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Effects of experimentally induced raised levels of organic flux and oxygen depletion on a continental slope benthic foraminiferal community

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Abstract

A laboratory experiment was carried out with 10 mesocosms containing sediment from a 550 m deep station in the Bay of Biscay. Station B is well-oxygenated throughout the year and material for this study was collected just after the spring bloom in May 2000. The aim of the experiment was to assess the separate effect of the principal environmental parameters, oxygen concentration and organic flux, on the benthic foraminiferal assemblage. Oxygen appears to induce the strongest changes, especially on the vertical distribution of the foraminifera. When subjected to anoxic conditions most species, except some intermediate to deep infaunal taxa (*Melonis barleeanus*, *Globobulimina* spp.), migrate towards the sediment water interface, apparently trying to escape the hostile conditions. Adding organic matter affected only some shallow living, opportunistic taxa (*Epistominella exigua*, *Adercotryma glomerata*). All other species display no significant response to enhanced food conditions, under either oxic or anoxic conditions. The outcome of our experiment suggests that the assemblages of this mesotrophic environment are influenced more strongly by variation in oxygen levels than by changes in organic flux on a short time scale (days to weeks). On a longer time scale organic flux is important in regulating abundances.

Keywords: Live benthic foraminifera; Organic matter flux; Oxygen depletion; Microhabitat; Mesocosm experiment; Bay of Biscay

1. Introduction

Although benthic foraminiferal patterns are certainly influenced by factors such as competition, predation and bioturbation (Jorissen, 1999), oxygen availability and organic flux (or food) seem to be the major parameters in benthic

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foraminiferal ecology (Van der Zwaan et al., 1999). This is substantiated by a number of field studies and experiments that demonstrated the impact of organic supply and changes in oxygen concentration (e.g. Widbom and Elmgren, 1988; Bernhard, 1989; Gooday and Turley, 1990; Bernhard and Reimers, 1991; Schmiedl et al., 1997; Moodley et al., 1998a; Kuhnt et al., 1999; Pfannkuche et al., 1999; Gooday et al., 2000; Schmiedl et al., 2000; Witbaard et al., 2000; Wollenburg and Kuhnt, 2000). Especially in deep-sea environments where organic flux is limiting, certain species respond immediately to pulses of food (Gooday, 1993). Conditions of anoxia in the sediment or bottom water, simulated under laboratory conditions or observed in the field, have been shown to be less limiting than previously expected (Bernhard, 1996; Moodley et al., 1997; Bernhard and Sen Gupta, 1999; Gustafsson and Nordberg, 1999). Yet, most species are negatively affected by low oxygen contents.

Loubere and Fariduddin (1999) review the present state of our knowledge on the relationship between benthic foraminifera and the flux of organic carbon to the seafloor. Jorissen (1999) gives a comparable review of the relationship between the benthic foraminiferal microhabitat and the oxygen concentration. In a third review Van der Zwaan et al. (1999) discuss both organic flux and oxygen as structuring parameters in benthic foraminiferal ecology. What becomes clear from these reviews is that some general patterns can be recognized (e.g. Altenbach, 1992; De Rijk et al., 2000), but that the individual response of most taxa to different regimes of organic carbon flux or oxygen concentration is still unknown (Loubere and Fariduddin, 1999). One often observed pattern is that faunal densities correlate positively with organic flux (e.g. De Stigter, 1996). In muddy shallow coastal and shelf environments (within the euphotic zone) primary production is high, causing a high carbon flux to the seabed. Consequently, in such sediments oxygen consumption is high and oxygen penetration depth is very shallow. Often, these assemblages consist of a few opportunistic and anoxia-tolerant taxa (Barmawidjaja et al., 1992; Nordberg et al., 2000). In deeper water, especially in deep-sea environments, oxygen is a less limiting factor, but instead the amount of organic carbon arriving at the seafloor regulates the benthic deep-sea ecosystem (see Jorissen et al., 1995). The deep sea is a relatively stable environment, but episodic events such as benthic storms or surface phyto-plankton blooms with associated flux to the seafloor cause certain species to respond immediately and increase in abundance or even dominate assemblages (e.g. *Epistominella exigua*, *Alabaminella weddellensis* and *Globocassidulina subglobosa*; see Gooday and Rathburn, 1999 for a review and further Gooday, 1993; Smart and Gooday, 1997).

Individual responses of species or assemblages on variation in organic flux or oxygen content are not well known. This seriously hampers proper reconstructions of the impact of variation of organic flux in the past. In this context, laboratory experiments are important to improve our knowledge since the complex interplay of all the variables in the field makes it difficult to assess the effect of each factor on individual taxa. The use of micro- or mesocosms, in which foraminifera (from greater depth) are kept in their natural sediments, has proven to be a most successful way to culture them (Weinberg, 1990; Chandler et al., 1996; Gross, 2000; Heinz et al., 2001, 2002). Our own experience is that foraminifera kept in their natural sediments and regularly provided with food are able to survive and maintain life cycles for many years (unpublished data). Up to now, experiments have been directed mostly at assessing the effect of low oxygen contents disregarding the effects of organic flux (e.g. Alve and Bernard, 1995; Moodley et al., 1997, 1998b), or at the effect of organic flux under constant oxygen concentrations (e.g. Heinz et al., 2001, 2002). The significance of experimental studies with (benthic) foraminifera lies in the detailed knowledge on ecology and biology, which plays an important role in the use of foraminifera as tools or proxies in modern geochemical and paleoceanographical studies (Van der Zwaan et al., 1999). Microhabitat distribution, for example, is an important factor in the selection of taxa for isotopic studies (e.g. Mackensen et al., 2000).

Live (Rose Bengal stained) benthic foraminifera in the Bay of Biscay have been studied by

Fontanier et al. (2002) along a depth transect from 150 to almost 2000 m deep. Five stations were sampled and faunal composition, density and microhabitat distribution of the live benthic foraminiferal taxa was studied. The main conclusion of this study was that the environmental parameter responsible for the observed differences between the stations was the amount of organic flux arriving at the seabed. Fontanier et al. (2003) focused on station B (550 m water depth) situated at the continental slope. In this study the temporal changes of the foraminiferal populations and vertical habitat distributions are compared with the seasonal changes in the primary production in the surface waters. The oxygen concentration in the bottom and pore waters was shown to be very constant during the 2.5 year sample period. The reproductive response of the foraminiferal faunas to surface phytoplankton blooms appeared to be delayed by several weeks to months. Although in the field only the organic flux to the seabed appears to be the varying environmental parameter, we designed an experiment in order to study in more detail the separate impact of variation in oxygen concentration (oxygenated vs. anoxic conditions) and organic flux on the foraminiferal communities. In order to do so, we collected a live foraminiferal assemblage from this same station B as studied in Fontanier et al. (2003). The experimental design allowed 10 incubated mesocosms to be subjected to oxygenated and anoxic regimes, combined with or without addition of a dose of organic matter, for an experimental period of 19 days.

