Deep-Sea Research II 108 (2014) 27–32

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Algal pigments in Southern Ocean abyssal foraminiferans indicate pelagobenthic coupling

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ARTICLE INFO

Available online 6 August 2014

Keywords:
Southern Ocean
Antarctica
Pelago-benthic coupling
Diatoms
Haptophytes
Sedimentation
Pigments
Phytodetritus
Abyssal environment
Food
Foraminifera

ABSTRACT

The cytoplasm of four species of abyssal benthic foraminiferans from the Southern Ocean (around 51°S; 12°W and 50°S; 39°W) was analysed by High Performance Liquid Chromatography (HPLC) and found to contain large concentrations of algal pigments and their degradation products. The composition of the algal pigments in the foraminiferan cytoplasm reflected the plankton community at the surface. Some foraminiferans contained high ratios of chlorophyll *a*/degraded pigments because they were feeding on fresher phytodetritus. Other foraminiferans contained only degraded pigments which shows that they utilized degraded phytodetritus. The concentration of algal pigment and corresponding degradation products in the foraminiferan cytoplasm is much higher than in the surrounding sediment. It shows that the foraminiferans collect a diluted and sparse food resource and concentrate it as they build up their cytoplasm. This ability contributes to the understanding of the great quantitative success of foraminiferans in the deep sea. Benthic foraminiferans are a food source for many abyssal metazoans. They form a link between the degraded food resources, phytodetritus, back to the active metazoan food chains.

1. Introduction

The benthic life on the abyssal floor depends primarily on an input of mass and energy from the upper ocean. The quality and quantity of this input, the pelago-benthic coupling, will determine the structure and function of the communities (Dayton et al., 1994; Epping, 2013; Fabiano et al., 1997; Gooday, 2002; Graf, 1989; Graf et al., 1995; Grebmeier et al., 1988; Grebmeier and Barry, 1991; Hughes et al., 2007; Schnack-Schiel and Isla, 2005; Smith et al., 2006, 2013). This input occurs as sinking of particles produced at the surface (Asper et al., 1992; Fabiano et al., 1997). Faecal pellets and phytoplankton are the major source of such particles and they can sink individually or form aggregates (Asper et al., 1992; Isla et al., 2009). Aggregates, also called marine snow, sink faster than individual particles. The presence of ballast materials such as diatom frustules (opal) can increase the sinking speed (Iversen et al., 2010; Iversen and Ploug, 2010, 2013).

In recent years, attention is drawn upon an overlooked mechanism that can speed up the transportation of primary production to great depths. Active grazing of phytoplankton by large plankton organisms such as salps followed by their fast vertical migration to great depths where they are utilized by benthic organisms are alternative mechanisms that can by-pass the sedimentation of particles and aggregates. The combination of filtering of phytoplankton and vertical migration by salps forms a shortcut of the food chain. It reduces the loss of energy and makes the exchange between the surface layer and the bottom more efficient (Gili et al., 2006; Pfannkuche and Lochte, 1993; Schnack-Schiel and Isla, 2005). It has been estimated that salp carcasses deposit 16 t km^{-2} yr^{-1} of carbon in the Tasman Sea (Henschke et al., 2013).

Many factors affect the sinking particles and the largest part of the phytoplankton production is re-mineralized on its way down to the abyssal depths (Dayton et al., 1994; Grebmeier et al., 1988). It is estimated that only 0.01–1% remain after passage through the water column (Gooday, 2003).

The pelago-benthic coupling in the deep sea is demonstrated for various macro- and megafauna organisms. For example abyssal sponges (Kahn et al., 2012), cnidarians (Elias-Piera et al., 2013), holothurians (Hudson et al., 2004) and sea urchins (Campos-Creasey et al., 1994) contain large amounts of phytoplankton pigments that form the basis for their biological functions. Some of these organisms adapt their reproduction according to variation

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http://dx.doi.org/10.1016/j.dsr2.2014.07.017
0967-0645/

in the input of sedimenting algae, i.e. seasonal variation in primary production (Campos-Creasey et al., 1994).

Pelago-benthic coupling has been demonstrated for shelf foraminiferans (Cedhagen, 1988; Rathburn et al., 2001). But it has also been shown that many deep-sea foraminiferans are associated with phytodetrital aggregates (Cornelius and Gooday, 2004) and can give a fast response to pulses of phytodetritus (Gooday, 1988, 2002). The response of foraminiferans to phytodetritus exposure has been extensively documented both *in situ* and experimentally (Enge et al., 2011; Heinz et al., 2001; Nomaki et al., 2005, 2009; Witte et al., 2003). Indirectly, the distribution of benthic foraminiferal faunas, e.g., dominated by *Epistominella exigua* (Brady, 1884) in various Southern Ocean environments are a reflection of the importance of phytodetritus pulses (Mackensen et al., 1993, 1995).

The Antarctic is characterized by strong seasonality and vertical mixing due to oceanographic processes (Dayton et al., 1994; Schnack-Schiel and Isla, 2005; Smith et al., 2006). The food fluxes and their relations to oceanography are still not understood, but an extensive model in order to understand the structure and function of the food webs at multiple scales were developed by Murphy et al. (2012). The objective of the project SYSTCO II (SYSten COupling in the deep Southern Ocean II) was to investigate aspects of pelago-benthic coupling between 50°S and 60°S. Upwelling deep-water masses interact here with the atmosphere and are ultimately subduced at the Sub-Antarctic Front. Preliminary results from this expedition are gathered by Wolf-Gladrow (2013).

Benthic foraminiferans were collected for other purposes during the expedition (Cedhagen et al., 2013a). Some foraminiferans contained cytoplasm with a distinct brown or brown-green colour. We hypothesize that deep-sea foraminiferans contain pigments from algae that settled from the euphotic zone and were ingested fresh or degraded. We analysed the algal pigment contents of four foraminifera species collected at two deep-sea benthic stations characterized by high net primary productivities and high bottom chlorophyll *a* concentrations (Lins et al., 2014).

