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ABYSSAL BENTHIC FORAMINIFERA IN THE POLAR FRONT REGION (PACIFIC SECTOR): FAUNAL COMPOSITION, STANDING STOCK AND SIZE STRUCTURE

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We have evaluated the quantitative composition of Rose Bengal-stained benthic foraminiferal assemblages of surface samples from two box cores (ANTA98-28 bc; ANTA01-01 bc) collected at the Polar Front in the Pacific sector of the Southern Ocean. Size structure, faunal composition and standing stock were analysed for living (Rose Bengalstained) and dead foraminifera. The size fractions among $63-150$, $150-250$ and >250 µm were counted separately in order to study the foraminiferal size distribution and to compare our results with earlier Antarctic studies. The low organic carbon content of the sediment, and hence the limited food availability, is reflected by very low standing stocks and low diversity values. Calcareous taxa dominated dead foraminiferal assemblages that were more diverse than the stained assemblages. In the sediment samples of ANTA01-01 bc, the living fauna contained agglutinated taxa and soft-shelled monothalamous forms. Our data represent the southernmost record of benthic foraminiferal community $(63° S)$ from the Polar Front region in the Pacific sector. These samples provide further evidence for the occurrence of meiofaunal foraminifera in extreme environments, like the Antarctic region, where the uncoupled annual variations in temperature and production cause strong effects on the structure of benthic communities.

Keywords: Foraminifera; Soft-shelled monothalamous foraminifera; Ecology; Southern Ocean

1 INTRODUCTION

Benthic foraminifera are abundant in many marine habitats including polar and deep-sea regions where large agglutinated species may be a conspicuous element of the fauna (Lipps and Hickman, 1982; Gage and Tyler, 1991).

In Antarctic marine environments, during the austral summer, a large proportion of the surface phytoplankton production from the short and intense bloom is deposited on the seafloor. The resulting seasonal, pulsed food supply is predicted to have a marked effect on the structure of benthic foraminiferal communities, leading to faunal changes and a distinct physiological response by certain foraminiferal species. Foraminifera are a major component of benthic communities in cold oceans as well as the deep-sea. In these low-temperature environments, this group must play an important role in the initial breakdown of organic material at the sediment surface within the benthic community.

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Several studies have emphasised the oceanographic setting of the Southern Ocean (both Pacific and Atlantic sector) focusing on physical and biological processes. In this region, no attempt has been made to describe the Polar Front foraminiferal assemblages over its entire taxonomic and size spectrum. The aim of this article is to provide an overview on the total fauna (both dead and live individuals) in order to improve our sparse knowledge of this group in Antarctic Polar Front (APF) waters.

1.1 Environmental Setting

The Southern Ocean is characterised by several thermohaline fronts. These fronts are associated with energetic exchanges with the atmosphere, influencing regional and global climate. The location of the APF varies seasonally from $59^{\circ}50'$ to $63^{\circ}00'$ S (Fig. 1), showing a general tendency to retreat southward between spring and summer (Russo et al., 1999).

FIGURE 1 Location map: position of APF in according to Russo et al., (1999) and Nelson et al., (2002). Arrows show the spatial variation southward until 65° S of the APF during the seasonal/inter-annual oscillations.

However, changes in the APF position during its seasonal or interannual oscillations, are a matter of debate (Russo *et al.*, 1999; Nelson *et al.*, 2002). In Fig. 1 (arrows), we show the extent of spatial variations in its position as far south as 65° S. The APF marks an important boundary in terms of air–sea exchange, primary productivity, and downward biogenic fluxes. Specifically, the APF serves as the northern limit of wind-driven upwelling of deep water. The surface temperature of the upper-layer of this front is lower than $2^{\circ}C$ at depths shallower than 200 m (Orsi et al., 1995; Belkin and Gordon, 1996).

2. MATERIALS AND METHODS

The box cores selected for this study (28 bc; 01 bc) were recovered during cruises of the R/V Italica during austral summers (1998 and 2001, respectively), in the Southern Ocean $(ANTA98-28 \text{ bc: } 63^{\circ}14'$.42 S; $177^{\circ}13'$.21 E; 4114 m water depth; ANTA01-01 bc: 61°35'.72 S; 174°28'.04 E; 4153 m water depth) (Fig. 1).