2. Material and methods

2.1. Collection site and sampling

The material used in this study was collected during the OXYBENT 10 cruise in April/May 2000. The sampled station (station B in Fontanier et al., 2002; Fontanier et al., 2003) is situated in the Bay of Biscay (43 °50′N, 2 °23′W) at a water depth of 550 m (Fig. 1). The area is characterized by two large bloom periods, in spring and in fall; relatively oligotrophic conditions prevail in winter and summer (see Fontanier et al., 2003). During

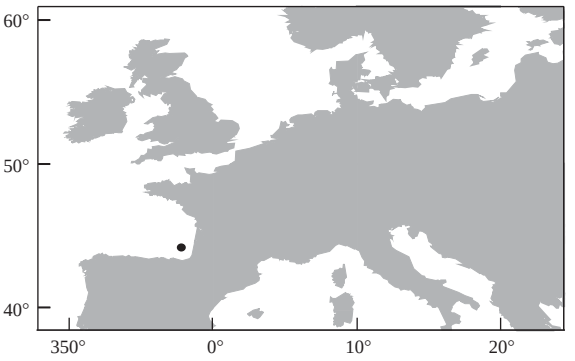

Fig. 1. Geographical position of station B in the Bay of Biscay.

the periods of peak production, labile organic matter can sink 500 m/day and in July 1993 Fernandez et al. (1995) observed a maximum vertical flux of 236 mg C/m^2/day of particulate organic carbon at a 150 m deep station in the Bay of Biscay. Average total flux to the seafloor at the sample site is estimated to be 9.2 g C/m^2/year (0.0025 mg C/cm^2/day), and the labile flux 6.6 g C/m^2/year (Fontanier et al., 2002).

Sampling was conducted with a Barnett multitube corer (eight tubes, surface area 72 cm^2); the collected sediment in the tubes appeared to be undisturbed. Immediately upon arrival on board (May 1, 2000), the top 10 cm of each core was sliced into two parts, the upper 5 cm (0–5 cm) and the lower 5 cm (5–10 cm). The material was not kept under ambient hydrostatic pressure since previous studies showed no necessity to do so with material from these, relatively, shallow depths (Weinberg, 1990; Turley et al., 1993). The material from the two sample intervals was stored and treated separately in polyethylene jars. The material was kept continuously, also during transport to the Netherlands, at 10 °C in cooling boxes. The jars were filled with ambient seawater and the water was aerated several times during transport to the Netherlands by removing the cap and gently stirring the water column.

2.2. Experimental design and set-up

Upon arrival in the Netherlands (May 4, 2000) the sediment from the jars was recombined to one volume (0–5 and 5–10 cm treated separately) and

sieved over a 500 μm sieve to remove the few larger organisms, no living forams were identified in the residue. The material was collected in two different containers after sieving and gently mixed to homogenise it. All treatments took place in a climate-controlled room at 10 °C. The sediment was not exposed to light, except for the time of the sieving and incubation treatments. Artificial seawater (Reef Crystals) was used in all treatments and the aquariums. The seawater was prepared with a salinity of 35.5, continuously checked with a salinity meter (WTW, type LF 330). At 4 days after the initial sieving treatment (May 9, 2000) the sediment was settled sufficiently and the mixed sediments from the lower 5–10 cm interval were incubated in Perspex mesocosms (Fig. 2a). The mesocosms are 20 cm in height, and 6 cm in diameter. After 24 h (May 10, 2000) to allow settling, material from the 0 to 5 cm interval was placed on top of the already incubated sediment. In this way, each mesocosm was filled with a sediment column of about 7 cm. Another 24 h later (May 11, 2000), the mesocosms were incubated in aquariums. After a period of 28 days (June 8, 2000), the mesocosms were considered to have re-equilibrated to ambient conditions, all specimens having had sufficient time to re-migrate to a preferred microhabitat (Ernst et al., 2002). The day before the treatment started (June 7, 2000), cultured algae (*Dunaliella salina*) and diatoms (*Amphiprora* sp., *Phaeodactylum* sp. and some unidentified species) were harvested by centrifuging large amounts of Erdschreiber medium (Cifuentes et al., 1992) on which the cultures took place. The concentrated mix of algae and diatoms was stored and finally heat-killed by placing the beaker for 30 min in water of 60 °C. Two mesocosms were left untreated (*Biox*). Two other mesocosms were fed with 2 ml of the concentrated algal/diatom mix and aerated (*Bioxf*). The resulting flux consisted of 0.007 mg N/cm^2 and 0.054 mg C/cm^2 (measured with a Fisons NA1500 NCS Elemental Analyzer). Two mesocosms received the same organic matter dose but were subsequently sealed in order to generate anoxic conditions (*Bianoxf*). Two other mesocosms were closed but received no organic load (*Bianox*). The mesocosms were put in three separate aquariums

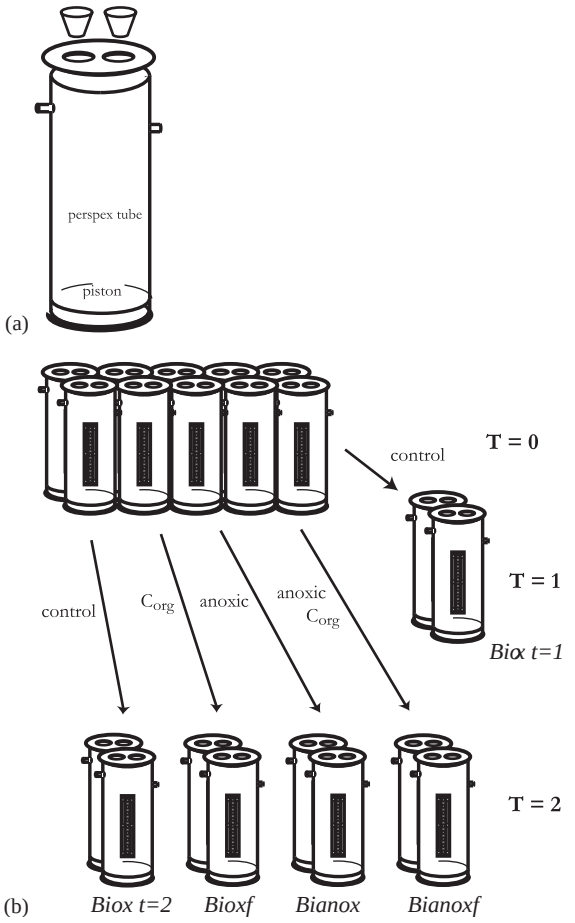

Fig. 2. (a) Mesocosm design. (b) Schematic representation of the experiment.

in order to avoid contamination between the mesocosms or exchange of algae/diatoms by resuspension. The first aquarium contained the oxygenated mesocosms without additional organic load; the second contained the mesocosms with organic load; and the third aquarium the anoxic mesocosms. The remaining two mesocosms (*Biox* $t = 1$) were sampled to function as control at the start of the treatment. After 19 days (June 27, 2000) the remaining mesocosms were harvested. Fig. 2b gives a schematic summary of the experimental design. Sampling was done by slicing the cores in intervals; the top 2 cm was sampled in 0.5 cm layers, and the remainder was sliced in 1 cm layers. The samples were fixed and stained with 1 g

Rose Bengal per litre ethanol (96%), and subsequently sieved (37–63, 63–150, >150 μm). Counting of the three size fractions took place in a mix of equal parts ethanol and water. Total samples were studied, and of each mesocosm the >150 μm size fraction was counted in the upper 5 cm. The size fractions 37–63 and 63–150 μm were counted in the upper 2 cm of each mesocosm.