2. Material and methods

Material was sampled during the PS79 expedition with the research vessel *Polarstern* to the Southern Ocean in 2012 (ANT-XXVIII/3). Sampling with Agassiz trawl (AGT) equipped with a net of 500 µm mesh size at two stations resulted in numerous very large foraminiferans (Cedhagen et al., 2013a). Stations 141-8 and 175-3 were sampled at comparable water depths (~4100 m) during the austral summer on the 18th of February and the 3rd of March, respectively (Table 1). The first station is located under a very high sea-surface primary production being exported while the second station is located north of South Georgia, in an area of constantly high production during the austral summer (Jones et al., 2012; Lins et al., 2014). Extensive data about all stations are available in Janussen et al. (2013). The samples were already washed to a great extent when they reached the deck because the mesh size of the Agassiz trawl is primarily designed for large macro- and megafauna organisms. The remaining foraminiferans were sieved in cold seawater in a +0 °C lab container and all further handling was done on ice. They were sorted under a stereomicroscope (Wild M5) and photographed with a Canon EOS 500D camera with a double flash (Canon Macro Twin Lite MT-24EX) and an ocular adaptor from LM-Scope. The samples were then immediately shock-frozen in eppendorf tubes in liquid nitrogen and stored at −80 °C until further pigment analysis using high performance liquid chromatography (HPLC) technique at Alfred-Wegener-Institute in Bremerhaven, Germany. Pigment contents were also analysed in sediment samples collected with a multicorer at the same stations as the Agassiz trawl samples. Collection date and coordinates of the multicorer samples are available in Cedhagen et al. (2013c). A summary of the pigment data from these replicates is given in Table 2.

Prior to HPLC analysis, foraminiferan samples were first weighted with a special accuracy balance. Afterwards samples were cleaned with MilliQ water on a Petri slide. Following the method of Knight and Mantoura (1985), the organisms were crushed using a glass rod and then centrifuged (730 g for 3 min). The supernatant was removed into a syringe previously wetted with 90% acetone, and its volume was recorded. Further 50 µl of 90% acetone was added and crushing, mixing and centrifugation repeated. Some samples with highly dense pigments were diluted with 90% acetone prior to HPLC analysis. All samples were analysed based on the HPLC method of Barlow et al. (1997), as detailed in Hoffmann et al. (2006). This method was adapted to our instrument (Waters 600, Waters, USA) and quality controlled as described in detail in Taylor et al. (2011).

Table 1
Stations where foraminiferans were sampled with Agassiz trawl.

Station number	Date	Lat.	Long.	Depth (m)
PS 79/141-8	2012-02-18	51°16.0′S	12°37.5′W	4110
PS 79/175-3	2012-03-03	51°49.95′S	39°24.0′W	4150

3. Results

Various benthic foraminiferans collected at all the abyssal stations during the expedition were observed to contain a cytoplasm that was more or less green or brown. The pigments in the cytoplasm became obvious when very large foraminiferans were collected with a sampling gear designed for macro- and megafauna organisms. Four species were isolated for pigment analyses (Fig. 1). They were *Bathysiphon* aff. *filiformis* M. Sars, 1872 (resembles Jones, 1994, pl. 26, Fig. 15; Wiesner, 1931, pl. III, Fig. 28); *Botellina* aff. *labyrinthica* Brady, 1881 (resembles Jones, 1994, pl. 29, Fig. 8; Wiesner, 1931, pl. XIII, Fig. 158 and pl. XIV, Fig. 159); *Nodosinum gaussicum* (Rhumbler, 1913) (resembles Jones, 1994, pl. 31, Fig. 1-2, 5; Wiesner, 1931, pl. IX, Fig. 108), and *Miliolinella* aff. *subrotunda* (Montagu, 1803) (resembles Jones, 1994, pl. 4, Fig. 3; Wiesner, 1931, pl. XI, Fig. 178).

The following pigments were analysed but gave negative results: chlorophyll *b* (divinyl chlorophyll *a* and divinyl chlorophyll *b*, but not expected to appear in the Southern Ocean), peridinin, 19′-butanoyloxyfucoxanthin, neoxanthin, violaxanthin, astaxanthin, dinoxanthin, lutein, gyroxanthin diesters, α-carotene, and chlorophyllide *a*.

The analysis was, however, positive for the pigments listed in Table 3 and plotted in Fig. 2. The ratio between chlorophyll *a* and degraded chlorophyll *a* pigments (Pheo *a*, *i.e.* sum of pheophorbide *a*, pyropheophorbide *a*, and pheophytin *a*) was 0.19 µg/g in

Table 2
Pigments in sediment samples. Pigment values are expressed as µg per liter sediment.

Station+cast number	PS 79/141-10	PS 79/175-8
Date	2012-02-19	2012-03-04
Latitude	51°16.01'S	50°46.63'S
Longitude	12°37.04'W	39°25.37'W
Bottom depth (m)	4116.5	4154.2
Chlorophyll *a*	0.700440883	0.906729312
Chlorophyll *c*1+*c*2	0	0.906729312
Fucoxanthin	0.622332781	0.79477652
Diadinoxanthin	0.159665768	0
Diatoxanthin	0.132801238	0.145186646
Zeaxanthin	0	0.146178391