On board, the box cores are sampled every centimetre and sediment samples are preserved in ethanol with Rose Bengal stain $(1 g L^{-1})$. The use of Rose Bengal to distinguish living foraminifera has been under debate since the introduction of the method. Numerous studies, however, have shown that staining by Rose Bengal is still the best method available to separate specimens, which were alive or recently alive at the time of collection from dead individuals (Boltovskoy and Wright, 1976; Douglas, 1979; Bowser et al., 1985; Bernhard, 1988; Murray, 1991). In the laboratory, the sub-samples (8 cm^3) are sieved on 250-, 150and 63-micron meshes and sorted in water under a binocular microscope for stained benthic foraminifera. Most of the well-stained calcareous and agglutinated specimens are mounted dry on micropaleontological slides to provide taxonomic reference material. All soft-shelled monothalamous foraminifera are placed in glycerol in a glass cavity slide (Gooday, 1988a). At the end of the analyses, all the sieve residues are dried and weighed. Subsequently, the dead foraminiferal fauna is identified and counted from the total samples because of the low density in the residues.

The sampling procedures include the size fractions analysis $(250, 150, 63 \,\mu m)$ in order to estimate the abundance of foraminifera in different size structure and their distribution. Here, we report the dead and live benthic foraminiferal assemblages. For standing stock analyses, counts of living foraminifera were standardised to a volume of 10 cm^3 . We calculate the diversity as number of species of benthic foraminiferal assemblages.

3 RESULTS

3.1 Size Structure

In Fig. 2 the size structure of foraminifera among different fractions reveals, in both box cores, the preponderance of tiny individuals $(63-150 \,\mu m)$ in the Rose Bengal-stained assemblages. Large individuals $(150-250 \,\text{µm})$ dominate the dead assemblage of box core bc-28, whereas dead foraminifera were concentrated in the finer size fraction $(63-150 \,\mu m)$ of box core bc-01.

3.2 Standing Stock

Box core bc-28 shows generally low standing stock values which further decrease downcore (from 34 to $2 n/10$ cm³); the standing stock values of box core bc-01 are lower ranging from 5 to $10 n/10$ cm³ with a peak in the second centimetre (Tab. I).

FIGURE 2 Size structure: number of dead and Rose Bengal-stained foraminifera in 8 cm³ in the different size fractions.

3.3 Taxonomic Composition

Most of the important species have hyaline, calcareous tests (suborder Rotaliina) or multilocular agglutinated tests (suborder Textulariina) as specified in the Taxonomic List in the Appendix. In Fig. 3, we illustrate the taxonomic distribution of the assemblages (both dead and live individuals). In the box core bc-28 calcareous foraminifera dominate the dead fauna (Epistominella exigua, Ehrenbergina glabra, Globocassidulina biora, Nuttalides umbonifer, Oridorsalis umbonatus, Pullenia bulloides), while the agglutinated taxa predominate in the Rose Bengal-stained fauna (Ammolagena clavata, Ammolagena contorta, Haplophragmoides spp., Hormosinella dentaliniformis, Portatrochammina spp., Rhabdammina spp., Reophax difflugiformis, Trochammina spp. (Fig. 3; a selection of

Sample	Interval (cm)	Fraction (μm)	Standing stock $(n/10 \text{ cm}^3)$	Diversity		
				Stained fauna	Dead fauna	TOC (%)
Anta 98-BC 28	$0 - 3$ $0 - 1$ $1 - 2$ $2 - 3$	>63	61 34 25 $\overline{2}$	23 17 11 2	65 36 33 37	0.35
Anta 01 -BC 01	$0 - 3$ $0 - 1$ $1 - 2$ $2 - 3$	>63	20 5 10 5	10 3 5 4	41 38 31 21	0.27

TABLE I Standing stock, diversity and organic carbon.

agglutinated taxa is illustrated in Plates 1 and 2). In the dead fauna, agglutinated taxa are abundant in the coarser residues $(>250 \,\mu m)$ while calcareous specimens predominate in the finest fractions (63–150 and 150–250 μ m). We find similar trend in the samples from box core bc-01 where the dead fauna is characterised by the same calcareous specimens

FIGURE 3 Taxonomic composition: percentage of the three categories analysed in the two box-corer versus sediment depth (cm). The oblique lines indicate the calcareous foraminifera; the grey colour indicates the agglutinated foraminifera; the white colour indicates the soft-shelled foraminifera.

