food capture and digestion occur infrequently (DeLaca et al. 1980, 1981). The low levels of zooplankton markers found in the tree-morph of *N. hyalinosphaira* (we analyzed only early season spe-

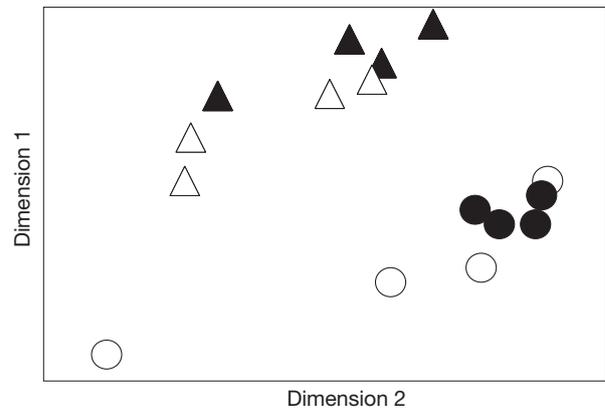


Fig. 2. *Astrammmina rara* and *Crithionina delacai*. MDS plot of full fatty acid profiles (weight %, untransformed data; 5 specimens per replicate) of the 2 species from Explorers Cove in early (November 7, 2001) and late (January 31, 2002) austral summer. Stress = 0.05. ▲: *A. rara* (early season), ●: *C. delacai* (early season), △: *A. rara* (late season), ○: *C. delacai* (late season)

cimens) may be explained simply by the absence or low abundances of metazoans on the sampling occasion.

The high content of 20:4(n-6) observed in the tree-morph was 10 times greater than in that of the quartz ball. Arachidonic acid is a major cell membrane constituent in deep-sea organisms and is thought to facilitate low temperature and pressure adaptation in bacteria (Yano et al. 1997) and some temperate and polar marine bivalves (Gillis & Ballantyne 1999, Hall et al. 2002). The higher relative amount of this fatty acid in the tree-morphs may reflect the greater cell surface area in comparison to the quartz ball, in which the cell forms a simple sphere.

Crithionina delacai

In conjunction with the comparatively low amounts of zooplankton biomarker found in *Crithionina delacai*, the significant difference in the content of PUFAs between early and late in the season suggests direct uptake of fresh phytoplankton-derived material. This is consistent with earlier SEM observations of food vacuole contents of this species, which contained diatom frustules as well as detrital material (Goody et al. 1995), indicating an omnivorous feeding behaviour that includes herbivorous and detrital feeding. This is also consistent with the lower efficiency of prey capture by *C. delacai* in the feeding experiments.

Astrammmina rara

Our results confirm early suggestions of a carnivorous diet for this species (DeLaca 1986), which is

highly efficient in prey capture (see Fig. 3 in Bowser et al. 1992) and ingests a wide variety of co-occurring metazoa as prey. The presence of zooplankton biomarker in our fatty acid analyses indicates that carnivory occurs *in situ*, and that the high amounts of PUFAs in this species originate from ingested metazoa, rather than from direct uptake of phytoplankton. Differences in the relative amounts of metazoan biomarker fatty acids found in *A. rara* early compared to late in the season may indicate enhanced ingestion of metazoans by the Foraminifera on the earlier sampling occasion, or conversely the uptake of consistent amounts of zooplankton throughout the season, with the late season zooplankton containing higher amounts of fresh material from sea-ice primary production.

The benthic environment at Explorers Cove

The presence of large amounts of PUFAs in the Foraminifera throughout the summer season indicates both the continual availability of fresh organic matter from microalgal primary production at the sampling site during this time, as well as ingestion of this material by all 3 species either directly or indirectly through the capture of herbivorous metazoa. Selective uptake of phytoplankton-derived material high in polyunsaturated fatty acids by benthic Foraminifera in the Antarctic was shown by Suhr et al. (2003) and Suhr & Pond (2006). There is also evidence from ^{13}C tracer experiments conducted *in situ* in Sagami Bay, Japan, for ingestion of fresh phytodetrital material (Nomaki et al. 2005). Our new observations suggest that the Explorers Cove site is less oligotrophic, relative to eastern McMurdo Sound, than previous studies suggest (Dayton & Oliver 1977, Palmisano & Sullivan 1983, Rivkin & DeLaca 1990). It seems likely that intense primary production by sea-ice algae and (to a much smaller extent) by sea-ice associated bacteria is the primary source of food for the benthic community in Explorers Cove, which has been suggested for this site by DeLaca et al. (1980) and was later shown to be the case elsewhere in the Antarctic (McMinn 1996, McMinn et al. 2000). The biomass of algae in fast ice can reach up to 300 mg chl $a\ m^{-2}$, with average values in the range of 50 to 100 mg chl $a\ m^{-2}$ (Palmisano & Sullivan 1983, Palmisano et al. 1988, Trenerry et al. 2002). High concentrations (40 to 51%) of PUFAs were found in sea-ice communities at other sites in McMurdo Sound (Nichols et al. 1993, McMinn et al. 1999), indicating intense primary production below the ice. It is remarkable how closely the relative amount of PUFAs in these studies matched those in the Explorers Cove Foraminifera that we analyzed.