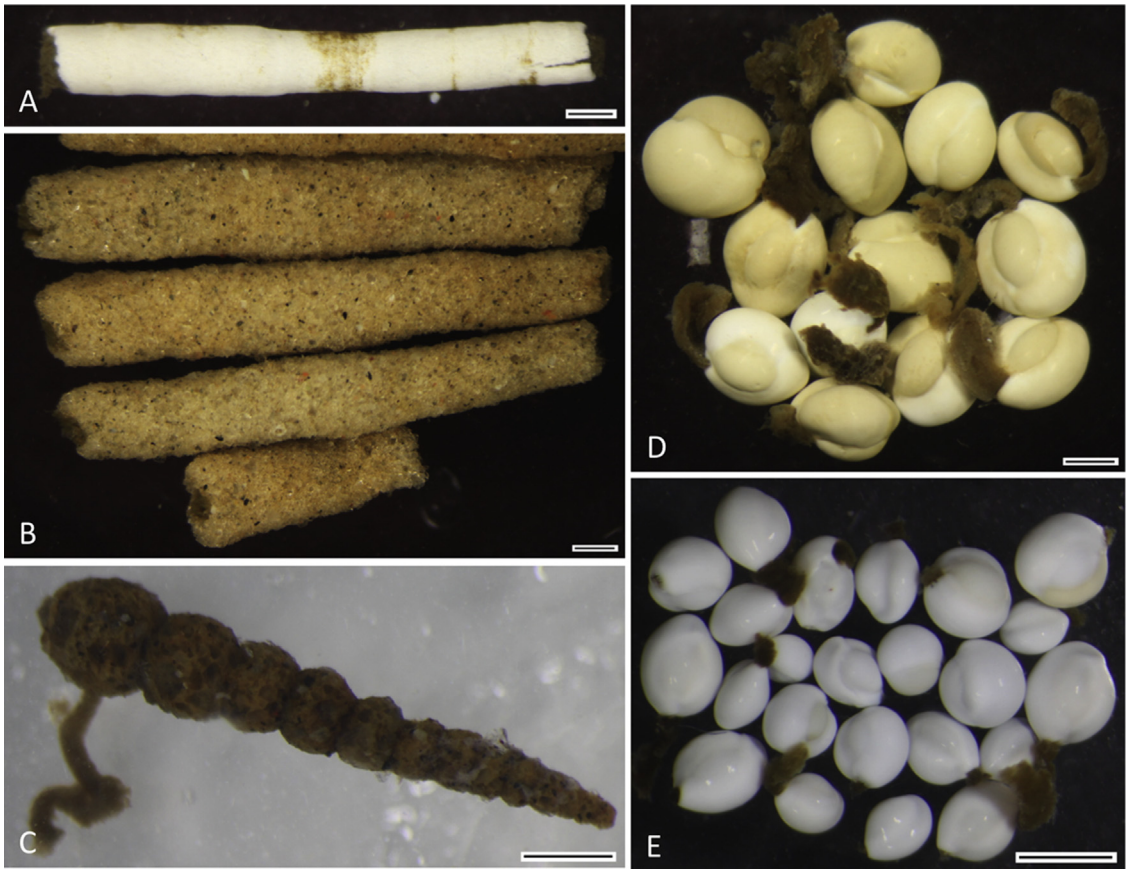

Fig. 1. Living abyssal foraminiferans with cytoplasm coloured by algal pigments: (A) *Bathysiphon* aff. *filiformis*; (B) *Botellina* aff. *labyrinthica*; (C) *Nodosinum gaussicum*; (D) and (E) *Miliolinella subrotunda*. (A) and (B)+(D) from station 175(3); (C)+(E) from station 141(8). Scale bars=1 mm.

Botellina 1; 0.058 in *Botellina* 3; 0.13 μg/g in *Nodosinum* 2; 0.23 in *Miliolinella*-1; 0.84 in *Miliolinella*-2. Some foraminiferans such as *Miliolinella* 3 contained no chlorophyll *a* but only Pheo-*a* pigments.

The pigments in foraminiferan cytoplasm in Table 3 primarily originate from diatoms and secondarily from haptophytes. Indicative for both groups are fucoxanthin, chlorophyll *c1*, chlorophyll *c2*, chlorophyll *c3*, diadinoxanthin and diatoxanthin (Roy et al., 2011). Only 19′-hexanoyloxyfucoxanthin (19-hex) is present in haptophytes but not in diatoms. Except for *Nodosinum* 2, the concentration of 19-hex is either much lower than fucoxanthin or not present in all samples which shows that diatoms were the primary pigment source. This is supported by the global relationship between fucoxanthin and chlorophyll *a* of 1.41 for living diatoms and between 19-hex and chlorophyll *a* of 1.27 for haptophytes (see Uitz et al., 2006). After chlorophyll *a* and pheophorbide *a*, fucoxanthin and pheophytin *a* were the most abundant. Except for *Miliolinella* 2, fucoxanthin was always detected in higher concentrations than chlorophyll *a*, and was even present in those cases when chlorophyll *a* was absent. The former pigment degrades much slower than the later. Low concentrations of alloxanthin, indicative of cryptophytes, and even lower concentrations of zeaxanthin, indicative for prokaryotes (cyanobacteria), are found in the *Botellina* 1 to 3; the later pigment is also found in *Nodosinum 2* samples. In one sample (*Miliolinella* 2), β-carotene, a photoprotective pigment common in many algal groups such as haptophytes and diatoms, was observed. There are no pigments from chrysophytes, prasinophytes or dinoflagellates.

Different foraminiferal species contain different pigments. One sample of *Nodosinum* (*Nodosinum* 1) contained no pigments at all, whereas *Bathysiphon* 1 contained only low concentrations of fucoxanthin. Concentrations of photoprotective pigments (diadinoxanthin, diatoxanthin, alloxanthin and β-carotene) were generally much lower than the photosynthetic pigments (all chlorophylls, fucoxanthin, 19-hex), which may indicate that light-inhibition for algae had been low. Some species contain higher concentrations of photosynthetic pigments (e.g. *Miliolinella* 1 and 2) while most other species (e.g. all *Botellina*, *Miliolinella* 3, and *Bathysiphon* 2) contain higher concentrations of degradation products such as pheophytin *a* and pheophorbide *a*. It shows that some species fed on fresh algae whereas others fed on degraded phytodetritus.