2.3. Rose Bengal staining

While it has been argued that ATP analysis is a better method to determine living foraminiferal densities than Rose Bengal (Bernhard, 1988), the latter is also reported to be an accurate and reliable method (Murray and Bowser, 2000). In the case that there are high proportions of empty tests and dead specimens (i.e., this study), Alve and Bernhard (1995) concluded that Rose Bengal is more practical to determine foraminiferal densities than the ATP method, since the former permits examination of more specimens.

2.4. Oxygen and salinity measurements

Oxygen concentrations in the water and in porewater of the sediments were measured simultaneously with two electrodes each time the mesocosms were sampled. Sediment oxygen concentrations were measured with oxygen microelectrodes (Microscale Measurements, The Netherlands, $\varnothing = 1$ mm) with Ag/AgCl reference electrode (Philips R11-D-SC) and nano Amp-meter (EDB-RUG MB05 NA). Salinity was measured (WTW, type LF 330) at the start of the treatment ($t = 1$) and at time of sampling ($t = 2$).

2.5. Average living depth

Average living depths (ALD, see Jorissen et al., 1995) were calculated by using the formula:

$$\mathrm{ALD}_x = \sum_{i=1,x} (n(i) \times D(i))/N,$$

with x being the lower boundary of deepest sample, n the number of individuals of a species in interval i, D the average depth of interval i, and N the total number of individuals counted in the mesocosm.

The ALD_5 of the most frequent taxa are calculated for the >150 μm size fraction in the upper 5 cm, and further, ALD_2 are calculated based on total numbers (all specimens >37 μm) of the upper 2 cm of the mesocosms. ALDs were only calculated when the abundance concerned five or more specimens per mesocosm.

2.6. Statistical analyses

PCA-analysis (Canoco 4.0, GLW-CPRO) was used to identify in multivariate space relationships between environmental factors, such as oxygenated or anoxic conditions and organic flux (treatments) on the one hand, and the relative abundance of species and samples on the other.

Any observed changes between the different treatments in vertical distribution and abundances of taxa were tested for significance by performing an analysis of variance; single factor and two-factor without replication ANOVA's (Microsoft Excel, Analysis Toolpack) by using the abundance data of the total assemblage (>37 μm) of the upper 2 cm of two duplicate samples for each treatment.

2.7. Taxonomy

In total, about 70 foraminiferal species were identified in the samples (see Appendix C for a list of taxa not included in the discussion). As seen in Table 1, 16 of these taxa attributed about 70–75% to the average total standing stock (TSS), of which 13 species were identified at the species level (*Adercotryma glomerata, Bolivina alata, Bulimina marginata, Clavulina cylindrica, E. exigua, Globobulimina affinis, Globobulimina pyrula, Haplophragmoides bradyi, Melonis barleeanus, Siphogenerina columellaris, Uvigerina peregrina, U. mediterranea, U. elongatastriata*). Three taxa were identified at genus level and placed in open nomenclature (*Nonionella* sp., *Textularia* sp., and *Stainforthia* sp.). *G. pyrula* and *G. affinis* were grouped in *Globobulimina* spp. The group of *Bolivina* spp. consisted of a number of smaller (mainly <150 μm) *Bolivina* species, namely *B. subspinescens, B. subaenariensis, B. spathulata* and a number of unidentified specimens. In the

Table 1
Abundances of the selected species in the different experimental treatments for the three size fractions

	37–63 μm						
	Biox t = 1	*Biox t = 2*	*Bioxf*	*Bianox*	*Bianoxf*	Total	%
Adercotryma glomerata	4	29	45	4	10	92	4.0
Bolivina alata							
Bolivina spp.	183	128	159	103	122	695	30.4
Bulimina marginata	2	4	8		2	16	0.7
Clavulina cylindrica							
Epistominella exigua	120	61	192	10	79	462	20.2
Globobulimina spp.							
Haplophragmoides bradyi							
Melonis barleeanus					4	4	0.2
Nonionella sp.	22	10	43	19	5	99	4.3
Siphogenerina columellaris		2				2	0.1
Stainforthia sp.	36	7	27	42	14	126	5.5
Textularia sp.	17	14	19	10	11	71	3.1
Uvigerina elongatastriata					2	2	0.1
Uvigerina mediterranea							
Uvigerina peregrina							
Uvigerina spp.	6	1	8			15	0.7
Rest	211	106	209	72	103	701	30.7
Total	601	362	710	260	352	2285	100

	63–150 μm						
	Biox t = 1	*Biox t = 2*	*Bioxf*	*Bianox*	*Bianoxf*	Total	%
Adercotryma glomerata	9	7	14	24	10	64	3.4
Bolivina alata	48	69	62	64	35	278	14.6
Bolivina spp.	67	44	45	83	48	287	15.1
Bulimina marginata	14	1	5	12	4	36	1.9
Clavulina cylindrica		3	5	5	1	14	0.7
Epistominella exigua	72	24	42	24	59	221	11.6
Globobulimina spp.				5	1	6	0.3
Haplophragmoides bradyi	10	25	29	27	20	111	5.8
Melonis barleeanus	19	25	33	29	14	120	6.3
Nonionella sp.	20	6	40	13	11	90	4.7
Siphogenerina columellaris	1	6	3	3	8	21	1.1
Stainforthia sp.							
Textularia sp.	8	14	13	4	5	44	2.3
Uvigerina elongatastriata		4	14	11	6	35	1.8
Uvigerina mediterranea	6	3	2	3	2	16	0.8
Uvigerina peregrina	13	9	3	4	9	38	2.0
Uvigerina spp.							
Rest	151	99	91	113	71	525	27.5
Total	438	339	401	424	304	1906	100

Table 1 (*Continued*)

