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Ecology and nutrition of the large agglutinated foraminiferan *Bathysiphon capillare* in the bathyal NE Atlantic: distribution within the sediment profile and lipid biomarker composition

Andrew J. Gooday[1,*], David W. Pond[1], Samuel S. Bowser[2]

[1]Southampton Oceanography Centre, Empress Dock, Southampton SO14 3ZH, United Kingdom
[2]Wadsworth Center, New York State Department of Health, PO Box 509, Albany, New York 12201-0509, USA

ABSTRACT: The large agglutinated foraminiferan *Bathysiphon capillare* de Folin (Protista) was an important component of the macrofauna in box core samples recovered at a 950 m site on the southern flank of the Wyville-Thomson Ridge, northern Rockall Trough. The long, narrow, very smooth, flexible tubes of *B. capillare* reached a maximum length of almost 10 cm. Densities ranged from 100 to 172 ind. m^{-2}, a figure that represents at least 5 to 9% of metazoan macrofaunal densities. This infaunal species usually adopted a more or less horizontal orientation within the upper 5 cm layer of brownish sandy silt. Its cytoplasm yielded a diverse spectrum of fatty acids. These included various monounsaturated fatty acids (39% of total), mainly 18:1(n-7), 20:1(n-9) and 22:1(n-7), the polyunsaturated fatty acids (PUFA) 20:4(n-6), 20.5(n-3) and 22.6(n-3), and non-methylene diene-interrupted fatty acids (NMIDS), particularly 22:2Δ7,13 and 22:2Δ7,15. The spectrum of PUFAs is consistent with the ingestion by *B. capillare* of phytodetrital material. However, the presence of NMIDS, reported here for the first time in a protist, provides evidence for a substantial bacterial component in the diet. Viewed by scanning electron microscopy (SEM), the cytoplasm occupied a narrow space between the inner organic test lining and an inner core of detritus around which it formed a sheath. The core material included numerous spherical structures (2 to 10 µm diameter) that we interpret as stercomata (waste pellets composed largely of mineral grains). Taken together, our observations suggest that *B. capillare* is a deposit feeder, consuming sediment, detritus and associated bacteria. Other deep infaunal foraminiferans probably have a similar diet, leading us to speculate that these protists, which are often abundant in dysoxic settings, may contribute significantly to carbon cycling in the deep sea. Since *B. capillare* and similar large *Bathysiphon* species can be recovered in good condition from bathyal depths, they may prove to be ideal experimental subjects for addressing some fundamental issues in the lipid biochemistry of deep-sea benthic organisms.

KEY WORDS: Deep sea · Diets · Fatty acids · Foraminiferans · Lipids · Macrofauna · NMIDS · PUFA

INTRODUCTION

Most species of foraminiferans belong to the meiofauna, but in deep-sea settings, these sarcodine protists can also constitute a substantial element of the macrofauna (Hessler & Jumars 1974, Tendal & Hessler 1977, Gooday et al. 2001). Delicate, soft-bodied agglutinated taxa such as komokiaceans are extremely abundant in oligotrophic central oceanic areas. Samples collected on more eutrophic bathyal continental margins often yield numerous large foraminiferans belonging to agglutinated taxa, such as *Bathysiphon, Hyperammina, Marsipella* and *Rhabdammina*, which have relatively robust, tubular tests (Gooday 1990, Gooday et al. 1997). These are visually conspicuous epifaunal organisms, often protruding from box core surfaces and sometimes clearly visible to the unaided eye in seafloor photographs or from submersibles (Levin et al. 1991, Gooday et al. 1992a). The ecological

*Email: ang@soc.soton.ac.uk

role of these large foraminiferans is not well understood. However, they are capable of consuming fresh organic matter (Levin et al. 1999) and, in some areas, probably play an important role in the degradation of detritus derived from photosynthetic primary production (Meyer-Reil & Köster 1991, Moodley et al. 2002). There is evidence that some species undergo a rapid physiological 'reawakening' following periods of dormancy, which is presumably an adaptation to a fluctuating food supply (Linke 1992, Linke et al. 1995). Their tests also help to create habitat structure that can be utilised by other foraminiferans and metazoan meiofauna and macrofauna (Levin 1991).

Much less is known about large agglutinated foraminiferans that live below the sediment/water interface. Infaunal species are rarely reported in deep-sea settings, and virtually no information is available regarding their autecology and role in benthic ecosystems. During RRS 'Discovery' Cruise 248 (Bett et al. 2001), we obtained box core and multicore samples at water depths of approximately 950 m in the northern Rockall Trough, immediately to the south of the Wyville-Thomson Ridge. Large agglutinated foraminiferans were sampled in this area during the 'Lightning' and 'Porcupine' expeditions of 1867 to 1868, the earliest serious attempts to investigate life in the deep ocean (Carpenter 1868, Carpenter et al. 1870, Rice 1986). By far the most abundant large agglutinated species present in core samples from this site was *Bathysiphon capillare* de Folin 1886. A redescription of this poorly known species was given by Gooday (1988) and its wall structure was investigated by Gooday & Claugher (1989).

The present paper aims to clarify possible roles of *Bathysiphon capillare* in deep-sea food webs. We address several specific questions: (1) Where does this long tubular species live in relation to the sediment/water interface? (2) How abundant is it compared to the metazoan macrofauna? (3) How important are food sources such as bacteria and phytodetritus in its diet? Fatty acid analyses are a central feature of our study. This approach has been used for some years to investigate the diets of planktonic, benthic and nektobenthic marine animals (Sargent et. al. 1987, Graeve et al. 1997, Pond et al. 1997b, 1998). Recently, Moodley et al. (2000, 2002) analysed ^{13}C enrichment of selected polar lipid-derived fatty acids (PLFA) in an experimental study of algal carbon uptake by benthic foraminiferans. However, ours is the first comprehensive attempt to analyse lipids in a foraminiferan species. Together with stable isotope experiments (Levin et al. 1999, Moodley et al. 2000, 2002), this method has considerable potential for clarifying the role of foraminiferans, numerically one of the most important of benthic taxa, in deep-sea food webs (Gooday et al. 1992b).

MATERIALS AND METHODS

The study site. The study area is characterised by an extensive field of low (5 m elevation) carbonate mounds (the 'Darwin Mounds'), discovered in 1998 during an environmental survey of part of the UK continental margin (Bett 1999, Bett et al. 2001, Masson et al. in press). Photographs taken using the WASP (Wide-Angle Survey Photography) vehicle revealed sparse patches of the deep-water coral *Lophelia pertusa* and other suspension-feeding organisms on the mounds. Most of the mound area, however, was composed of quartz sands rather than biogenic material. The large xenophyophore *Syringammina fragilissima* Brady, first described by Brady (1883) on the basis of material collected during the 'Triton' expedition, was conspicuous on the seafloor in certain areas (Bett et al. 1999, Roberts et al. 2000). Mean water temperatures around the Darwin Mounds range from 7.5 to 8.5°C and salinity is approximately 35.0 to 35.2‰ (Holliday et al. 2000).