4. Discussion

The following pigments were analysed but gave negative results: chlorophyll *b*, peridinin, 19′-butanoyloxyfucoxanthin, neoxanthin, violaxanthin, astaxanthin, dinoxanthin, lutein, gyroxanthin diesters, α-carotene, and chlorophyllide *a*. The absence of peridinin, neoxanthin, lutein, and chlorophyll *b* suggests that dinoflagellates and chlorophytes were absent (Roy et al., 2011). Algae corresponding to these pigments were not found in the plankton samples (Klaas et al., 2013).

Some foraminiferans contained large amounts of pigments which shows that they were feeding on phytoplankton transported to the abyssal depth before being degraded, or on degraded algae. The composition of algal pigments in the foraminiferans reflects the plankton community that is dominated by diatoms, primarily *Fragilariopsis kerguelensis* (O'Meara, 1877), *Pseudonitzschia* spp. and *Thalassiothrix antarctica* Schimper ex Karsten, 1905 (Klaas et al., 2013). Salps have been shown to act as a mechanism that can increase the transportation of primary production to great depths (see above). Dense populations of the salp species *Salpa thompsoni*

Table 3
Algal pigments in abyssal foraminiferans from the Southern Ocean: *Bathysiphon* aff. *filiformis*; *Botellina* aff. *labyrinthica*; *Nodosinum gaussicum*; *Miliolinella subrotunda*. All values are in μg pigment per gram foraminiferan dry weight.

Foram. species	*Bathysiphon* 1	*Bathysiphon* 2	*Botellina* 1	*Botellina* 2	*Botellina* 3	*Nodosinum* 1	*Nodosinum* 2	*Miliolinella* 1	*Miliolinella* 2	*Miliolinella* 3
Sampling station	141_8	175_3	175_3	175_3	175_3	141_8	141_8	141_8	141_8	175_3
Chlorophyll *a*	0	0	1.96646343	0	0.735986393	0	0.090145364	16.5159044	45.58436167	0
Chlorophyll *c*1 + *c*2	0	0.260717642	0.337025139	0.224022069	0.217744319	0	0.014407376	5.831234029	6.207723694	1.999782336
Chlorophyll *c*3	0	0	0	0	0	0	0	4.127554644	3.291799132	0.714940609
Fucoxanthin	0.251115369	1.862968483	3.860092787	1.842812548	1.802951371	0	0.151205913	38.20594732	20.34032223	13.79591737
19′-Hexanoyloxyfucoxanthin	0	0	0.908778652	0.749077999	0.752693636	0	0.144902252	5.995547736	6.115436153	4.350800293
Diadinoxanthin	0	0	0	0	0	0	0	0	1.026341361	0
Alloxanthin	0	0	0.477308766	0.234383586	0.288093858	0	0	0	0	0
Diatoxanthin	0	0	0.15373216	0	0.102065814	0	0.02024509	1.702737857	0.547255973	1.256458503
Zeaxanthin	0	0	0.11945335	0.109344646	0.078161173	0	0.012022841	0	0	0
β-carotene	0	0	0	0	0	0	0.020937538	0	0.884402011	0
Pheophorbide *a*	0	4.664634745	6.743302427	3.421647712	9.839928555	0	0	50.50484137	34.65425639	10.15424834
Pyropheophorbide *a*	0	0	0	0	0	0	0.704752759	0	0	15.49884487
Pheophytin *a*	0	0	3.64237693	2.381897749	2.833146469	0	0	21.96106094	19.55995834	25.31745302
Sum of Pheo *a*	0	4.664634745	10.38567936	5.803545461	12.67307502	0	0.704752759	72.46590231	54.21421473	50.97054623
Chl *a*:Pheo *a* ratio	–	–	0.189343746	–	0.058074808	–	0.127910622	0.227912768	0.840819366	–

Foxton, 1961 were found in the investigated area (Pakhomov and Hunt, 2013) and could probably have contributed to the downward transport of the fresh phytodetritus. Both *Miliolinella* 1 and 2 samples from station 141_8 contain very high concentrations (16.52 and 45.58 μg/g, respectively) of chlorophyll *a* and the ratio between chlorophyll *a* and Pheo *a* pigments is also high (Table 3). It shows that they have been feeding on fresh phytodetritus. Some miliolid species from continental slope and deep-sea environments have been found to sit elevated on long tubes high above the sediment – a structure facilitating suspension feeding (Altenbach et al., 1993; Cedhagen et al., 2013b). Murray (2006) classified *Miliolinella* as a passive suspension feeder. The importance of the phenomenon could be grossly evaluated by counting the proportion of foraminiferans displaying greenish cytoplasm, as observed experimentally for a deep-sea benthic species (Barras et al., 2009).

Niche separation between different surface-sediment feeding foraminiferans is demonstrated by the composition of algal pigments in the cytoplasm, confirming previous experimental results (Heinz et al., 2001; Nomaki et al., 2005, 2009; Witte et al., 2003). The high ratios of chlorophyll *a* and Pheo *a* pigments in *Miliolinella* 1 and *Miliolinella* 2 shows that they were feeding on fresh phytodetritus. The lower chlorophyll *a*/Pheo *a* ratios, on the contrary, shows that other specimens were feeding on degraded phytodetritus. The availability of food might have been better sustained in station 175 as the benthos lied below extremely productive phytoplankton communities dominated by *Chaetoceros* spp., which contributed to a longer and more efficient export of carbon as compared to the communities of station 141, dominated by *Fragilariopsis* (Assmy et al., 2013).