PLATE 1 (1) Ammobaculites filiformis (Bc 01; 0-1 cm; >63 µm); (2) Ammobaculites filiformis, apertural view (Bc 01; 0–1 cm; >63 mm); (3,4) Glomospira charoides (Bc 01; 0–1 cm; >63 mm); (5) Glomospira charoides, apertural view (Bc 01; 0–1 cm; >63 μ m); (6) Heronallenia kempii, dorsal side (Bc 01; 0–1 cm; >63 μ m); (7) Heronallenia kempii, ventral side (Bc 01; 0–1 cm; >63 mm); (8) Heronallenia kempii, apertural view (Bc 01; 0–1 cm; >63 mm); (9) Reophax difflugiformis (Bc 01; 1–2 cm; >150 mm); (10) Reophax sp. (Bc 01; 1–2 cm; $>150 \,\mu$ m); (11) Reophax pilulifer (Bc 01; 1–2 cm; $>150 \,\mu$ m); (12) Spiroplectammina biformis (Bc 01; 0–1 cm; >63 mm); (13) Spiroplectammina biformis, apertural view (Bc 01; 0–1 cm; >63 mm); (14) Textularia pseudogramen (Bc 01; 0-1 cm; >63 µm); (15) Textularia pseudogramen, apertural view (Bc 01; 0-1 cm; >63 µm).

PLATE 2 (1) Cyclammina trullissata (Bc 28; 0-1 cm; >250 µm); (2) Cyclammina trullissata, apertural view (Bc 28; 0–1 cm; >250 mm); (3,4) Deuterammina sp., ventral side. The test consists entirely of agglutinated barium crystal (Bc 01; 0–1 cm; >250 μ m); (5) Deuterammina sp., particular of aperture (Bc 01; 0–1 cm; >250 μ m); (6) Deuterammina sp., particular of suture (Bc 01; 0-1 cm; >250 µm); (7,9) Rhizammina algaeformis (Bc 28; 1–2 cm; >250 μm); (8) Rhizammina algaeformis, particular (Bc 28; 1–2 cm; >250 μm); (10) Rhizammina algaeformis, particular (Bc 28; 1-2 cm; >250 µm); (11) Rhizammina algaeformis, particular (Bc 28; 1-2 cm; $>250 \,\mu m$); (12) *Trochammina* sp. (Bc 01; 0–1 cm; $>250 \,\mu m$).

of box bc-28 (E. exigua, E. glabra, G. biora, N. umbonifer, O. umbonatus) with the occurrence of *Alabaminella weddellensis* abundant in the first centimetre and completely absent in the other box core.

In box core bc-01, the Rose Bengal-stained assemblages especially consist of agglutinated taxa (Hormosina normanni, H. dentaliniformis, Lagenammina difflugiformis, Proteonina difflugiformis) as well as soft-shelled monothalamous foraminifera (allogromiids, saccamminids and psammosphaerids). These single-chambered species with either agglutinated or organic-walled shells (suborders Allogromiina and Astrorhizina) are abundant in the finest fractions (63–150 and 150–250 μ m).

3.4 Diversity and Vertical Distribution in the Sediment

In the dead assemblages, in both box cores, the diversity is high. However, only N . umbonifer, (17–129 specimens per sample) is common and about half the species are represented by single individuals. The diversity of the Rose Bengal-stained fauna is low and remarkably uniform. Within the upper 3 cm of sediment, most foraminifera occur in the top 1 cm and there is a steep decrease in density below this level (Tab. I). Hyaline, calcareous species are concentrated in the uppermost 1 cm (G. biora, Marginulina glabra, Nonion cf. affinis, O. umbonatus, P. bulloides), agglutinated species are more abundant between 1 and 3 cm (A. filiformis, A. clavata, A. contorta, Cyclammina cancellata, Glomospira charoides, L. difflugiformis, Martinottiella communis, Portatrochammina spp., Psammosphaera fusca, R. difflugiformis, Reophax group, Rhizammina algaeformis, Trochammina wiesneri). Some of the abundant species (A. filiformis, Portatrochammina spp., T. wiesneri) are concentrated in the surface layer $(0-1 \text{ cm})$ while others peak between 1 and 3 cm (C. cancellata, G. charoides, M. communis, Reophax group see Taxonomic List). Below 3 cm depth in the sediment, stained benthic foraminifera disappear.