The Darwin Mounds area is underlain by a contourite sand sheet deposited under the influence of a bottom current. Near-bottom flows are strongly tidal with maximum velocities of 34 to 35 m s^{-1} being recorded over a 20 d period in July 2000 (Masson et al. in press). Many sediment areas imaged using the WASP system were rippled. Cores with *Bathysiphon* comprised approximately 10 cm of sandy silt overlying sticky mud. Surficial sediment from a multicore (13816#4) was dominated by particles >63 µm; the 63 to 125 µm fraction yielded 66% and the 125 to 300 µm fraction yielded 0.6% of the sediment mass. The total organic carbon content of the sediment was low (0.1 to 0.2%; K. Kiriakoulakis pers. comm.). Fresh, undegraded lipids occurred in highest concentrations at a depth of 5 to 6 cm within the sediment on the mounds and their associated tails (Kiriakoulakis et al. 2000). This probably reflects bioturbation and suggests that the sediments were oxygenated to at least this level. At the control sites, however, lipids were concentrated at the sediment surface (Kiriakoulakis et al. 2000).

Sample collection and processing. Samples were collected close to the carbonate mounds using an undivided USNEL box corer (surface area 0.25 m^2) and a Barnett-Watson multiple corer equipped with 12 core tubes, each 57 mm internal diameter (surface area 25.5 cm^2) (Barnett et al. 1984) (Table 1). Four complete box cores (13834#2; 13840#1; 13842#3; 13842#4; total surface area 1 m^2) were carefully dissected using a small knife and a spatula, and all *Bathysiphon* specimens encountered were documented before being extracted and fixed in 10% borax-buffered formalin. Some individuals were photographed *in situ* using an Olympus D450 digital camera before being picked out. Additional specimens were obtained from other cores,

Table 1. Positions of box core (BC) and multicorer (MC) samples examined for this study. In 'Remarks', the numbers of specimens of large agglutinated foraminifera species removed are indicated in parentheses. Macrofaunal densities (see text) are from Hepburn (2001)

Stn and series	Gear	Latitude (° N)	Longitude (° W)	Depth (m)	Location	Remarks
13816#1	BC	58° 48.83′	7° 22.73′	946	Tail of mound	Macrofaunal densities
13816#3	BC	58° 48.85′	7° 22.71′	946	Tail of mound	Macrofaunal densities
13816#4	MC	59° 48.85′	7° 22.68′	947	Tail of mound	Granulometric analysis
13821#2	BC	58° 48.76′	7° 21.67′	960	Mound	Macrofaunal densities
13826#2	BC	59° 48.82′	7° 22.60′	948	Tail of mound	Macrofaunal densities. Selected specimens of *Bathysiphon capillare*; also *Astrorhiza arenaria* (1), *Rhabdammina abyssorum* (2)
13826#3	BC	59° 48.82′	7° 22.57′	946	Tail of mound	Macrofaunal densities
13827#1	BC	59° 48.95′	7° 22.52′	948	Tail of mound	Selected specimens of *B. capillare* retained
13834#2	BC	59° 49.09′	7° 21.49′	958	Background	All specimens of *B. capillare* (26) removed
13835#1	MC	59° 36.01′	7° 41.86′	904	Pockmark area, sandy sediments	No large agglutinated foraminifera
13835#2	MC	59° 36.00′	7° 41.86′	905	Pockmark area, muddy sediments	12 MCs yielding: *A. arenaria* (11), *R. discreta* (3), *Pelosina* sp. (4)
13840#1	BC	59° 49.09′	7° 21.51′	958	Background	All specimens of *B. capillare* (43) removed
13842#3	BC	59° 49.08′	7° 21.51′	961	Background	All specimens of *B. capillare* (25), *R. abyssorum* (2) removed
13842#4	BC	59° 49.08′	7° 21.50′	959	Background	All specimens of *B. capillare* (35), *A. arenaria* (3) removed

being picked either directly from the core or from sieved residues (>250 µm fraction) (Table 1). Fixed specimens were used for a variety of purposes, including length measurements, and comparison with previously collected material. Specimens for scanning electron microscopy (SEM) were picked as soon as practical, and processed as described in Bowser & Travis (2000). After critical point-drying, they were mounted on stubs using carbon tape and viewed, either directly or after sputter coating with gold, using a LEO 1550VP FESEM.

Lipid analyses. Specimens of *Bathysiphon capillare* for lipid analysis (5 replicates of 8 specimens) were removed from box core 13840#1, as described above, and stored in chloroform:methanol (2:1, v/v) until analysis. Total lipid was extracted following Folch et al. (1957) and subsequently transesterified in methanol containing 1.5% sulphuric acid at 50°C for 16 h to generate fatty acid methyl esters (FAME; Christie 1982). FAMEs were then purified by thin layer chromatography using a hexane:diethyl ether:acetic acid (90:10:1, v/v/v) solvent system. Purified FAMEs were dissolved in hexane to a concentration of 2 mg ml^{-1} and analysed by gas chromatography on a Carlo Erba (Trace 2000 series) fitted with a ZBWAX fused silica capillary column (30 × 0.32 mm internal diameter) using hydrogen as the carrier gas. Fatty acids were identified using the procedures detailed in Pond et al. (1998).

RESULTS

The test of *Bathysiphon capillare* and its contents

A total of 129 intact specimens of *Bathysiphon capillare* picked from the 4 carefully dissected box cores

were between 8 and 68 mm (mean 34.8 mm, SD 15.2 mm) long and 180 to 540 µm (wider end) and 140 to 480 µm (narrower end) in width. The 2 largest individuals (selected specimens from box core 13827#1) were 105 and 95 mm long, tapering in width from 600 to 440 and 640 to 420 µm, respectively. The tube usually follows a curved, sometimes sinuous course and the apertural end is constricted. The test surface is white, very smooth, with a variably developed, silvery reflective sheen. Examination by SEM (Fig. 1A,B) confirmed that the wall structure of *Bathysiphon capillare* comprises a very thin, outer layer of imbricated, micaceous grains underlain by a much thicker, loose aggregate of mixed composition (Gooday & Claugher 1989).