We propose the following pattern for primary production in Explorers Cove: throughout the winter, primary production by shade-adapted benthic microalgae, primarily diatoms (Palmisano et al. 1985, Kottmeier & Sullivan 1987, Robinson et al. 1995), takes place at low levels, providing food for the benthic community during this period. Beginning in mid to late November, the spring-bloom of ice algae sets in, and increasing concentrations of ice algae that subsequently attenuate light penetrating the ice limit benthic algal production (Palmisano et al. 1987). Throughout the summer, organic carbon is transferred from the ice to the benthic community. By late January, divers in Explorers Cove observed the release of large amounts of organic carbon from ice algal production from the melting sea ice, which are deposited on the seafloor (S. S. Bowser pers. obs.).

Carnivory in Foraminifera

For over a century, certain planktonic Foraminifera have been known to take metazoan prey such as copepods (reviewed by Bé & Anderson 1976). Less is known about metazoan carnivory by benthic species, although it has been documented in some sublittoral species (Buchanan & Hedley 1960). The only review of the topic focuses on the question of whether or not Foraminifera actively kill their prey (Langer & Bell 1995). Our laboratory feeding experiments expand our knowledge of the range of metazoan prey taken by *Astrammmina rara*, and microscope imagery together with fatty acid biomarker analysis support the interpretation that carnivory occurs *in situ* and that metazoans are part of the diet of this species. In addition, the entrapment of metazoans by most of the other Foraminifera examined in the feeding experiment indicates that carnivory may be more prevalent within this group than previously believed.

Previous studies on interactions between Foraminifera and metazoan meio- and macrofauna focused on competition between the 2 groups (Chandler 1989) or on the role of large Foraminifera as habitats for metazoa (Levin 1991, Hughes & Gooday 2004). However, Bernstein et al. (1978) highlighted the impact that large, carnivorous Foraminifera may have on the structure of benthic communities, and our study provides corroborating evidence. The high abundance of large agglutinated Foraminifera in Explorers Cove (Gooday et al. 1996) raises the possibility that predation by large Foraminifera on metazoans (besides competition for resources such as space or food) explains the low macrofaunal densities observed in Explorers Cove by Dayton & Oliver (1977). The results also suggest that carnivorous Foraminifera may affect settlement pat-

terns of planktonic larvae of megafauna. This is consistent with the fact that many of the successful megafauna in Explorers Cove, e.g. the bivalve *Adamussium colbecki* (Stockton 1984) and echinoids (Dayton & Oliver 1977), have juvenile settling strategies or brood protection behaviors that reduce their contact with benthic predators such as large carnivorous Foraminifera. Similarly, the only larvae not consumed by *Astrammmina rara* in our feeding experiment was *Acodontaster* sp., which may have effective chemical defenses against predators, as previously shown for most other lecithotrophic offspring of Antarctic asteroids (McClintock & Baker 1997, McClintock et al. 2003).

Large, monothalamous agglutinated Foraminifera are abundant and presumably play an important ecological role in deep sublittoral and upper bathyal settings in other parts of the world (e.g. Levin et al. 1991, Cedhagen 1993, Gooday et al. 1996, A. J. Gooday pers. obs.). Although information on the role of large Foraminifera in benthic communities is increasing, much work and directed study remain to be done. Future experiments at Explorers Cove (bearing in mind the severe logistical constraints of working out of a remote sea-ice field camp in the Antarctic) could include *in situ* sediment trays to study the colonization of substrata by metazoan larvae in the presence and absence of Foraminifera, and detailed combined studies of foraminiferal and macrofaunal communities to determine the degree to which large Foraminifera may structure benthic communities on at least the macro- and megafaunal scale.