The concentration of algal pigment in the foraminiferal cytoplasm was very much higher than in the surrounding sediment, in which degraded chlorophylls were absent (Table 2) indicating an important mechanism. Pheo *a*, which could have resulted from zooplankton grazing and/or senescent cells (Jeffrey, 1974), have been applied recently as marker of detritus in the Southern Ocean (Wright et al., 2010). Diluted and degraded phytodetritus is a food resource of relatively low quality. Many foraminiferans cover a fairly large sediment surface area with their pseudopodia and gather food particles that are transported to, and concentrate in their cytoplasm. Photographs of foraminiferans with extended pseudopodial networks gathering food particles are published by Travis and Bowser (1991), Cedhagen (1988, 2010), Richardson and Cedhagen (2001), and Goldstein (1999). The granuloreticular pseudopodia are able to collect even a sparse food resource. This phenomenon – covering a large area with numerous granuloreticulopodia without spending much energy on active searching for food – gives the foraminiferans an advantage over other organisms and contributes to the explanation of their great quantitative success, particularly in the deep sea. The proportion of benthic foraminiferans is generally increasing by depth in the deep sea where they gradually become the dominant organism group (Gage and Tyler, 1999). Moreover, one Agassiz trawl encompasses diverse foraminiferal communities resulting from the great patchiness of the deep-sea benthos. Indeed, subsamples taken within a single sediment core can greatly differ in terms of taxonomic composition, as shown using environmental DNA sequencing (Lejzerowicz et al., 2014). From our four species, only a relative of *Bathysiphon* could be sequenced while numerous species washed through the Agassiz trawl mesh such as those belonging to the small genus *Epistominella* may also contribute to the phytodetritus uptake (Enge et al., 2011; Gooday, 1988).

The *Miliolinella subrotunda* specimens were unusually large. We have no explanation for this particular phenomenon but gigantism has been described in other organisms from the deep Southern Ocean (Moran and Woods, 2012). Most foraminiferans in Fig. 1 show large amounts of cytoplasm outside their tests. Similar reactions have been observed in sublittoral foraminiferans as a

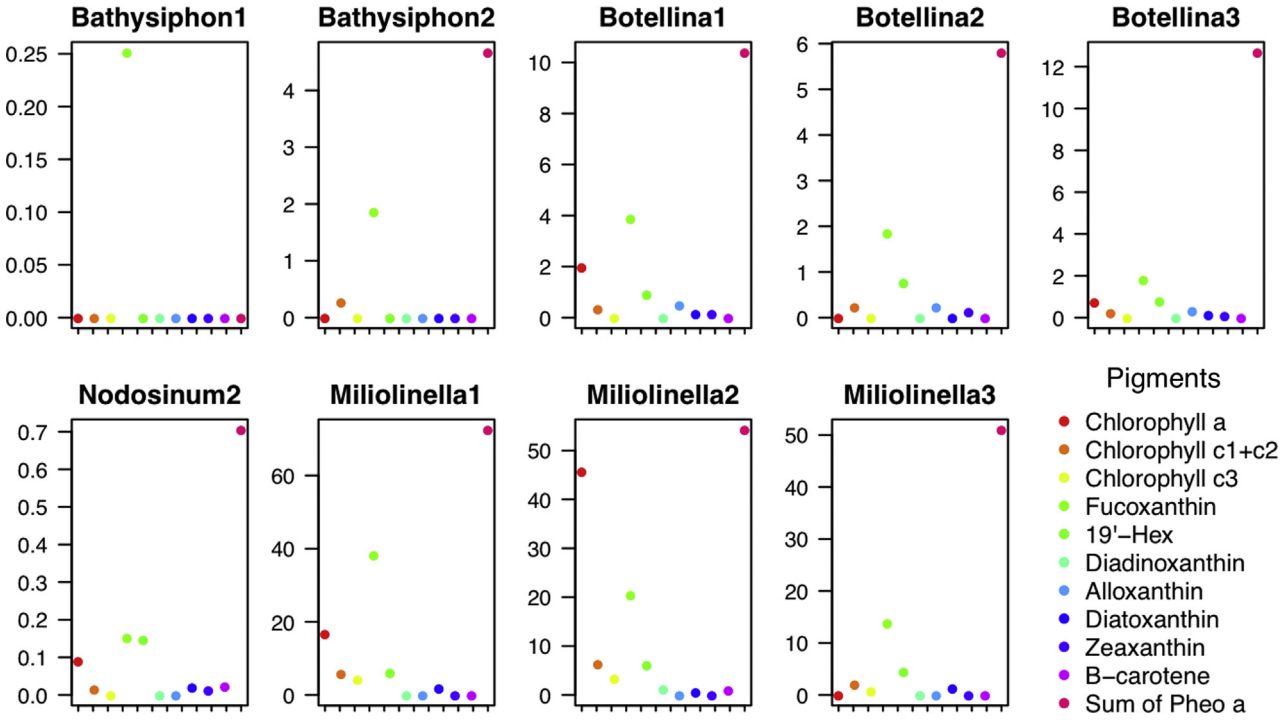

Fig. 2. Pigment concentration in the 9 foraminifera specimens found positive for the presence of algal pigments. For each specimen, concentrations are indicated in μg pigment per gram of foraminiferan dry weight. Note the *y*-axis scale variation. 19′-Hex: 19′-hexanoyloxyfucoxanthin.

response to unfavourable conditions, particularly increased temperature (Cedhagen, 1993).

Foraminiferans create food resources for benthic metazoans by concentrating phytodetritus and building up their own biomass. Some megabenthos such as holothurians are adapted to directly feed on the phytodetritus but some other groups in the deep sea do not easily utilize this food resource directly. Deep-sea foraminiferans are known to be an important food source for isopods, a common organism group in the deep sea (Brökeland et al., 2010 and further references therein). It shows that foraminiferans are an important mechanism for using the residual of the settling primary production, also degraded algae, and transferring it back to the active food chains in the deep sea.