In some dried specimens, the agglutinated wall was easily teased away. SEM of such preparations revealed that the test was occupied by a dense core of granular material surrounded by a thin, tubular sheath of cytoplasm (Fig. 1C). In certain areas, this cytoplasmic sheath merged into typical reticulopodia which encircled the detrital core (not illustrated) or ramified along the lumenal (i.e. inner) face of the inner organic lining of the test (Fig. 1E,F). Visible on broken surfaces of the core material (Figs. 1D & 2A,B) were a number of identifiable particles including sponge spicules, occasional coccoliths, and parts of crustacean appendages (not illustrated). The most numerous structures, however, were more or less spherical bodies, 2 to 10 µm in diameter, with a surface texture that was rough and uneven at high magnifications (Figs. 1D & 2C,D). Preliminary X-ray microanalysis revealed peaks for Al, Si and O, suggesting the presence of mineral grains, and C, N, and P, suggesting the presence of an organic component. We interpret these structures as stercomata, pellets of waste material that are present in large numbers in certain foraminiferans, for example, komokiaceans (e.g. Cartwright et al.1989). They probably represent the consolidated remains of ingested, fine-grained sedimentary material. Cytoplasmic structures were not visible within the granular contents of the tube, which therefore appear to be extracellular. However, branching reticulopodia were clearly evident on the inner surfaces of the inner organic lining of the test (Fig. 1E). One of the reticulopodia gave rise to a food cup closing around what appeared to be a bacterium (Fig. 1F).

Abundance and distribution within the sediment

Specimens recovered from the 4 systematically studied box-cores were all filled with the dark greenish-brown, granular material described above. Those examined by SEM had pseudopodia. All specimens were therefore presumed to be alive when captured. Tubes of *Bathysiphon capillare* are fragile, but since these specimens were carefully excavated from the sediment, we regard them as intact individuals. The number in each core was 26 (13834#2), 43 (13840#1), 25 (13842#3) and 35 (13842#4), corresponding to a density of 104, 172, 100 and 135 ind. m^{-2}. Additional data on the abundance of *Bathysiphon capillare* in the northern Rockall Trough were obtained from box-cores sieved for macrofauna (L. Hepburn & J. D. Gage unpubl.). The 0 to 10 cm layer (>500 µm fraction) of 3 undisturbed cores (13816#1, 13816#3 and 13826#3) from the Darwin Mounds area yielded 11, 57 and 23 specimens, respectively, of this species, while a core from a nearby mound field (13821#2) contained 57 specimens. Most of these tubes were obvious fragments and their densities cannot be compared directly to those of intact individuals.

Bathysiphon capillare occurred at all depths in the sediment down to about 50 mm, but most specimens were observed between 15 and 40 mm below the surface (Fig. 3). Three individuals from box core 13842#4 protruded from the surface. The other 126 specimens from the 4 systematically examined cores occurred below the sediment surface within a 5 cm layer of brownish sand (Fig. 4A,B). The tubes were not observed within the underlying greyish sand (5 to 10 cm depth) or in the dense mud that occupied the lower part of the core (>10 cm depth). The orientation of the tubes was usually approximately horizontal but occasional specimens curved downwards at one end, usually the broader one. Their lateral distribution within the 5 cm thick layer of brownish sand was fairly even, although paired individuals sometimes occurred (Fig. 4C). Specimens were never observed to be associated with burrows or biogenic structures. *Bathysiphon* tubes also occurred infaunally in cores that were not studied systematically.

The only other large agglutinated foraminiferans present in the 4 carefully dissected box-cores were occasional ($n \leq 3$ per core) triradiate specimens of *Rhabdammina abyssorum* Sars, and its biradiate variant '*Rhabdammina discreta*', tubes of which sometimes protruded from the sediment surface. In addition, 3 specimens of *Astrorhiza arenaria* lay flat on the surfaces of 2 box-cores (13842#4 and 13826#2) from the main Darwin Mounds study area. Both these species, and particularly *R. abyssorum*, are often fairly common in the sieved residues (>500 µm) of box-cores obtained in this area, although fragmentation during sieving made quantification impossible. Other large agglutinated species encountered as fragments in these samples were *Hyperammina laevigata, H. fragilis* (both at Stn 13821#2) and *Technitella legumen* (13826#2).