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LITERATURE CITED

- Albers CS, Kattner G, Hagen W (1996) The compositions of wax esters, triacylglycerols and phospholipids in Arctic and Antarctic copepods: evidence of energetic adaptations. *Mar Chem* 55:347–358
- Auel H, Harjes M, da Rocha R, Stübing D, Hagen W (2002) Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. *Polar Biol* 25:374–383
- Basov IA (1974) Biomass of benthic foraminifera in the region of the South Sandwich Trench and Falkland Islands. *Oceanology* 14:277–279
- Bé AW, Anderson OR (1976) Gametogenesis in planktonic Foraminifera. *Science* 192:890–892
- Bernstein BB, Hessler RR, Smith R, Jumars PA (1978) Spatial dispersion of benthic Foraminifera in the abyssal central North Pacific. *Limnol Oceanogr* 23:401–416
- Bowser SS, Travis JL (2000) Methods for structural studies of reticulopodia, the vital foraminiferal 'soft part'. *Micropaleontology* 46(Suppl 1):47–56
- Bowser SS, DeLaca TE, Rieder CL (1986) Novel extracellular matrix and microtubule cables associated with pseudopodia of *Astrammmina rara*, a carnivorous Antarctic foraminifer. *J Ultrastruct Mol Struct Res* 94:149–160
- Bowser SS, Alexander SP, Stockton WL, DeLaca TE (1992) Extracellular matrix augments mechanical properties of pseudopodia in the carnivorous Foraminifera *Astrammmina rara*: role in prey capture. *J Eukaryot Microbiol* 39:724–732
- Buchanan JB, Hedley RH (1960) A contribution to the biology of *Astrorhiza limicola* (Foraminifera). *J Mar Biol Assoc UK* 39:549–560
- Carr MR (2001) PRIMER (Plymouth Routines in Multivariate Ecological Research), Vers. 5.1. Plymouth Marine Laboratory, Plymouth
- Cedhagen T (1993) Taxonomy and biology of *Pelosina arborescens* with comparative notes on *Astrorhiza limicola* (Foraminifera). *Ophelia* 37:143–162
- Chandler GT (1989) Foraminifera may structure meiobenthic communities. *Oecologia* 81:354–360
- Cripps GC, Atkinson A (2000) Fatty acid composition as an indicator of carnivory in Antarctic krill, *Euphausia superba*. *Can J Fish Aquat Sci* 57(Suppl 3):31–37
- Dayton PK, Oliver J (1977) Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. *Science* 197:55–58
- DeLaca TE (1982) Use of dissolved amino acids by the foraminifer *Notodendrodes antarctikos*. *Am Zool* 22:683–690
- DeLaca TE (1986) The morphology and ecology of *Astrammmina rara*. *J Foraminifer Res* 16:216–224
- DeLaca TE, Lipps JH, Hessler RR (1980) The morphology and ecology of a new large agglutinated Antarctic foraminifer (Textulariina: *Notodendroididae* nov.). *Zool J Linn Soc* 69:205–224
- DeLaca TE, Karl DM, Lipps JH (1981) Direct use of dissolved organic carbon by agglutinated benthic Foraminifera. *Nature* 289:287–289
- DeLaca TE, Bernhard JM, Reilly AA, Bowser SS (2002) *Notodendrodes hyalinosphaira* (sp. nov.): structure and autecology of an allogromiid-like agglutinated foraminifer. *J Foraminifer Res* 32:177–187
- Falk-Petersen S, Hagen W, Kattner G, Clarke A, Sargent J (2000) Lipids, trophic relationships, and biodiversity in Arctic and Antarctic krill. *Can J Fish Aquat Sci* 57(Suppl 3) 178–191
- Fileman TW, Pond DW, Barlow RG, Mantoura RFC (1998) Vertical profiles of pigments, fatty acids and amino acids: evidence for undegraded diatomaceous material sedimenting to the deep ocean in the Bellingshausen Sea, Antarctica. *Deep-Sea Res I* 45:333–346
- Gillis TE, Ballantyne JS (1999) Influences of subzero thermal acclimation on mitochondrial membrane composition of temperate zone marine bivalve mollusks. *Lipids* 34:59–66
- Goldstein ST (1999) Foraminifera: a biological overview. In: Sen Gupta BK (ed) *Modern Foraminifera*. Kluwer Academic Publishers, Norwell, MA, p 37–55
- Gooday AJ (2002) Organic-walled allogromiids: aspects of their occurrence, diversity and ecology in marine habitats. *J Foraminifer Res* 32:384–399
- Gooday AJ, Levin LA, Linke P, Heeger T (1992) The role of