4 DISCUSSION

In this study, we document the size range of foraminiferal taxa present in the samples, an approach that is rarely attempted because it is time consuming. However, the data set has limitations because it represents a small view of the fauna during a single season (summer) of two years that are not consecutive (1998 and 2001). Despite of its limitations, the information is sufficient to establish the overall character of the foraminiferal fauna in relation to seasonal variability of food supply. In fact the taxonomic composition of the benthic foraminiferal fauna of the two box cores is quite similar but the standing stock and diversity values for box core bc-01 (austral summer 2001) are much lower than those for box core bc-28. These differences probably reflect the rapidly changing environmental conditions near the Polar Front.

This area as well as the Southern Ocean are the largest of several high-nutrient, lowchlorophyll regions in the world's oceans. However, several studies based on satellite ocean colour, sea-surface temperature and irradiance data, applied to temperature-dependent photosynthesis/irradiance models (Antoine et al., 1996; Behrenfeld and Falkowski, 1997; Moore and Abbott, 2000), indicate primary productivity of $\lt 50 \text{ g cm}^{-2} \text{ yr}^{-1}$ throughout most of the Antarctic Circumpolar Current (ACC) south of 55° S. This result implies that most of the ACC is less productive on an annual basis than even the classically oligotrophic mid-ocean areas.

In the box core bc-01 tiny individuals $(63-150 \,\mu m)$ dominate in the living and dead assemblages. Information available on foraminiferal population dynamics are rather scarce; especially for deep-sea faunas there is evidence that important interspecific difference in test production and size may exist (Murray, 1991; Jorissen and Wittling, 1999; Gooday and Hughes, 2002). Foraminiferal longevity is supposed to vary from 1 month to 2 years, whereas one individual produces several hundreds of juveniles during asexual reproduction (Murray, 1991). Only a small number of juveniles, however, become adults, and are found ultimately in size fractions larger than $125 \mu m$. This situation can be correlated to pulsed trophic resources and hydrographic conditions. The size distribution of dead benthic foraminifera in the box core bc-28 indicates a preponderance of large individuals $(150-250 \,\mu m)$. The living fauna can be influenced by seasonal variations in the organic flux to the benthic ecosystem reflecting the ontogenetic cycle of specimens. The dead assemblage represent the addition of many generations overtime and therefore may record the occurrence of larger individuals. As written by Mackensen *et al.* (1993) the composition of the dead assemblages differs from the corresponding live assemblages and this is quite normal because the live assemblage represents only the time of sampling, whereas the dead fauna represents many generations added over a long period of time.

Our Polar Front fauna comprises a variety of hard and soft-shelled taxa including species with calcareous, agglutinated and proteinaceous tests. Multilocular agglutinated taxa predominate in the Rose Bengal-stained assemblages with the occurrence of soft-bodied monothalamous foraminifera (suborders Allogromiina and Astrorhizina). Agglutinated taxa, which form their test by sediment particles glued together with organic cement, rapidly disintegrate after death. These species, which make up the majority of the living fauna, decrease in the dead assemblages (Wollenburg and Mackensen 1998; Jorissen and Wittling, 1999; Gooday and Hughes, 2002). Most investigations are based on dried residues and therefore biased towards the calcareous and more robust agglutinated taxa, which survive desiccation. A number of soft-bodied monothalamous foraminifera have been already described (for example, Nyholm, 1974 and earlier papers; Goldstein and Barker, 1988; Gooday, 1990; Bernhard and Bowser, 1992; Gooday and Fernando, 1992) but these delicate taxa are not normally considered as part of the foraminiferal community. Soft-bodied monothalamous foraminifera are reported from marine habitats ranging from supralittoral sands and intertidal mudflats to deep-sea trenches. These delicate foraminifera often account for 10–20% of individuals and species in deep-sea samples. At Polar coastal sites influenced by turbid glacial meltwater, and in some estuaries, allogromiids (including saccamminids) represent an even higher proportion of live foraminifera, in some case >90% (Gooday, 2002).