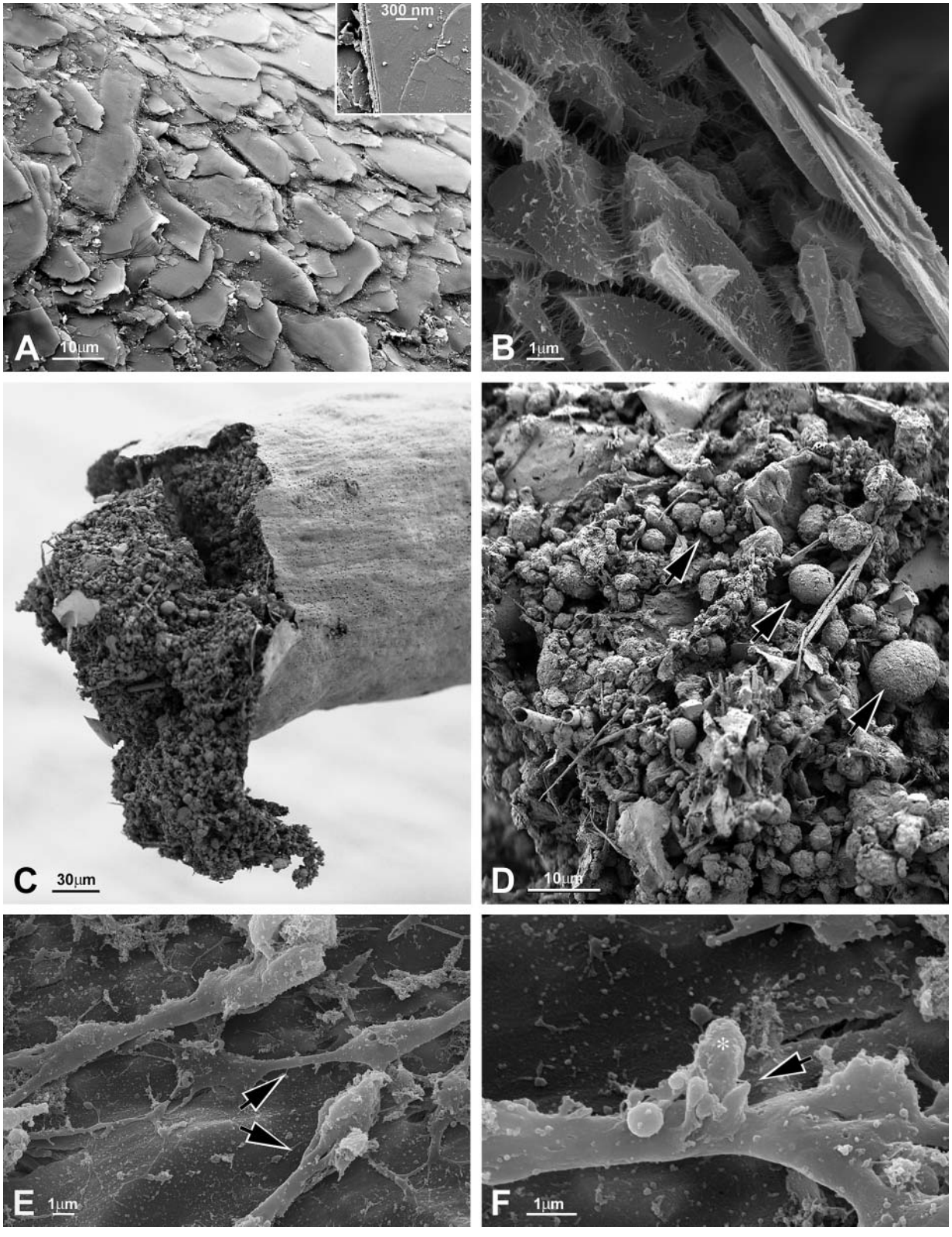

Fig. 1. Scanning electron micrographs of *Bathysiphon capillare*. (A) Outer surface of test consisting of imbricated, plate-like mineral grains that give the test surface a very smooth finish on a scale of µm. Inset shows mica-like cleavage pattern of the outer grains. (B) Broken surface of wall showing thin, surface layer of micaceous grains and underlying grains held together by cobweb-like strands of organic cement. (C) Granular contents of tube bounded by a thin sheath of cytoplasm. (D) Detailed view of granular contents, showing stercomata (arrowed), detrital grains, sponge spicules and other debris indicative of deposit feeding. (E) Branching reticulopodia (arrowed) attached to lumenal (inner) aspect of inner organic lining. (F) Detail of reticulopod giving rise to a food cup engulfing what appears to be a bacterium (*)

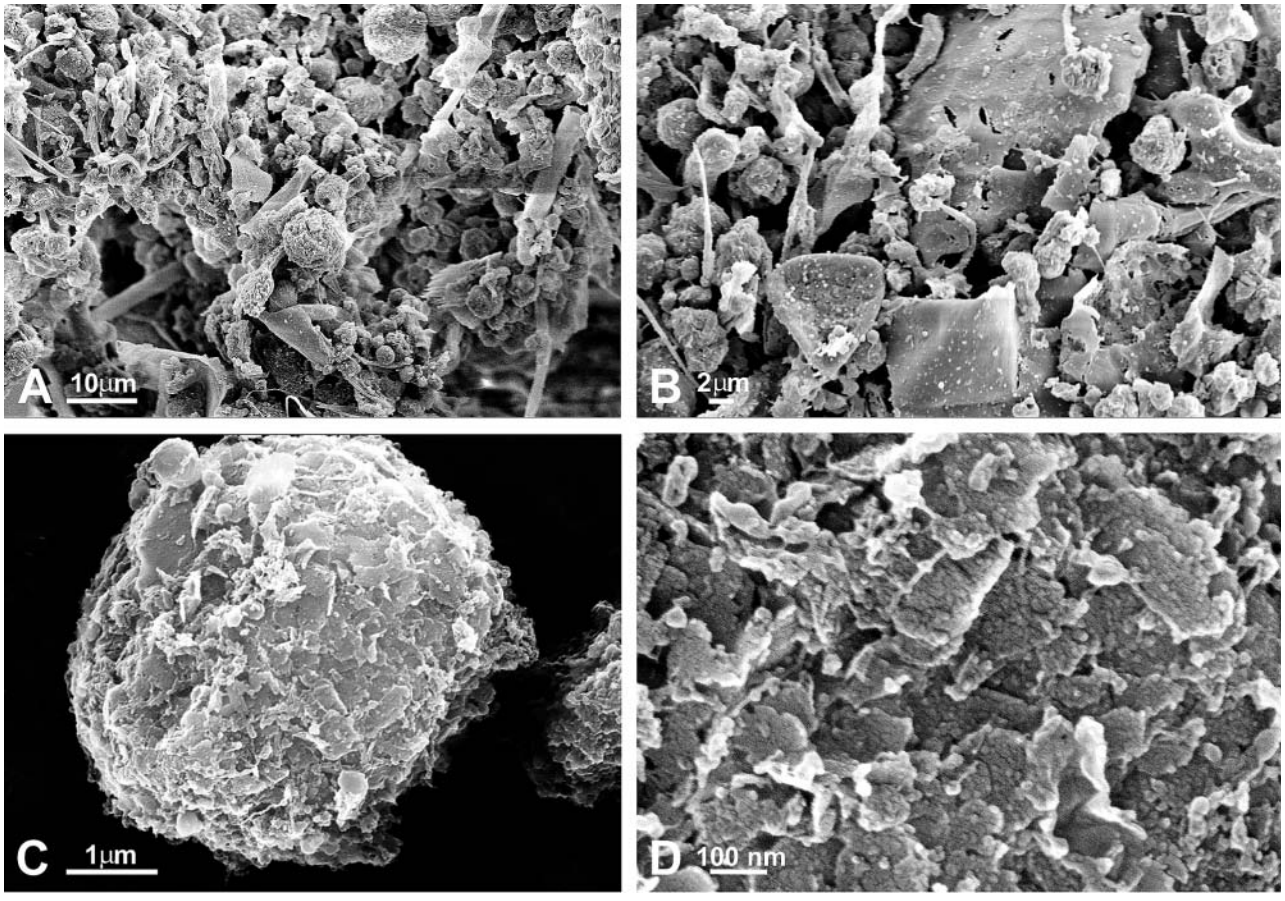

Fig. 2. Scanning electron micrographs of *Bathysiphon capillare*. (A,B) Details of granular material that fills lumen of tube. Among the particles present are stercomata and sponge spicules. (C) Single stercome. (D) Surface of stercome showing tiny constituent grains

Fatty acid composition

Bathysiphon capillare contained a diverse spectrum of fatty acids, which were dominated by monounsaturated fatty acids (~39% of the total, Fig. 5). These monenoic fatty acids comprised mostly 18:1(n-7), 20:1(n-9) and 22:1(n-7) with lesser amounts of 16:1(n-9), 18:1(n-9) and 20:1(n-7). Percentages of total saturated, diunsaturated and polyunsaturated fatty acid (PUFA) were similar, ranging from 18 to 22%. Non-methylene diene interrupted fatty acids (NMIDs) were present in substantial amounts, particularly 22:2Δ7, 13 and 22:2Δ7,15 (Fig. 5). The single most abundant fatty acid in *B. capillare* was 20:4(n-6) which accounted for 16% of total fatty acids, while the long chain PUFA of the n-3 series, i.e. 20:5(n-3) and 22:6(n-3), were present in much lower amounts (~1 and 4%, respectively).