	>150 μm						
	Biox t = 1	*Biox t* = 2	*Bioxf*	*Bianox*	*Bianoxf*	Total	%
Adercotryma glomerata							
Bolivina alata	13	35	33	18	21	120	15.4
Bolivina spp.							
Bulimina marginata		3	3	2	1	9	1.2
Clavulina cylindrica	23	18	11	27	13	92	11.8
Epistominella exigua							
Globobulimina spp.	8	5	4	6	10	33	4.2
Haplophragmoides bradyi	4	2	1	2		9	1.2
Melonis barleeanus	5	15	6	10	5	41	5.3
Nonionella sp.							
Siphogenerina columellaris	6	6	4	9	2	27	3.5
Stainforthia sp.							
Textularia sp.							
Uvigerina elongatastriata	10	28	35	25	28	126	16.2
Uvigerina mediterranea	42	16	32	32	45	167	21.5
Uvigerina peregrina	6	10	3	14	8	41	5.3
Uvigerina spp.							
Rest	17	30	29	25	12	113	14.5
Total	134	168	161	170	145	778	100

The relative share of the taxa in all mesocosms in each size fraction is given in the final row. *Uvigerina* spp. concerns specimens in the 37–63 μm size fraction of which it was not possible to identify them at the species level.

smaller size fraction these boliviniids are difficult to identify at species level. For further details see Appendix A and Plates I and II.

3. Results

3.1. Geochemistry

Oxygen was measured at the start and end of the experiment (Fig. 3). In Fig. 2 the grey and black lines and dots indicate the results for the two electrodes used at the same time in each individual mesocosm. The measurements were carried out in both control mesocosms at $t = 1$; for the other treatments the results are shown for a single mesoscosm. The oxygenated mesocosms showed similar oxygen profiles at both $=1$ and $t = 2$. The mesocosms subjected to both a supply of organic matter and aeration (*Bioxf*) were very similar to the control situation (*Biox*). Between $t=1$ and 2 perhaps a slight increase in the depth of oxygen penetration could be observed; at $t = 1$ the oxic/anoxic boundary was found at 1.75 cm in both mesocosms, and at $t = 2$ around 2 cm. Anoxic conditions are in the field met at depths varying between 1.7 and 2.6 cm (Fontanier et al., 2003). The anoxic mesocosms (*Bianox* and *Bianoxf*) were indeed depleted in oxygen, both the water column and the pore water in the sediment being anoxic (Fig. 3). Salinity was fairly constant throughout the experimental period in the various aquariums. At $t = 1$, salinity was 35.9 in the aquarium with mesocosms that were subjected to an organic flux pulse, and 36.0 in the aquariums containing mesocosms without this pulse (*Biox*). The anoxic mesocosms were sealed and no salinity changes were observed there ($S = 35.5$).

3.2. Foraminiferal abundances and distribution

Table 1 gives the standing stocks of the 16 selected taxa in the three size fractions (see Appendix B for the countings of all taxa). The total standing stocks of the anoxic treatments were

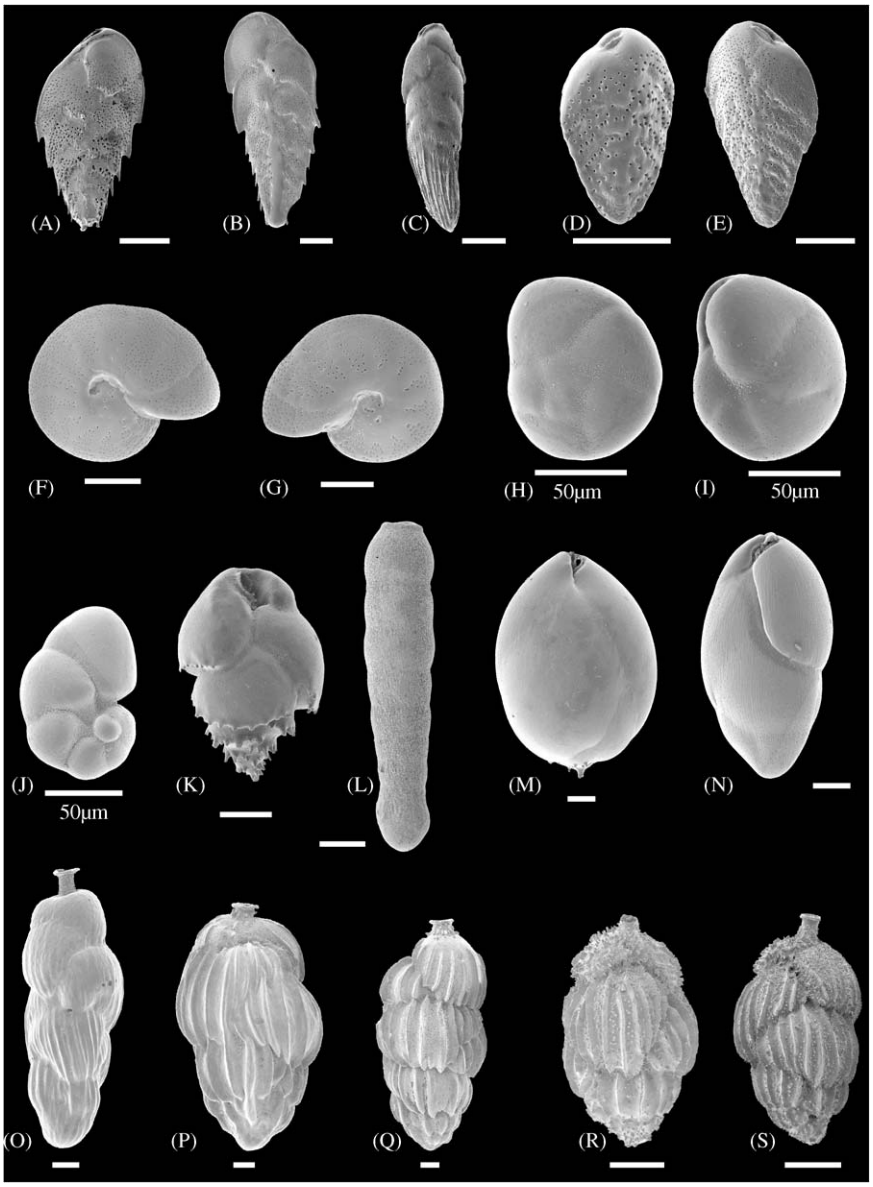

Plate I. The scale bars represent 100 µm, but for some figures the scale bar represents 50 µm. If this is the case, it is noted in the plate. Plate I, Figures: A,B = *Bolivina alata*; C = *Bolivina striatula*; D,E = *Bolivina spathulata*; F,G = *Melonis barleeanus*; H,I = *Epistominella exigua*; J = *Nonionella* sp.; K = *Bulimina marginata*; L = *Siphogenerina columellaris*; M = *Globobulimina pyrula*; N = *Globobulimina affinis*; O = *Uvigerina elongatastriata*; P,Q = *Uvigerina mediterranea*; R,S = *Uvigerina peregrina*.