Our study emphasises the importance of these organisms, which are particularly abundant in the sediment samples from box core bc-01, constituting about 30% of all foraminifera in the >63 -µm fraction.

Probably, the diets of deep-sea soft-bodied monothalamous foraminifera may be less closely linked to inputs of organic matter than those of calcareous foraminifera. There is evidence for a bacterial diet among organic-walled allogromiids and other monothalamous soft-bodies foraminifera (Gooday, 2002). In the box core ANTA01-01 bc, where the carbon flux is very low, living benthic foraminiferal assemblage is represented also by these delicate taxa.

The organic carbon content of the sediments in the Southern Ocean is low, as in many open-ocean environments (Van Bennekom et al., 1988; DeMaster et al., 1991). The annual downward flux of particulate organic carbon decreases dramatically with depth and the most efficient transport of particulate organic carbon (POC) to the sea floor appears to occur south of the APF (61.5–65.5° S), where POC values that rain to the sea floor are 0.15–0.21 mol cm⁻² yr⁻¹ (Nelson et al., 2002). Most (97–99%) of the POC that reaches the sea floor is remineralised in the upper sediment and diffuses back to the water column as dissolved inorganic carbon. Comparison with POC fluxes shows that the biogenic silica $(BSiO₂)$ flux decreases much less with depth than POC flux; moreover the southern ACC between 61.5° S and 65.5° S represents a local maximum in almost every Si flux estimated in the upper ocean, the deep ocean or the seabed (Nelson et al., 2002). Organic carbon values are 0.35% in superficial sediments of bc-28 decreasing downcore to a mean value of about 0.20% at 4 cm depth, while the value of the organic carbon for the core top of bc-01 is 0.27% (Tab. I) (personal communication of L. Langone). The abundance of living benthic foraminifera (standing stock) seems to be positively correlated to the carbon contents measured in our samples (Tab. I). The diversity of living foraminifera correlates well with standing stock values. Highest standing stock and diversities are observed in the first 2 cm of sediment samples.

Foraminiferal associations consisting of E. exigua, N. umbonifer, O. umbonatus, P. bulloides and G. biora are related to low and seasonal fluctuating organic matter fluxes. Epistominella exigua is an opportunistic species reproducing during short pulses of phytodetritus deposition (Gooday, 1988b), while N. *umbonifer* is the dominant element in bottom waters with low temperature and salinity (Mead and Kennet, 1987). G. biora and O. umbonatus seem to be adapted to relatively oligotrophic and well-oxygenated environments, which in turn is strongly dependent on the organic matter fluxes to the sea floor (Mackensen *et al.*, 1995). Large populations of A . weddellensis only in the box core bc-01 can be attributed to organic food resource; probably the absence of E . exigua in the same samples can be attributed to the different nature of organic aggregates present in January 2001 and virtually absent in January 1998. Many of the foraminifera at our study site live epifaunally, on or above the sediment surface, others favour a shallow or more deeply infaunal microhabitats. The ability of some species to switch trophic mode may contribute to their success in a regime characterised by a strongly fluctuating food supply.

Our data can be compared with that provided by Mackensen et al. (1993). As reported in the Table I there are three samples useful for our discussion located in the Polar Front region. The standing stock values are quite similar but the interval and the fractions studied are not directly comparable. The composition of the foraminiferal assemblage is also similar but the diversity is higher.

5 CONCLUSIONS

The distribution of foraminiferal fauna on the Polar Front region (Southern Ocean) essentially mirrors the association zonations of the deep environments, where standing stock and distribution of foraminiferal associations are predominantly controlled by the availability of food. Differences in the taxonomic composition of stained and dead assemblages from sediment samples of different years are believed to reflect inter-annual chemical, physical and biological processes. In both box cores, whereas the dead assemblages include a wide range of taxa, the stained assemblages from the same samples are dominated by agglutinated foraminifera, particularly belonging to suborder Textulariina. Rose Bengal-stained assemblages are less diverse than dead assemblages. The foraminiferal fauna from 1998 and 2001 is very similar in terms of the dominant species but not in terms of abundance that is lower in the living assemblages.

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A APPENDIX

Taxonomic List: Data are related to Cushman, (1948) and Loeblich and Tappan, (1984, 1987) and are referred to genus.

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