Acknowledgements

Prof. Angelika Brandt is thanked for active support of the authors and for boosting the SYSTCO project. The captain and crew of R/V *Polarstern* are thanked for their competence and indefatigable helpfulness. Funding for T.C. was given by Carlsberg Foundation, Denmark (project no. 2011_01_0574). Funding for A.B. and W.C. was supplied by the Helmholtz Association and AWI via the project "Phytooptics". Funding for F.L. was provided by the Swiss National Science Foundation Grant no. 31003A-140766 (Jan Pawlowski) and by G & L Claraz Donation (J.P.). We thank Mariana Altenburg-Soppa for her assistance during the cruise and Sonja Wiegmann for HPLC pigment analysis, Prof. Gerhard Schmiedl for insightful critics on the manuscript and Prof. Andrew J. Gooday for help with the identification of foraminiferans.

References

Altenbach, A.V., Heeger, T., Linke, P., Spindler, M., Thies, A., 1993. *Miliolinella subrotunda* (Montagu), a miliolid foraminifer building large detritic tubes for a temporary epibenthic lifestyle. Mar. Micropaleontol. 20, 293–301.

Asper, V.L., Deuser, W.G., Knauer, G.A., Lohrenz, S.E., 1992. Rapid coupling of sinking particles between surface and deep ocean waters. Nature 357, 670–672.

Assmy, P., Smetacek, V., Montresor, M., Klaas, C., Henjes, J., Strass, V.H., Arrieta, J.M., Bathmann, U., Berg, G.M., Breitbarth, E., Cisewski, B., Friedrichs, L., Fuchs, N., Herndl, G.J., Jansen, S., Krägefsky, S., Latasa, M., Peeken, I., Röttgers, R., Scharek, R., Schüller, S. E., Steigenberger, S., Webb, A., Wolf-Gladrow, D., 2013. Thick-shelled, grazer-protected diatoms decouple ocean carbon and silicon cycles in the iron-limited Antarctic Circumpolar Current. Proc. Natl. Acad. Sci. USA 110, 20633–20638.

Barlow, R.G., Cummings, D.G., Gibb, S.W., 1997. Improved resolution of mono- and divinyl chlorophylls a and b and zeaxanthin and lutein in phytoplankton extracts using reverse phase C-8 HPLC. Mar. Ecol. Prog. Ser. 161, 303–307.

Barras, C., Geslin, E., Duplessy, J.C., Jorissen, F.J., 2009. Reproduction and growth of the deep-sea benthic foraminifer *Bulimina marginata* under different laboratory conditions. J. Foraminifer. Res. 39, 155–165.

Brökeland, W., Gudmundsson, G., Svavarsson, J., 2010. Diet of four species of deep-sea isopods (Crustacea: Malacostraca: Peracarida) in the South Atlantic and the Southern Ocean. Mar. Biol. 157, 177–187.

Campos-Creasey, L.S., Tyler, P.A., Gage, J.D., John, A.W.G., 1994. Evidence for coupling the vertical flux of phytodetritus to the diet and seasonal life history of the deep-sea echinoid *Echinus affinis*. Deep-Sea Res. I 41, 369–388.

Cedhagen, T., 1988. Position in the sediment and feeding of *Astrorhiza limicola* Sandahl, 1857 (Foraminiferida). Sarsia 73, 43–47.

Cedhagen, T., 1993. Taxonomy and biology of *Pelosina arborescens* with comparative notes on *Astrorhiza limicola* (Foraminiferida). Ophelia 37, 143–162.

Cedhagen, T., 2010. Encelliga djur som andas nitrat. HavsUtsikt 2010 (1), 4–5.

Cedhagen, T., Lejzerovicz, F., Pawlowski, J., 2013a. Foraminifera of the deep Southern Ocean: bentho-pelagic distribution and past and present metagenetics. Ber. Polar-Meeresforsch. 661, 81–83.

Cedhagen, T., Aungtonya, C., Banchongmanee, S., Sinniger, F.A., Pawlowski, J., 2013b. Gromiids and monothalamous foraminiferans (Rhizaria) from the Andaman Sea, Thailand – taxonomic notes. Phuket Mar. Biol. Cent. Res. Bull. 72, 1–17.

Cedhagen, T., Hauquier, F., Jörger, K., Lejzerowicz, F., Mulsow, S., Würzberg, L., Zinkann, A.-C., 2013c. Foraminifera of the deep Southern Ocean: MUC deployments. Ber. Polar- Meeresforsch. 661, 76–78.

Cornelius, N., Gooday, A.J., 2004. 'Live' (stained) deep-sea benthic foraminiferans in the western Weddell Sea: trends in abundance, diversity and taxonomic composition along a depth transect. Deep-Sea Res. II 51, 1571–1602.

Dayton, P.K., Mordida, B.J., Bacon, F., 1994. Polar marine communities. Am. Zool. 34, 90–99.

Elias-Piera, F., Rossi, S., Gili, J.M., Orejas, C., 2013. Trophic ecology of seven Antarctic gorgonian species. Mar. Ecol. Prog. Ser. 477, 93–106.

Enge, A.J., Nomaki, H., Ogawa, N.O., Witte, U., Moeseneder, M.M., Lavik, G., Ohkouchi, N., Kitazato, H., Kucera, M., Heinz, P., 2011. Response of the benthic foraminiferal community to a simulated short-term phytodetritus pulse in the abyssal North Pacific. Mar. Ecol. Prog. Ser. 438, 129–142.

Epping, E., 2013. Life in an oceanic extreme. Nat. Geosci. 6, 252–253.

Fabiano, M., Chiantore, M., Povero, P., Cattaneo-Vietti, R., Pusceddu, A., Micic, C., Albertelli, G., 1997. Short-term variations in particulate matter flux in Terra Nova Bay, Ross Sea. Antarct. Sci. 9 (2), 143–149.