somewhat lower compared to the oxic treatments. The share of these 16 taxa in the total standing stock averages about 73%. A large number of undetermined specimens were present in the smallest size fractions where identification at the species level was difficult. *E. exigua*, *Bolivina* spp., *B. alata* and *U. mediterranea* are the most abundant taxa. Especially the very small *E. exigua* and *Bolivina* spp. were dominantly present, but mostly found in the 37–63 µm fraction. In the >150 µm size fraction *U. mediterranea* was the most abundant taxon, as seen in the field

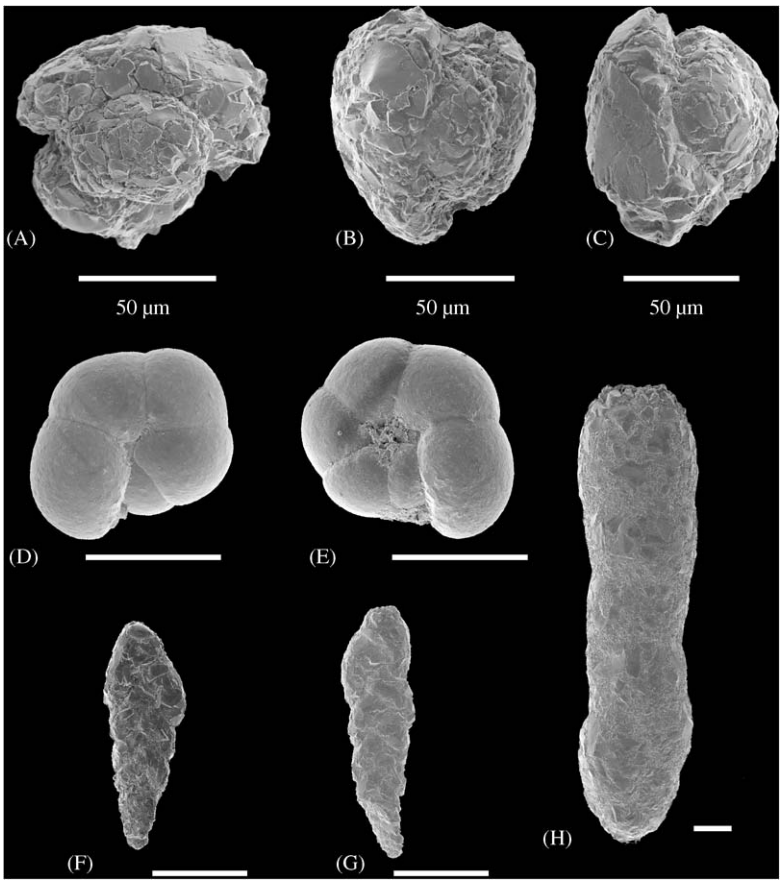

Plate II. The scale bars represent 100 µm, but for some figures the scale bar represents 50 µm. If this is the case, it is noted in the plate. Plate II, Figures: A–C = *Adercotryma glomerata*; D,E = *Haplophragmoides bradyi*; F,G = *Textularia* sp.; H = *Clavulina cylindrica*.

(Fontanier et al., 2003). The 63–150 µm size fraction had in general the highest diversity and most taxa, except *Stainforthia* sp., were present.

For analyses concerning the upper 2 cm all three size fractions were summed. During the experiment the TSS in the control mesocosms (*Biox* $t =$ 1 and 2) decreased (Fig. 4). The mesocosms that additionally received fresh organic matter (*Bioxf*) had a higher TSS and this was especially noticeable near the sediment–water interface (Fig. 4). The TSS in the anoxic mesocosms (*Bianox*) was lower and the vertical distribution shows that most living specimens are found near the surface of the mesocosms. The anoxic mesocosms that received organic matter (*Bianoxf*) also had lower TSS and similar microhabitat distribution as in the unfed anoxic mesocosms.

Fig. 5 shows the relative distribution in depth of the three size classes in all treatments. In the control mesocosms (*Biox*), the foraminifera larger than 63 and 150 µm are distributed over the upper 2 cm. In these *Biox* mesocosms a relatively high number of specimens of the size 37–63 µm were found in the upper 5 mm of the sediment (40–70%). In the *Bioxf* treatment over 80% of the specimens in the size fraction 37–63 µm were found in the upper 5 mm of the sediment, the two larger size fractions were more evenly distributed in depth. The distribution of the different size fractions in the anoxic mesocosms (*Bianox* and *Bianoxf*) was very similar; in all mesocosms over 70% of all size fractions was found in the upper 5 mm of the sediment.