- benthic Foraminifera in deep-sea food webs and carbon cycling. In: Rowe GT, Pariente V (eds) Deep-sea food chains and the global carbon cycle. Kluwer, Amsterdam, p 63–91
- Gooday AJ, Bernhard JM, Bowser SS (1995) The taxonomy and ecology of *Crithionina delacai* sp. nov., an abundant large agglutinated foraminifer from Explorers Cove, Antarctica. *J Foraminif Res* 25:290–298
- Gooday AJ, Bowser SS, Bernhard JM (1996) Benthic foraminiferal assemblages in Explorers Cove, Antarctica: a shallow-water site with deep-sea characteristics. *Prog Oceanogr* 37:117–166
- Graeve M, Albers C, Kattner G (2005) Assimilation and biosynthesis of lipids in Arctic *Calanus* species based on feeding experiments with a ¹³C labelled diatom. *J Exp Mar Biol Ecol* 317:109–125
- Hall JM, Parrish CC, Thompson RJ (2002) Eicosapentaenoic acid regulates scallop (*Placopecten magellanicus*) membrane fluidity in response to cold. *Biol Bull* 202:201–203
- Howell KL, Pond DW, Billett DSM, Tyler PA (2003) Feeding ecology of deep-sea seastars (Echinodermata: Asteroidea): a fatty-acid biomarker approach. *Mar Ecol Prog Ser* 255:193–206
- Hughes JA, Gooday AJ (2004) Associations between living benthic foraminifera and dead tests of *Syringammina fragilissima* (Xenophyophorea) in the Darwin Mounds region (NE Atlantic). *Deep-Sea Res I* 51:1741–1758
- Kottmeier ST, Sullivan CW (1987) Late winter primary production and bacterial production in seaice and seawater west of the Antarctic Peninsula. *Mar Ecol Prog Ser* 36:287–298
- Kottmeier ST, Grossi SM, Sullivan CW (1987) Sea ice microbial communities. VIII. Bacterial production in annual Seaice of McMurdo Sound, Antarctica. *Mar Ecol Prog Ser* 35:175–186
- Langer M, Bell CJ (1995) Toxic Foraminifera: innocent until proven guilty. *Mar Micropaleontol* 24:205–214
- Levin LA (1991) Interactions between metazoans and large, agglutinating protozoans: implications for the community structure of deep-sea benthos. *Am Zool* 31:886–900
- Levin LA, Childers SE, Smith CR (1991) Epibenthic agglutinating foraminiferans in the Santa Catalina Basin and their response to disturbance. *Deep-Sea Res* 38:465–483
- Lipps JH (1983) Biotic interactions in benthic Foraminifera. In: Tevez MJJ, McCall PL (eds) Biotic interactions in recent and fossil benthic communities. Plenum Press, New York, p 331–376
- Lipps JH, Valentine JW (1970) The role of foraminifera in the trophic structure of marine communities. *Lethaia* 3:279–286
- McClintock JB, Baker BJ (1997) Palatability and chemical defense of eggs, embryos and larvae of shallow-water Antarctic marine invertebrates. *Mar Ecol Prog Ser* 154:121–131
- McClintock JB, Mahon AR, Peters KJ, Amsler CD, Baker BJ (2003) Chemical defences in embryos and juveniles of 2 common Antarctic sea stars and an isopod. *Antarct Sci* 15:339–344
- McGrath Grossi S, Kottmeier ST, Sullivan CW (1984) Sea ice microbial communities. III. Seasonal abundance of microalgae and associated bacteria, McMurdo Sound, Antarctica. *Microb Ecol* 10:231–242
- McMinn A (1996) Preliminary investigation of the contribution of fast-ice algae to the spring bloom in Ellis Fjord, east Antarctica. *Polar Biol* 16:301–307
- McMinn A, Skerratt J, Trull T, Ashworth C, Lizotte M (1999) Nutrient stress gradient in the bottom 5 cm of fast ice, McMurdo Sound, Antarctica. *Polar Biol* 21:220–227
- McMinn A, Ashworth C, Ryan KG (2000) *In situ* net primary production of an Antarctic fast ice bottom algal community. *Aquat Microb Ecol* 21:177–185
- Moodley L, Middelburg JJ, Boschker HTS, Duineveld GCA, Pel R, Herman PMJ, Heip CHR (2002) Bacteria and Foraminifera: key players in a short-term deep-sea benthic response to phytodetritus. *Mar Ecol Prog Ser* 236:23–29
- Nichols DS (2003) Prokaryotes and the input of polyunsaturated fatty acids to the marine food web. *FEMS Microbiol Lett* 219:1–7