DISCUSSION

Bathysiphon capillare has been reported previously from bathyal localities in the tropical and temperate NE Atlantic (off NW Africa, the Iberian margin, the Bay of Biscay, Porcupine Seabight, Rockall Trough and Norwegian fjords) (Gooday 1988, Schiebel 1992, Timm 1992, Bender 1995, Schönfeld 2001). Many of the records are from water depths of 800 to 1200 m. The only previous Rockall Trough record is from 'Goldseeker' Station 228 (57° 55.55′ N, 10° 34′ W; 1160 m), although reports of *Bathysiphon filiformis* from the warm-water area to the south of the Wyville-Thomson Ridge (Pearcey 1890, Murray & Taplin 1984) probably refer to *B. capillare.* Some individuals (a fifth of all those carefully collected) from the Darwin Mounds were >50 mm in length (in 1 case 105 mm), compared to the lengths of 10 to 20 mm reported in earlier studies (Gooday 1988). This probably reflects the fact that

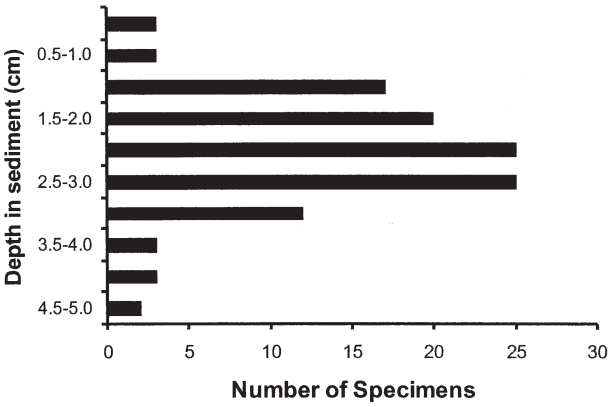

Fig. 3. Vertical distribution of *Bathysiphon capillare* within the sediment profile. Data are based on pooled data from 4 carefully excavated box cores (13834#2, 13840#1, 13842#3 and 13842#4)

earlier material was collected using towed gear (dredge or epibenthic sledge) and therefore subjected to considerable fragmentation. In other respects, the new material resembles the description of *B. capillare* given by previous authors (de Folin 1886, Gooday 1988).

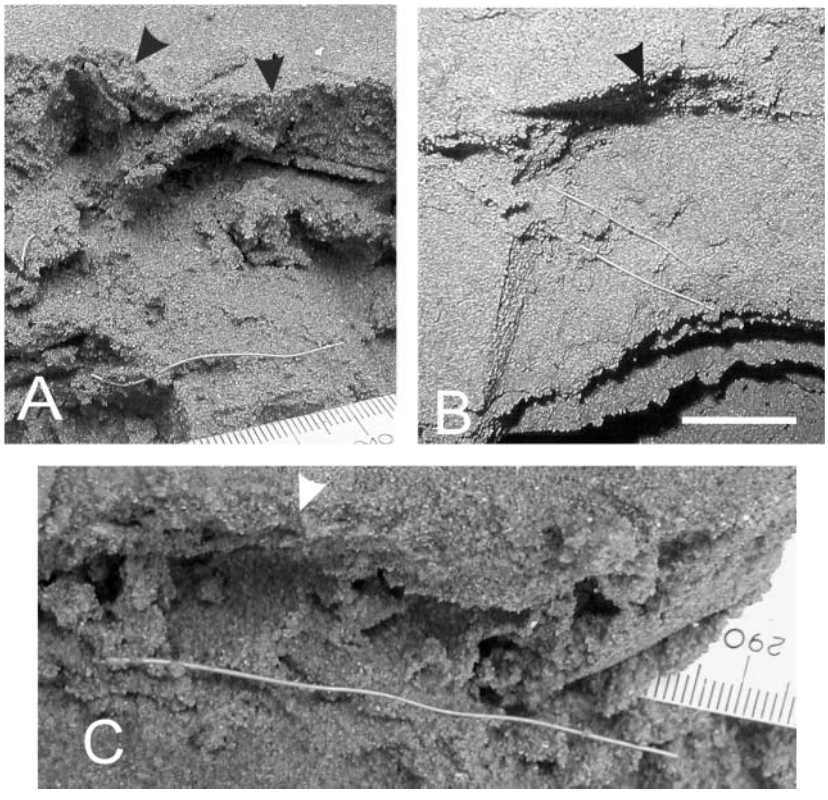

Fig. 4. *Bathysiphon capillare.* (A,C) Individuals of *Bathysiphon capillare* photographed *in situ* in box cores from the Darwin Mounds area. The specimens have been revealed by carefully excavating away the surrounding sediment; the arrowheads indicate the edge of the undisturbed sediment surface. (B) Two individuals lying side by side in an excavated box core; scale bar is 2 cm

The relative scarcity of large agglutinated foraminiferans in cores from the Darwin Mounds area is surprising given the abundance of such forms in samples obtained during early oceanographic expeditions (e.g. 'Lightning', 'Porcupine' and 'Triton'). For example, Brady (1882) reported that a sample from his 'Triton' Stn D, located close to our study area (59° 37' N, 7° 19' W, water depth 530 fathoms = 970 m), was very rich in taxa such as *Astrorhiza, Rhabdammina* and *Marsipella.* This difference presumably reflects the use by the Victorian naturalists of a dredge. Dredges and other towed gears can yield huge numbers of large foraminiferal specimens because they concentrate individuals from a wide tract of seafloor that may encompass different sedimentary habitats and faunal patches (Bandy & Rodolfo 1964, Herb 1971). In fact, 1 of the species reported by Brady (1882), *Astrorhiza arenaria,* was common (11 complete individuals in 12 cores, total surface area 306 cm^2) in muddy sediments recovered during 1 deployment of the multicorer (13835#2) in an area close to the Darwin Mounds, characterised by pockmark-like features (Bett et al. 2001). Another complete set of multicorer samples (13835#1) obtained approximately 100 m away yielded sandy sediments devoid of large agglutinated foraminiferans, suggesting that the distribution of *A. arenaria* on the seafloor is distinctly patchy.