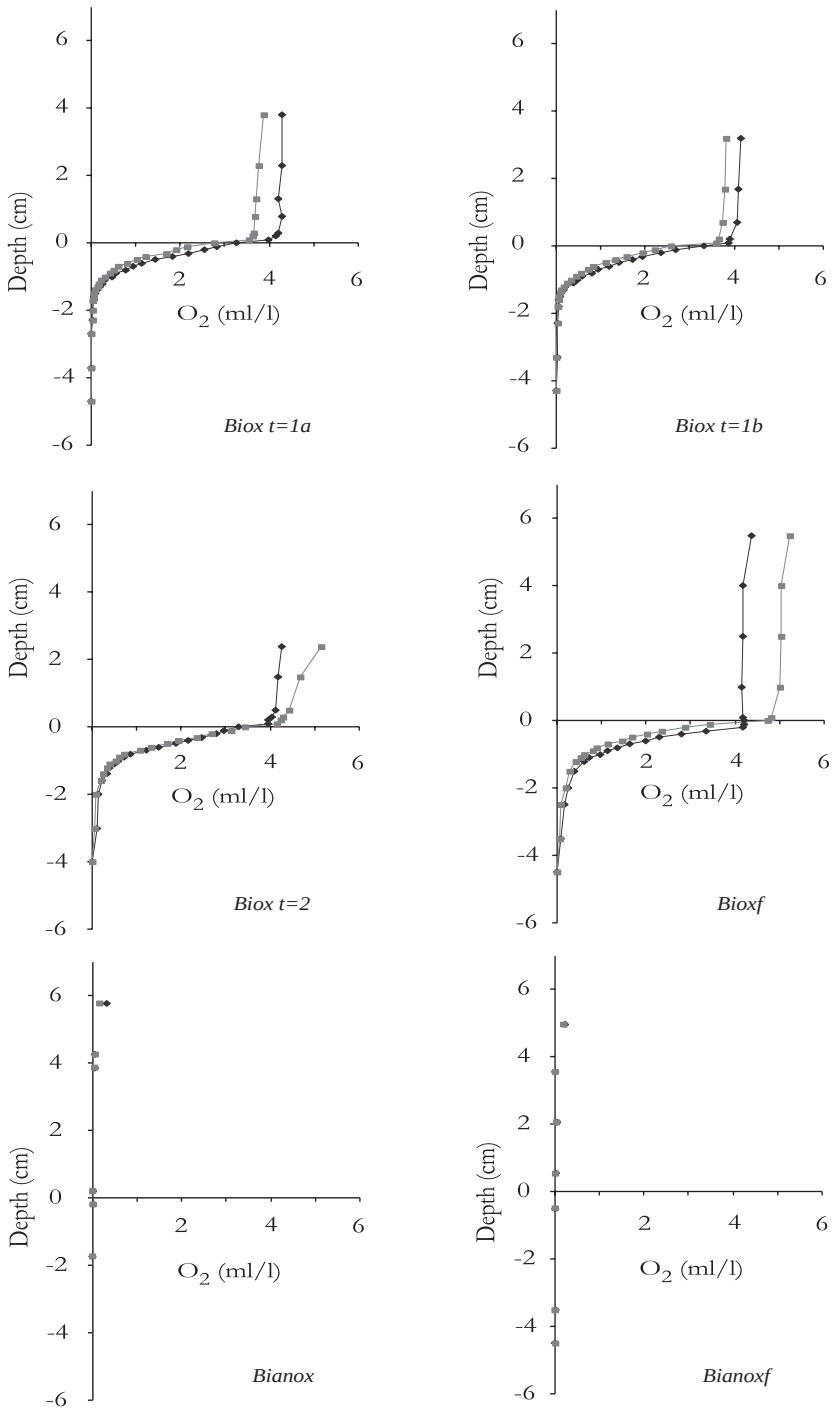

Fig. 3. Sediment oxygen profiles in the different treatments at $t = 1$ and 2. The sediment–water interface is located at the depth of 0 cm. All measurements were made simultaneously with two different electrodes (grey and black lines and dots) in a single mesocosm. The control mesocosms at $t = 1$ were both measured (*Biox* $t = 1$a and *Biox* $t = 1$b).

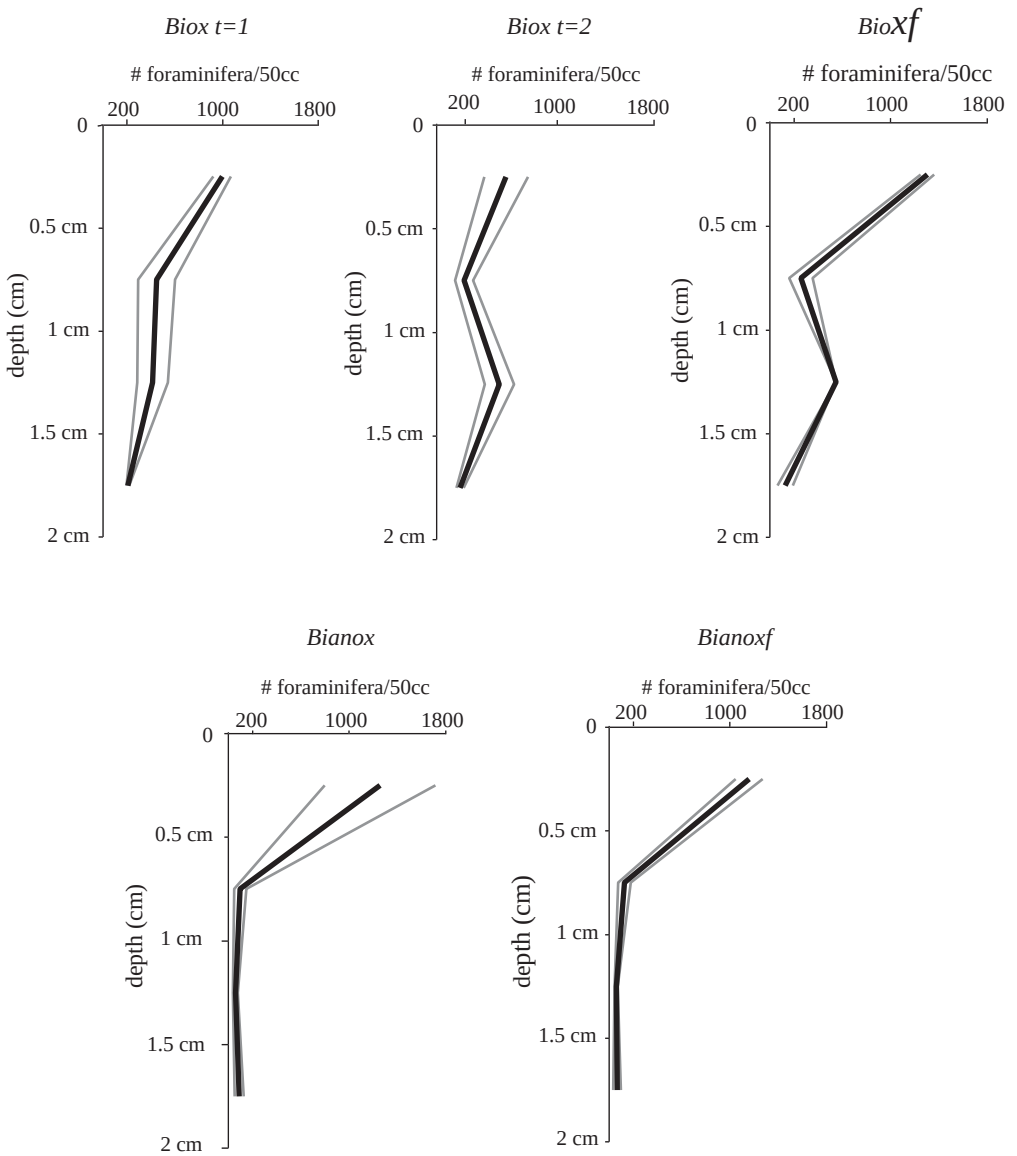

Fig. 4. The vertical distribution of the total standing stocks (TSS) per treatments. The TSS include all foraminifera $>37\,\mu m$ per $50\,cm^3$ sediment. The black lines represent the average value of the two replicates of each treatment, the grey lines represent the values of the two individual replicates.