Gage, J.D., Tyler, P.A., 1999. Deep-Sea Biology: A Natural History of Organisms at the Deep-sea Floor. Cambridge University Press, Cambridge p. 504.
Gili, J.-M., Rossi, S., Pagès, F., Orejas, C., Teixidó, N., López-González, P.J., Arntz, W.E., 2006. A new trophic link between the pelagic and benthic systems on the Antarctic shelf. Mar. Ecol. Prog. Ser. 322, 43–49.
Goldstein, S., 1999. Foraminifera: a biological overview. In: Sen Gupta, B.K. (Ed.), Modern Foraminifera. Kluwer Academic Publishers, Dortrech, pp. 37–55.
Gooday, A.J., 1988. A response by benthic Foraminifera to the deposition of phytodetritus in the deep sea. Nature 332, 70–73.
Gooday, A.J., 2002. Biological responses to seasonally varying fluxes of organic matter to the ocean floor: a review. J. Oceanogr. 58, 305–332.
Gooday, A.J., 2003. Benthic Foraminifera (Protista) as tools in deep-water palaeoceanography: environmental influences on faunal characteristics. Adv. Mar. Biol. 46, 1–90.
Graf, G., 1989. Benthic–pelagic coupling in a deep-sea benthic community. Nature 341, 437–439.
Graf, G., Gerlach, S.A., Linke, P., Queisser, W., Ritzrau, W., Scheltz, A., Thomsen, L., Witte, U., 1995. Benthic–pelagic coupling in the Greenland-Norwegian Sea and its effect on the geological record. Geol. Rundsch. 84, 49–58.
Grebmeier, J.M., McRoy, C.P., Feder, H.M., 1988. Pelagic–benthic coupling on the shelf of the northern Bering and Chukchi Seas. I. Food supply source and benthic biomass. Mar. Ecol. Prog. Ser. 48, 57–67.
Grebmeier, J.M., Barry, J.P., 1991. Influence of oceanographic processes on pelagic–benthic coupling in polar regions: a benthic perspective. J. Mar. Syst. 2, 495–518.
Heinz, P., Kitazato, H., Schmiedl, G., Hemleben, C., 2001. Response of deep-sea benthic foraminifera from the Mediterranean Sea to simulated phytoplankton pulses under laboratory conditions. J. Foraminifer. Res. 31, 210–227.
Henschke, N., Bowden, D.A., Everett, J.D., Holmes, S.P., Kloser, R.J., Lee, R.W., Suthers, I.M., 2013. Salp-falls in the Tasman Sea: a major food input to deep-sea benthos. Mar. Ecol. Prog. Ser. 491, 165–175.
Hoffmann, L.J., Peeken, I., Lochte, K., Assmy, P., Veldhuis, M., 2006. Different reactions of Southern Ocean phytoplankton size classes to iron fertilization. Limnol. Oceanogr. 51, 1217–1229.
Hudson, I.R., Pond, D.W., Billett, D.S.M., Tyler, P.A., Lampitt, R.S., Wolff, G.A., 2004. Temporal variations in fatty acid composition of deep-sea holothurians: evidence of bentho-pelagic coupling. Mar. Ecol. Prog. Ser. 81, 109–120.
Hughes, J.A., Smith, T., Chaillan, F., Bett, B.J., Billett, D.S.M., Boorman, B., Fisher, E.H., Frenz, M., Wolff, G.A., 2007. Two abyssal sites in the Southern Ocean influenced by different organic matter inputs: environmental characterization and preliminary observations on the benthic foraminifera. Deep-Sea Res. II 54, 2275–2290.
Isla, E., Gerdes, D., Palanques, A., Gili, J.-M., Arntz, W.E., König-Langlo, G., 2009. Downward particle fluxes, wind and a phytoplankton bloom over a polar continental shelf: a stormy impulse for the biological pump. Mar. Geol. 259, 59–72.
Iversen, M.H., Nowald, N., Ploug, H., Jackson, G.A., Fischer, G., 2010. High resolution profiles of vertical particulate organic matter export off Cape Blanc, Mauritania: degradation processes and ballasting effects. Deep-Sea Res. I 57, 771–784.
Iversen, M.H., Ploug, H., 2010. Ballast minerals and the sinking carbon flux in the ocean: carbon-specific respiration rates and sinking velocity of marine snow aggregates. Biogeosciences 7, 2613–2624.
Iversen, M.H., Ploug, H., 2013. Temperature effects on carbon-specific respiration rate and sinking velocity of diatom aggregates – potential implications for deep ocean export processes. Biogeosciences 10, 4073–4085.
Janussen, D., Brandao, S., Cedhagen, T., Hauquier, F., Havermans, C., Jörger, K., Lejzerowicz, F., Meyer-Löbbecke, A., Schnurr, S., Schwabe, E., Vortkamp, M., Würzberg, L., Zinnkann, A.C., Brandt, A., 2013. Agassiz trawl (AGT) deployments. Ber. Polar- Meeresforsch. 661, 115–117.
Jeffrey, S.W., 1974. Profiles of photosynthetic pigments in the ocean using thin-layer chromatography. Mar. Biol. 26, 101–110.
Jones, R.W., 1994. The Challenger Foraminifera, VII+151. Oxford University Press, Oxford p. 117.
Jones, E.M., Bakker, D.C., Venables, H.J., Watson, A.J., 2012. Dynamic seasonal cycling of inorganic carbon downstream of South Georgia, Southern Ocean. Deep-Sea Res. 59, 25–35.
Kahn, A.S., Ruhl, H.A., Smith, K.L., 2012. Temporal changes in deep-sea sponge populations are correlated to changes in surface climate and food supply. Deep-Sea Res. I 70, 36–41.
Knight, R., Mantoura, R.F.C., 1985. Chlorophyll and carotenoid pigments in Foraminifera and their symbiotic algae: analysis by high pressure liquid chromatography. Mar. Ecol. Prog. Ser. 23, 241–249.