Fossil *Bathysiphon* are reported from deep-water turbidite ('flysch') deposits in many parts of the world (e.g. Miller 1988, 1995). The tubes of these large, robust species had been transported by turbidity currents and deposited in basinal settings. In contrast, all specimens of *Bathysiphon capillare* that we examined contained a core of dark granular material and appeared to be intact. Their delicate tests are very unlikely to have survived transport by a turbidity current without severe damage. There is no evidence for turbidite deposits in our study area, which is underlain by a sandy contourite deposit. Although current speeds of up to 35 cm s^{-1} have been recorded in the area, and the sandy sediment surface is rippled (Masson et al. in press), there is no evidence that *B. capillare* and other faunal elements are anything other than indigenous.

Contribution to macrofaunal densities

The invertebrate fauna in the area of the Darwin Mounds is generally sparse. Few macrofauna were observed, either

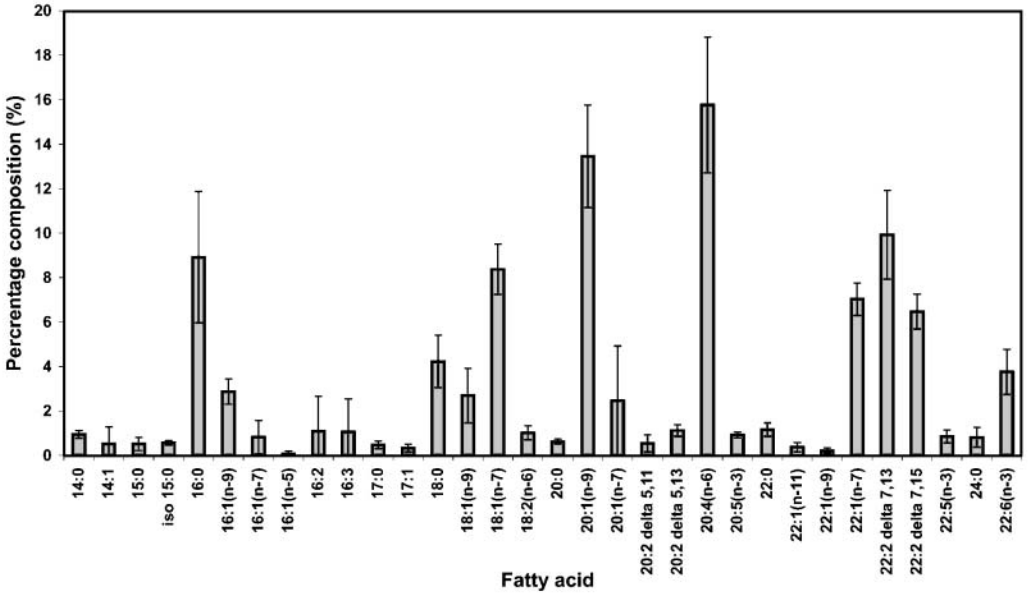

Fig. 5. Fatty acid composition of *Bathysiphon capillare*. Data are from box core 13840#1 (n = 5, SE bars are indicated on the figure)

on the sediment surface or within the cores, although small ophiuroids were quite common. Hepburn (2001) reports the following density values (ind. core^{-1}; >500 µm fraction) for metazoan macrofaunal taxa in 5 undisturbed box-cores collected around the Darwin mounds during the 'Discovery' cruise 248: Stn 13816#1, 233 ind. core^{-1}; Stn 13816#3, 269 ind. core^{-1}; 13821#2, 279 ind. core^{-1}; 13826#2, 112 ind. core^{-1}; 13826#3, 261 ind. core^{-1}; mean density value, 233 ind. core^{-1} (= 932 ind. m^{-2}). The core from Stn 13821 was located on a mound; the other cores were obtained from the tails of mounds. Densities of *Bathysiphon capillare* (100 to 172 ind. m^{-2}) represent 10.7 to 18.5 % of the mean metazoan macrofaunal density in these 5 cores.

Recent work on the UK continental margin comparing macrofauna (>500 µm) in box-cores and in cores recovered using a hydraulically damped megacorer (a larger version of the multicorer) suggests that box-corers underestimate macrofaunal densities by a mean factor of about 2.1 (Bett unpubl.). This, presumably, is because lighter-bodied, surface-dwelling organisms are blown away by the bow wave generated by the box-corer. Applying this factor to the mean macrofaunal density value of Hepburn (2001) gives a figure of 1957 ind. m^{-2}. Megacorer samples collected over the depth range from 706 to 1098 m in the northern Rockall Trough during the Atlantic Margin Environmental Survey (RRS 'Charles Darwin' Cruise 112C) yielded 1317 to 4841 (mean 2333) macrofaunal ind. m^{-2}.[1] The values for the 2 stations closest to the Darwin Mounds area (1BA5 and 1BA6) were 1825 and 3095 (mean 2460) ind. m^{-2}. If we assume a value of around 2000 ind. m^{-2} for metazoan macrofauna in the Darwin mounds area, then *Bathysiphon capillare* densities (100 to 172 ind. m^{-2}) are equivalent to about 5 to 9 % of macrofaunal densities. This should be considered to be a minimum figure since it assumes that, unlike the metazoan macrofauna, no individuals of *B. capillare* were swept away by the box-corer bow wave. Unfortunately, fragmentation makes it impossible to give accurate densities for the total foraminiferal macrofauna.

[1]Bett BJ (2000) Benthic ecology of the Faroe-Shetland channel. In: Environmental surveys of the seafloor of the UK Atlantic Margin, Atlantic Frontier Environmental Network (CD-ROM), section 4.3.2 (available from Geotek, Daventry, Northhants NN11 5EA, UK)

Autecology

Previous field (Christiansen 1971, Gooday et al. 1992a) and laboratory (Hannah & Rogerson 1997, Gross 1998, 2000, Heinz 1999) observations suggest that some *Bathysiphon* species protrude above the sediment surface, while others live below the sediment-water interface. At our study site, *B. capillare* clearly occupies an infaunal microhabitat within the upper 5 cm of sediment. Since the work of Corliss (1985), the occupancy of infaunal microhabitats by deep-sea benthic foraminiferans has been well documented (reviewed by Jorissen 1999). Most infaunal species are relatively tolerant of low oxygen concentrations, and some occur in sediment layers below the oxic/anoxic boundary (Moodley & Hess 1992, Bernhard 1993, Jorissen et al. 1998, Bernhard & Sen Gupta 1999, Schönfeld 2001). Although oxygen data are not available from our study site, *B. capillare* is clearly associated with the upper brownish layer of relatively loose, sandy sediment that probably contains some

oxygen. Schönfeld (2001) reported that oxygen levels (measured using a shipboard oxygen microelectrode) reached 0 around 5 cm sediment depth in 3 cores collected at a similar water depth (800 to 1200 m) on the Iberian margin. The 2.5 to 5.0 cm horizon of one of these cores (from 1085 m) yielded 4 specimens of *B. capillare,* considered by Schönfeld to be an indicator of dysoxic conditions (O_2 < 0.3 ml l^{-1}). Two small, undescribed *Bathysiphon* species are fairly common in the core region of the oxygen minimum zone (OMZ) in the NW Arabian Sea (bottom-water oxygen concentration ~0.13 ml l^{-1}), confirming that some species of this genus can withstand a substantial degree of oxygen depletion (Gooday et al. 2000).