3.3. Individual species patterns

The standing stock of the individual taxa (Table 1) was fairly constant comparing the different treatments. Comparing the two control mesocosms (*Biox* $t=1$ and 2) in time some taxa showed lowered abundances (*Bolivina* spp., *E. exigua*, *Nonionella* sp., *U. mediterranea*), others a higher abundance (e.g. *B. alata*, *A. glomerata*, *M. barleeanus*, *U. elongatastriata*). In the *Bioxf* mesocosms almost all taxa had equal or higher abundances compared to the control situation (*Biox* $t=2$). In the anoxic treatments (*Bianox* and *Bianoxf*) the abundances were generally somewhat

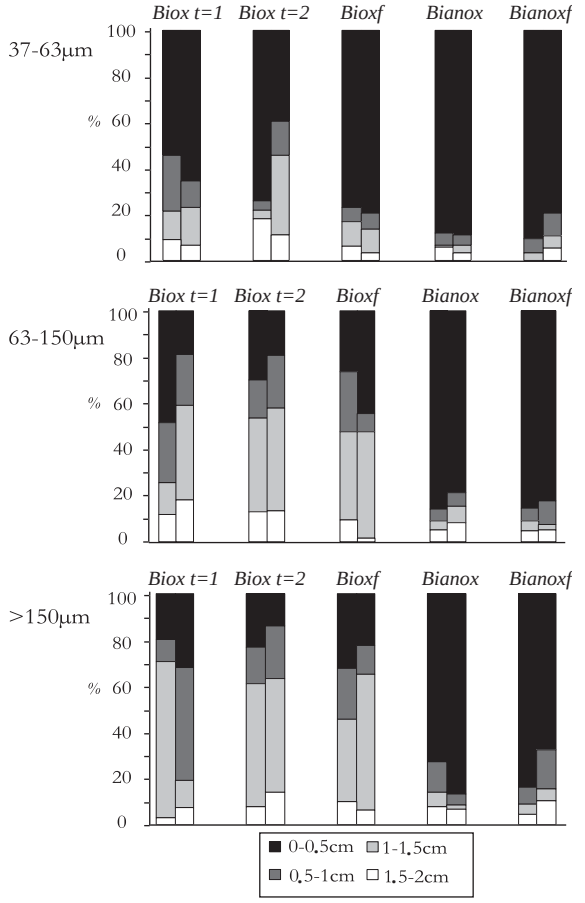

Fig 5. Relative vertical distribution in the upper 2 cm of the three different size fractions in all treatments (data of both replicates are shown).

lower, but none of the taxa was absent in any of the treatments. Finally, *E. exigua* showed the highest variation and increased its abundance strongly in the treatments with fresh organic matter (*Bioxf* and *Bianoxf*).

In Fig. 6 the average relative distribution of the selected taxa (all specimens $>37\,\mu m$) over the upper 20 mm of the sediment is given. The group consisting of *E. exigua, A. glomerata*, *U. peregrina*, *U. mediterranea* and *B. marginata* was found mainly in the upper 5 mm under oxygenated conditions (Fig. 6), and even more pronounced in the anoxic treatments (Fig. 6). In the *Bioxf* treatment, some taxa (e.g. *Haplophragmoides bradyi, S. columellaris, Nonionella* sp.) were relatively more frequent in the upper 5 mm compared to the control mesocosms (*Biox*). In the anoxic treatments almost all taxa migrated towards shallower depth. In the anoxic treatments *C. cylindrica, B. alata, U. elongatastriata*, and *Stainforthia* sp., were also predominantly found in the upper 5 mm of the sediment. However, the organic flux treatments did not appear to have a profound effect on the vertical distribution of these taxa. For *M. barleeanus* and especially for *Globobulimina* spp. the trigger to migrate towards the surface was less strong or absent, although the presented distribution in the upper 2 cm does not give the complete picture since most specimens of these taxa are found below a depth of 2 cm.

3.4. ALD

The average living depth is used here to summarize in a simple way the (average) microhabitat position in each treatment. In Fig. 7 the ALD_5 in both duplicate mesocosms of the most frequent taxa in the $>150\,\mu m$ in the experiment for the upper 5 cm is shown. None of the taxa was restricted to the surface layers. Most values of the replicates are very similar, only *U. mediterranea* and *U. peregrina* show a very distinct difference in the, respectively, *Bianox* and *Biox* $t = 2$ mesocosms. The ALD's of *B. alata*, *C. cylindrica* and *U. elongatastriata* are shallower in the anoxic treatments compared to the oxic treatments. In all treatments, *M. barleeanus* and *Globobulimina* spp. have deep ALDs; their shallowest ALD-values are around 2 cm deep. Anoxic conditions do not affect their ALD substantially. The addition of organic matter (*Bioxf*) did not trigger a clear shallowing ALD of taxa. Most taxa display similar ALD's values in the field as in this experiment compared with the distribution at the time of collection in the field (cores OB10B and $OB10^{bis}$, and the averaged weighed ALD_{10} of this station B over a 2.5 year period; data in Fontanier et al. (2003). The ALD_{10} data can be different because of the deeper samples and the use of different sample intervals. However, below 5 cm few living (staining) specimens are encountered in the field.

Fig. 8a–d shows the average ALD_2 of the selected taxa for all the specimens larger than

