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Algal pigments in Southern Ocean abyssal foraminiferans indicate pelagobenthic coupling

Tomas Cedhagen [a,*], Wee Cheah [b,1], Astrid Bracher [b], Franck Lejzerowicz [c]

[a] Aarhus University, Department of Bioscience, Section of Aquatic Biology, Building 1135, Ole Worms allé 1, DK-8000 Aarhus C, Denmark
[b] Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Bussetraße 24, D-27570 Bremerhaven, Germany
[c] Department of Genetics and Evolution, University of Geneva, Sciences III, 30, Quai Ernest Ansermet, CH 1211 Genève 4, Switzerland

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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

* Corresponding author. Tel.: +45 87156112; Mobile: +45 25374780.
E-mail addresses: cedhagen@biology.au.dk (T. Cedhagen), weecheah@gate.sinica.edu.tw (W. Cheah), astrid.bracher@awi.de (A. Bracher), franck.lejzerowicz@unige.ch (F. Lejzerowicz).
[1] Present address: Research Center for Environmental Changes, Academia Sinica, 128 Academia Road, Section 2, Taipei 11529, Taiwan.

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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