The very smooth outer surface (Fig. 1A,B) of *Bathysiphon capillare* tubes might suggest that specimens can move actively through the substrate. Subsurface movement in 'ant farm' aquaria by unidentified *Bathysiphon* spp. recovered from sublittoral and bathyal sites (water depths from <100 to 900 m) has been reported by several authors (Hannah & Rogerson 1997, Gross 1998, 2000, Heinz 1999). Rates of movement ranged from <2.5 to 7.3 µm min^{-1}. Both Gross (1998) and Heinz (1999) observed that *Bathysiphon* spp. created smooth-sided burrows, presumably reflecting their smooth test surfaces. However, these mobile species were very small; for example, the individual illustrated by Heinz (1999 Plate 1, Fig. G) was ~1.75 mm long. Due to increased frictional resistance and sediment overburden pressures (Severin & Erskian 1981, Severin 1987), the much larger (up to 10 cm long) *B. capillare* specimens from the Darwin Mounds area are less likely to be mobile. Possibly, these long tubes change their position by growth rather than by active locomotion.

Lipid composition

Insights into the diets and trophic dynamics of foraminiferans and other marine organisms can be obtained from their fatty acid composition (Scott et al. 1999). In the case of foraminiferans, which are unicellular protists and therefore lack guts, these biomarkers will be located either in the contents of food vacuoles or in the lipid inclusions that are sometimes a prominent feature of foraminiferal cytoplasm (e.g. Heeger 1990, Turley et al. 1993). Fatty acids that either lack double bonds (saturated) or include only a single double bond (monounsaturated) tend to be used as storage reserves and are extensively catabolised to generate metabolic energy. These fatty acids can be derived both from dietary sources and/or synthesised *de novo* by the organism. PUFAs containing 2 or more double bonds are particularly important for marine organisms since they serve crucial functional roles, for example within cell membranes. Many animals, particularly vertebrates, are either unable to produce PUFA or are unable to do so at a sufficient rate to satisfy their growth and reproductive demands. For these organisms, PUFA are 'essential' dietary components. However, it is not known whether PUFA are essential for marine heterotrophic protists. The main sources of PUFA in the marine environment are photosynthetic microplankton; for example, diatoms are rich in 20:5(n-3) and flagellated algae contain high amounts of 22:6(n-3) (Sargent et al. 1987). Thus, in deep-sea ecosystems, PUFAs are useful markers of comparatively undegraded organic phytodetrital material (Fileman et al. 1998).

The abundance of n-7 series fatty acids and NMIDs suggests a substantial bacterial component to the diet of *Bathysiphon capillare*, since (n-7) fatty acids and particularly 18:1(n-7) are abundant in most classes of bacteria (Sargent et al. 1987). The presence of NMIDs in *B. capillare* is notable since this is the first report of these compounds in a protist. As discussed extensively elsewhere (Ackman & Hooper 1973, Zhukova 1991, Fang et al. 1993), the production of NMIDs is typical of marine invertebrates that experience high dietary inputs of (n-7) 'bacterial' fatty acids. These compounds are thought to be synthesised first by chain elongation of bacterially produced 18:1(n-7) to 20:1(n-7), followed by Δ5 desaturation to 20:2Δ5,13, and finally by further chain elongation to 22:2Δ7,15. The NMIDs 20:2Δ5,11 and 22:2Δ7,13 are similarly produced, but in this instance, the precursor fatty acid is 18:1(n-9). The function of NMIDs in aquatic organisms is unknown, although they possibly compensate for a low dietary availability of PUFA (Fullarton et al. 1995, Pond et al. 1997a). The high amounts of NMIDs in *B. capillare* therefore provide evidence of a predominately bacterial/detrital diet with minor contributions of undegraded phytodetritus. The infaunal occurrence of this species, and the presence within the test of numerous stercomata-like bodies that probably represent the consolidated remains of ingested sediment (Fig. 1D), are also consistent with a bacterial/detrital diet.

The relatively large amounts of n-9 fatty acids, particularly 20:1(n-9), suggest that these fatty acids are synthesised *de novo* by *Bathysiphon capillare*, possibly as energy storage compounds. However, 20 and 22 carbon monounstaurated fatty acids are often major components of zooplankton, particularly those that inhabit the deep ocean (Pond et al. 2000), and so a detrital/zooplankton source for these compounds cannot be excluded. The PUFA 20:5(n-3) and 22:6(n-3), which are abundant in photosynthetic microplankton, are likely to derive from phytodetrital material and indicate that labile compounds of photosynthetic origin make some contribution to the diet of *B. capillare*. A

further possible source of the PUFA is from heterotrophic bacteria, since some strains isolated from the deep sea have been shown to produce these compounds (Russell & Nichols 1999). Bacteria in sediment samples from the Darwin mounds site, however, contained only very low amounts of PUFA (D. W. Pond et al. unpubl.). Given that other large deep-sea agglutinated foraminiferans have been shown to ingest phytodetrital material (discussed below), it is likely that the majority of 20:5(n-3) and 22:6(n-3) in *B. capilliare* was ultimately derived from photosynthetic microplankton. However, future research is required to assess the importance of bacterially derived PUFA in deep-sea ecosystems.

The high amount of 20:4(n-6) in *Bathysiphon capillare* is puzzling. This fatty acid is not particularly abundant in photosynthetic microplankton and unless it is highly conserved by *B. capillare,* phytodetritus is unlikely to be the sole source. A number of deep-sea organisms contain concentrations of 20:4(n-6) (Fullerton et al. 1995, Ginger et al. 2001). Why this should be is not known. More generally, however, it has been suggested that the unsaturated fatty acid composition of cell membranes can affect their fluidity (de Long & Ayes 1985). Under deep-sea conditions of low temperature and high pressure, 20:4(n-6) may possibly serve a crucial role in maintaining the integrity of cell membranes. The resolution of these issues will require the application of experimental tracer techniques to the study of deep-sea organisms.