Klaas, C., Altvater, F., Kottmeier, D., Kottmeier, R., Rueger, T., Schourup-Kristensen, V., 2013. Plankton assemblage composition, chlorophyll *a*, biogenic silica, particulate and dissolved carbon and nitrogen determination. Ber. Polar-Meeresforsch. 661, 56–59.
Lejzerowicz, F., Esling, P., Pawlowski, J., 2014. Patchiness of deep-sea benthic Foraminifera across the Southern Ocean: insights from high-throughput DNA sequencing. Deep-Sea Res. 108, 17–26.
Lins, L., Guilini, K., Veit-Köhler, G., Hauquier, F., Alves, R.M.S., Esteves, A.M., Vanreusel, A., 2014. The link between meiofauna and surface productivity in the Southern Ocean. Deep-Sea Research 108, 60–68.
Mackensen, A., Fütterer, D.K., Grobe, G., Schmiedl, G., 1993. Benthic foraminiferal assemblages from the eastern South Atlantic Polar Front region between 35° and 57°S: distribution, ecology and fossilization potential. Mar. Micropaleontol. 22, 33–69.
Mackensen, A., Schmiedl, G., Harloff, J., Giese, M., 1995. Deep-Sea Foraminifera in the South Atlantic Ocean: ecology and assemblage generation. Micropaleontology 41, 342–358.
Moran, A.L., Woods, H.A., 2012. Why might there be giants? Towards an understanding of polar gigantism. J. Exp. Biol. 215, 1995–2002.
Murphy, E.J., Cavanagh, R.D., Hofmann, E.E., Hill, S.L., Constable, A.J., Costa, D.P., Pinkerton, M.H., Johnston, N.M., Trathan, P.N., Klinck, J.M., Wolf-Gladrow, D.A., Daly, K.L., Maury, O., Doney, S.C., 2012. Developing integrated models of Southern Ocean food webs: including ecological complexity, accounting for uncertainty and the importance of scale. Prog. Oceanogr. 102, 74–92.
Murray, J.W., 2006. Ecology and Applications of Benthic Foraminifera. Cambridge University Press, Cambridge p. 426.
Nomaki, H., Heinz, P., Nakatsuka, T., 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.
Nomaki, H., Ohkouchi, N., Heinz, P., Suga, H., Chikaraishi, Y., Ogawa, N.O., Matsumoto, K., Kitazato, H., 2009. Degradation of algal lipids by deep-sea benthic foraminifera: an in situ tracer experiment. Deep-Sea Res. I 56, 1488–1503.
Pakhomov, E., Hunt, B., 2013. *Salpa thompsoni* biology: density, population structure and grazing. Ber. Polar- Meeresforsch. 661, 60–65.
Pfannkuche, O., Lochte, K., 1993. Open ocean pelago-benthic coupling: cyanobacteria as tracers of sedimenting salp faeces. Deep-Sea Res. 40, 727–737.
Rathburn, A.E., Perez, M.E., Lange, C.B., 2001. Benthic–pelagic coupling in the Southern California Bight: relationships between sinking organic material, diatoms and benthic foraminifera. Mar. Micropaleontol. 43, 261–271.
Richardson, K., Cedhagen, T., 2001. Quantifying pelagic–benthic coupling in the north sea: are we asking the righy questions? Senckenberg. Maritima 31 (2), 215–224.
Roy, S., Llewellyn, C.A., Egeland, E.S., 2011. Phytoplankton Pigments: Characterization, Chemotaxonomy and Applications in Oceanography. Cambridge University Press, Cambridge, p. 880.
Schnack-Schiel, S.B., Isla, E., 2005. The role of zooplankton in the pelagic–benthic coupling of the Southern Ocean. Sci. Mar. 69 (Suppl. 2), 39–55.
Smith, C.R., Mincks, S., DeMaster, D.J., 2006. A synthesis of bentho-pelagic coupling on the Antarctic shelf: food banks, ecosystem inertia and global climate change. Deep-Sea Res. II 53, 875–894.
Smith, K.L., Ruhl, H.A., Kahru, M., Huffard, C.L., Sherman, A.D., 2013. Deep ocean communities impacted by changing climate over 24 y in the abyssal northeast Pacific Ocean. Proc. Natl. Acad. Sci. USA 110 (49), 19838–19841.
Taylor, B.B., Torrecilla, E., Bernhardt, A., Taylor, M.H., Peeken, I., Röttgers, R., Piera, J., Bracher, A., 2011. Bio-optical provinces in the eastern Atlantic Ocean. Biogeosciences 8, 3609–3629. http://dx.doi.org/10.5194/bg-8-3609-2011.
Travis, J.L., Bowser, S.S., 1991. The motility of foraminifera. In: Lee, J.J., Anderson, O.R. (Eds.), Biology of Foraminifera. Academic Press, London, pp. 91–155.
Uitz, J., Claustre, H., Morel, A., Hooker, S., 2006. Vertical distribution of phytoplankton communities in open ocean: an assessment based on surface chlorophyll. J. Geophys. Res. 111 (1–23), C08005. http://dx.doi.org/10.1029/2005JC003207).
Wiesner, H., 1931. Die Foraminiferen der Deutschen Südpolar-Expedition 1901–1903. Dtsch. Südpolar Exped. 20, 49–165+24.
Witte, U., Wenzhöfer, F., Sommer, S., Boetius, A., Heinz, P., Aberle, N., Sand, M., Cremer, A., Abraham, W.-R., Jørgensen, B.B., Pfannkuche, O., 2003. In situ experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor. Nature 424, 763–766.
The Expedition of the Research Vessel "Polarstern" to the Antarctic in 2012 (ANT-XXVIII/3). Berichte zur Polar- und Meeresforschung 661. In: Wolf-Gladrow, D. (Ed.), iv+190; 2013.
Wright, S.W., van den Enden, R.L., Pearce, I., Davidson, A.T., Scott, F.J., Westwood, K. J., 2010. Phyto-plankton community structure and stocks in the Southern Ocean (30–80°E) determined by CHEMTAX analysis of HPLC pigment signatures. Deep-Sea Res. II 57, 758–778.