- Nichols DS, McMeekin TA (2002) Biomarker techniques to screen for bacteria that produce polyunsaturated fatty acids. *J Microbiol Methods* 48:161–170
- Nichols DS, Nichols PD, Sullivan CW (1993) Fatty acid, sterol and hydrocarbon composition of Antarctic sea-ice diatom communities during the spring bloom in McMurdo Sound. *Antarct Sci* 5:271–278
- Nomaki H, Heinz P, Nakatsuka K, Shimanaga M, Kitazato H (2005) Species-specific ingestion of organic carbon by deep-sea benthic foraminifera and meiobenthos: *in situ* tracer experiments. *Limnol Oceanogr* 50:134–146
- Palmisano AC, Sullivan CW (1983) Sea ice microbial communities (SIMCO). 1. Distribution, abundance, and primary production of ice microalgae in McMurdo Sound, Antarctica in 1980. *Polar Biol* 2:171–177
- Palmisano AC, Soohoo JB, White DC, Smith GA, Stanton GR, Burckle LH (1985) Shade adapted benthic diatoms beneath Antarctic sea ice. *J Phycol* 21:664–667
- Palmisano AC, Beeler Soohoo J, Moe RL, Sullivan CW (1987) Sea ice microbial communities. VII. Changes in under-ice spectral irradiance during the development of Antarctic seaice microalgal communities. *Mar Ecol Prog Ser* 35:165–173
- Palmisano AC, Lizotte MP, Smith GA, Nichols PD, White DC, Sullivan CW (1988) Changes in photosynthetic carbon assimilation in Antarctic sea-ice diatoms during spring bloom: variations in synthesis of lipid classes. *J Exp Mar Biol Ecol* 116:1–13
- Pollock NW, Bowser SS (1995) SCUBA collection of benthic Foraminifera in Explorers Cove, Antarctica: an accessible model of the deep-ocean benthos? In: Harper DE (ed) *Diving for science*. American Academy of Underwater Sciences, Nahant, MA, p 63–74
- Rivkin RB, DeLaca TE (1990) Trophic dynamics in Antarctic benthic communities. I. *In situ* ingestion of microalgae by Foraminifera and metazoan meiofauna. *Mar Ecol Prog Ser* 64:129–136
- Robinson DH, Arrigo KR, Iturriaga R, Sullivan CW (1995) Microalgal light-harvesting in extreme low-light environments in McMurdo Sound, Antarctica. *J Phycol* 31:508–520
- Russell NJ, Nichols DS (1999) Polyunsaturated fatty acids in marine bacteria—a dogma rewritten. *Microbiology* 145:767–779
- Smith KL, Baldwin RJ, Karl DM, Boetius A (2002) Benthic community responses to pulses in pelagic food supply: North Pacific Subtropical Gyre. *Deep-Sea Res I* 49:971–990
- Stockton WL (1984) The biology and ecology of the epifaunal scallop *Adamussium colbecki* on the west side of McMurdo Sound, Antarctica. *Mar Biol* 78:171–178
- Suhr SB, Pond DW (2006) Antarctic benthic Foraminifera facilitate rapid cycling of phytoplankton-derived organic carbon. *Deep-Sea Res II* 53:895–902
- Suhr SB, Pond DW, Gooday AJ, Smith CR (2003) Selective feeding by benthic Foraminifera on phytodetritus on the western Antarctic Peninsula shelf: evidence from fatty

acid biomarker analysis. *Mar Ecol Prog Ser* 262:153–162

Sullivan CW, Palmisano AC (1984) Sea ice microbial communities: distribution, abundance, and diversity of ice bacteria in McMurdo Sound, Antarctica, in 1980. *Appl Environ Microbiol* 47:788–795

Thiel H (1983) Meiobenthos and nanobenthos of the deep sea. In: Rowe GT (ed) *Deep-sea biology*. Wiley, New York, p 167–230

Trenerry LJ, McMinn A, Ryan KG (2002) *In situ* oxygen

microelectrode measurements of bottom-ice algal production in McMurdo Sound, Antarctica. *Polar Biol* 25:72–80

Wakeham SG, Lee C, Hedges JI, Hernes PJ, Peterson ML (1997) Molecular indicators of diagenetic status in marine organic matter. *Geochim Cosmochim Acta* 61:5363–5369

Yano Y, Nakayama A, Yoshida K (1997) Distribution of polyunsaturated fatty acids in bacteria present in intestines of deep-sea fish and shallow-sea poikilothermic animals. *Appl Environ Microbiol* 63:2572–2577

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