Deep-sea foraminiferal diets and implications for carbon cycling

The evidence from lipid biomarkers is consistent with our relatively sparse knowledge of foraminiferal dietary requirements. The extensive and highly mobile granuloreticulopodial networks of foraminiferans are very efficient food-gathering systems (Travis & Bowser 1991). Shallow-water species use them to collect and consume various small organisms, mainly pennate diatoms, small chlorophytes and bacteria in addition to yeasts, fungi and even small animals (Lipps & Valentine 1970, Lee & Muller 1973, Lee 1980, 1993, Lipps 1983, Rivkin & DeLaca 1990, Goldstein 1999). Culture studies suggest that feeding is selective (Muller 1975, Moodley et al. 2000) and that some species require bacteria in their diets in order to sustain reproduction (Muller & Lee 1969). Food acquisition is often very rapid and experimental studies suggest that algal particles are processed within hours of being deposited (Moodley et al. 2000).

Diets in deep-sea foraminiferans are probably broadly similar to those of shallow-water species. They also appear to reflect the preferences of individual species for particular microhabitats within the sediment profile (Jorissen 1999). Species living at or close to the sediment surface often consume phytodetritus (Gooday et al. 1992b). The cytoplasm of some epifaunal miliolids and rotaliids (calcareous foraminiferans) is reported to contain green algal cells derived from fresh phytodetrital deposits (Gooday & Turley 1990, Heeger 1990, Gooday et al. 1992b, Altenbach et al. 1993). Experiments and observations of living specimens indicate that large, surface-dwelling agglutinated foraminiferans (e.g. *Bathysiphon* spp., *Cribrostomoides subglobosa, Rhabdammina abyssorum*) also ingest substantial quantities of phytodetrital or algal material (Altenbach 1992, Linke 1992, Linke et al. 1995, 1999). It is likely that these larger agglutinated and smaller calcareous species play an important role in the degradation of labile freshly settled phytodetritus in various bathyal and abyssal settings (Gooday 1988, Meyer-Reil & Köster 1991, Levin et al. 1999, Köster & Meyer-Reil 2001, Moodley et al. 2002).

Other deep-sea foraminiferans may be less reliant on labile food sources. Komokiaceans and related taxa that accumulate large quantities of stercomata ingest sediment and presumably feed on the associated bacteria (Tendal & Hessler 1977, Gooday et al. 1997). These stercomata-bearing foraminiferans are characteristic of abyssal, oligotrophic regions, where fresh organic matter is scarce. Deep-infaunal foraminiferans ('Type C' vertical distribution pattern of Jorissen 1999), which are most abundant in high productivity areas, are also likely to be deposit feeders. Their abundance may reflect the availability of relatively non-labile food 'stored' within the sediments (Jorissen et al. 1998, Van der Zwaan et al. 1999). Deep-infaunal foraminiferans are typically associated with oxygen-depleted sediment porewaters, prompting some authors to speculate that, like some ciliates (e.g. Fenchel & Jansson 1966, Fenchel 1969, 1987, Goulder 1971), they feed on bacteria associated with redox fronts within the sediment (Jannink et al. 1998, Jorissen et al. 1998, Van der Zwaan et al. 1999, Schmiedl et al. 2000, Schönfeld 2001, Fontanier et al. 2002). Direct evidence about diets, however, is scarce and available only for calcareous species. When cultured in the laboratory at 1 atm, 2 deep-infaunal species (*Globobulimina* spp. and *Chilostomella ovoidea*) from Sagami Bay, Japan (1450 m water depth) consumed fresh, heat-killed algae (*Chlorella*) at a much slower rate than epifaunal/shallow infaunal species (Kitazato & Ohga 1995). Dried *Chlorella,* on the other hand, was utilised more quickly. Using transmission electron microscopy, Goldstein & Corliss (1994) investigated the contents of food vacuoles in *Uvigerina peregrina* and *Globobulimina pacifica*, shallow- and deep-infaunal species, respectively, collected at a 710 m site in the San Pedro Basin off

California. Both contained relatively large quantities of sediment particles, organic detritus and associated bacteria. The San Pedro Basin sediments had a higher organic carbon content (3.0 to 3.5%) than the Darwin Mounds sediments and were overlain by oxygen-depleted (<15 µM) bottom water. Our observations suggest that, despite these environmental differences, *Bathysiphon capillare* has a similar diet. There is also evidence that it consumes some fresh phytodetritus. In Sagami Bay, 2 other deep-infaunal species (*G. affinis* and *C. ovoidea*) both exhibited reproductive responses to phytodetritus deposition, and therefore may also be able to utilise labile material as well as more degraded detritus (Kitazato et al. 2000).

These observations have significant implications for carbon cycling. Infaunal foraminiferans are widely distributed in marine environments. They dominate foraminiferal faunas in areas of dysoxic bottom water (Bernhard & Sen Gupta 1999), but also occur in subsurface sediments overlain by well-oxygenated bottom water (Gooday et al. 2001, Fontanier et al. 2002). We speculate that deep-infaunal species, both agglutinated and calcareous, are deposit (sediment) feeders that consume bacteria and relatively degraded (refractory) detrital material in a variety of settings, and may represent an important route by which these carbon sources are made available to higher trophic levels. Their trophic role probably complements that of surface-dwelling foraminiferans, including large, agglutinated species such as *Astrorhiza arenaria* and *Rhabdammina abyssorum,* which are likely to include a higher proportion of fresh phytodetritus in their diets.

CONCLUDING REMARKS

Bathysiphon capillare was by far the most abundant large agglutinated foraminiferan present in box-cores from a site (~950 m water depth) at the northern Rockall Trough. This macrofauna-sized protist occurred infaunally within the top 5 cm of sediment, near the interface between brown (upper) and grey (lower) layers of silty sand. Lipid biomarkers, and the presence within the tubular test of a mass of material including probable stercomata (waste pellets), suggest that it is a deposit feeder, ingesting fine-grained sediment and associated bacteria together with a certain amount of fresher phytodetrital material. As a result, this species and other infaunal foraminiferans may play a significant role in carbon cycling on continental margins. *B. capillare* can be predictably sampled, and the protection afforded by its test and the surrounding sediment ensures that it can be recovered from the seafloor in good condition. Thus, *B. capillare*, and perhaps other large *Bathysiphon* species, such as *B. filiformis* and *B. major* (Gooday et al. 1992a), could provide an excellent experimental system, well suited to resolving fundamental issues regarding the lipid biochemistry of deep-sea organisms and hence, carbon pathways in deep-sea food webs.

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