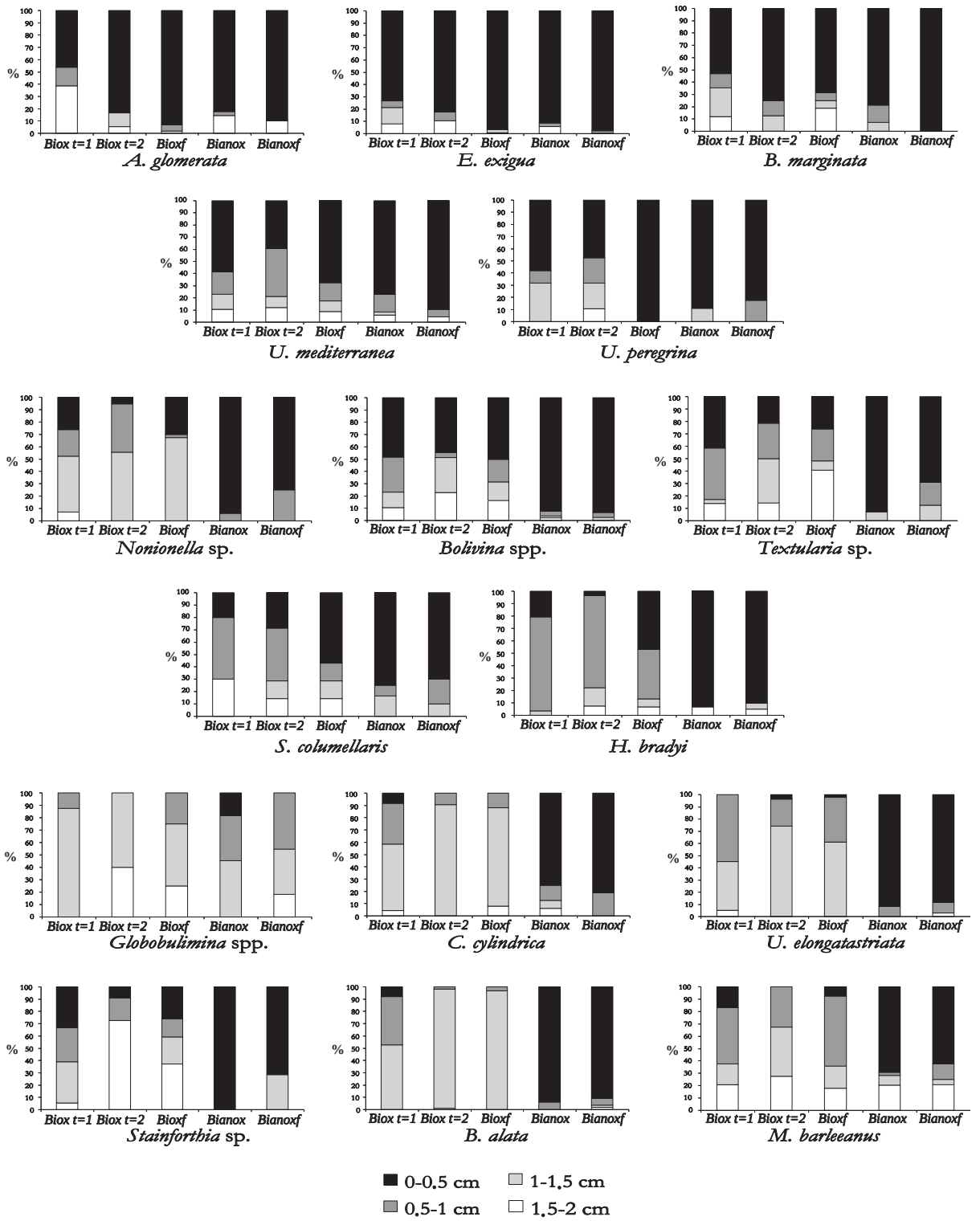

Fig. 6. Average relative distribution of the selected taxa (all foraminifera >37 μm) in the sample intervals in the upper 2 cm of the mesocosms.

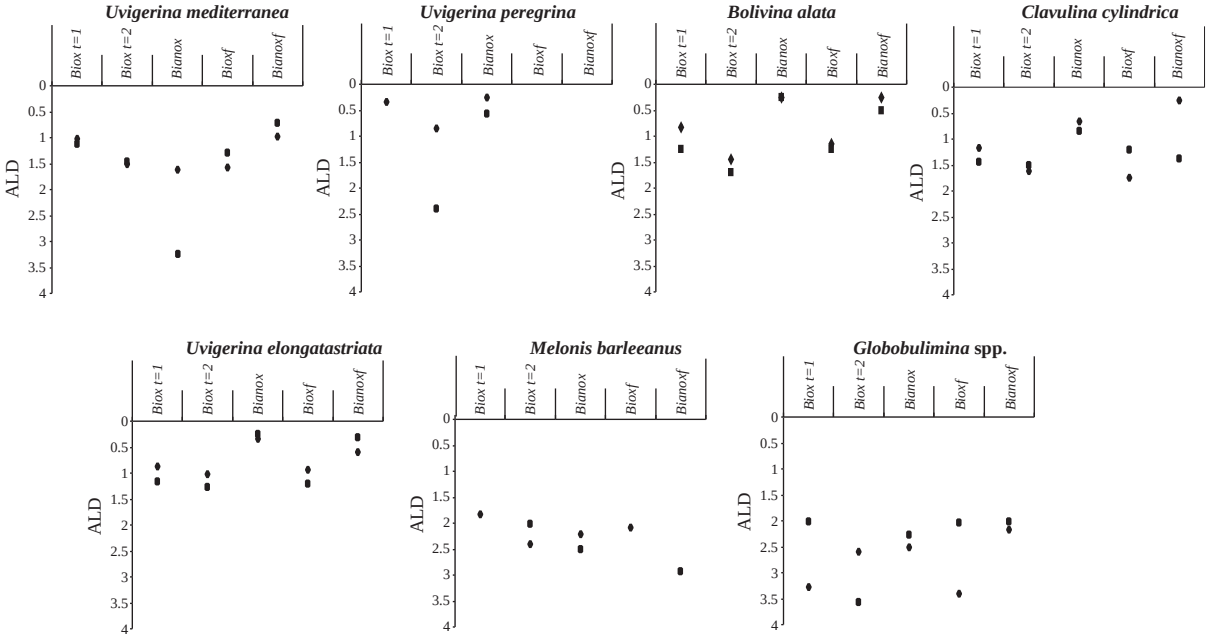

Fig. 7. ALD_5 of the seven most frequent taxa in the >150 μm size fraction in the different treatments of the experiment. The values of the ALDs are given for both replicates per treatment.

37 μm in the upper 2 cm of each mesocosm. In each graph two treatments are compared. In comparison, *Biox* $t = 1$ and *Biox* $t = 2$ (Fig. 8a) show for most taxa no strong differences in time, although at $t = 2$ some taxa have shallower ALDs (e.g. *A. glomerata* and *B. marginata*) and others have deeper ALDs (e.g. *Stainforthia fusiformis*). With *Bioxf* and *Biox* $t = 2$ put side to side (Fig. 8b), the organic flux pulse appears to have affected the depth distribution of most taxa; the ALD values are for many taxa lower in the *Bioxf* mesocosms, especially for *U. peregrina*. Comparison of *Biox* $t = 2$ with the anoxic *Bianox* treatments (Fig. 8c) suggests that almost all species had a shallower ALD under anoxic conditions. Most species were found in the upper sediment layers in both anoxic experiments (*Bianox* vs. *Bianoxf*, Fig. 8d); the ALD data do not reflect a clear trend in difference between the two treatments.

E. exigua, *B. marginata*, *A. glomerata*, *U. mediterranea* and *U. peregrina* have shallow ALDs and are shallow infaunal taxa. *S. columellaris*, *H. bradyi*, *Textularia* sp., *Bolivina* sp., and *Nonionella* sp. have deeper ALD's and can be categorized as shallow to intermediate infaunal taxa. The species *U. elongatastriata*, *B. alata*, *Stainforthia* sp. and *C. cylindrica* are intermediate to deep infaunal taxa. *M. barleeanus* and especially *Globobulimina* spp. were found almost exclusively in deep infaunal habitats.

3.5. Statistics

Principal component analysis (Canoco 4.0, GLW-CPRO) on the data set was performed and the result is shown in Fig. 9. The first and second axes explain 77.1% of the species variance, and 86.8% of the variance in species–environment relation. In the presented analysis, relative abundance data of the taxa, the experimental treatments and the environmental variables oxygen vs. anoxia (*oxygen*), the flux of organic matter (*organic carbon flux*) and the time passed since the start of the experiment (*time*) were projected.

Most species show a relationship with oxygen. Some deeper-dwelling taxa, such as *C. cylindrica*, *M. barleeanus*, *Stainforthia* sp., *B. alata*, *H. bradyi*, appear to be less dependent on high oxygen concentrations. *S. columellaris*, *Globobulimina* spp.

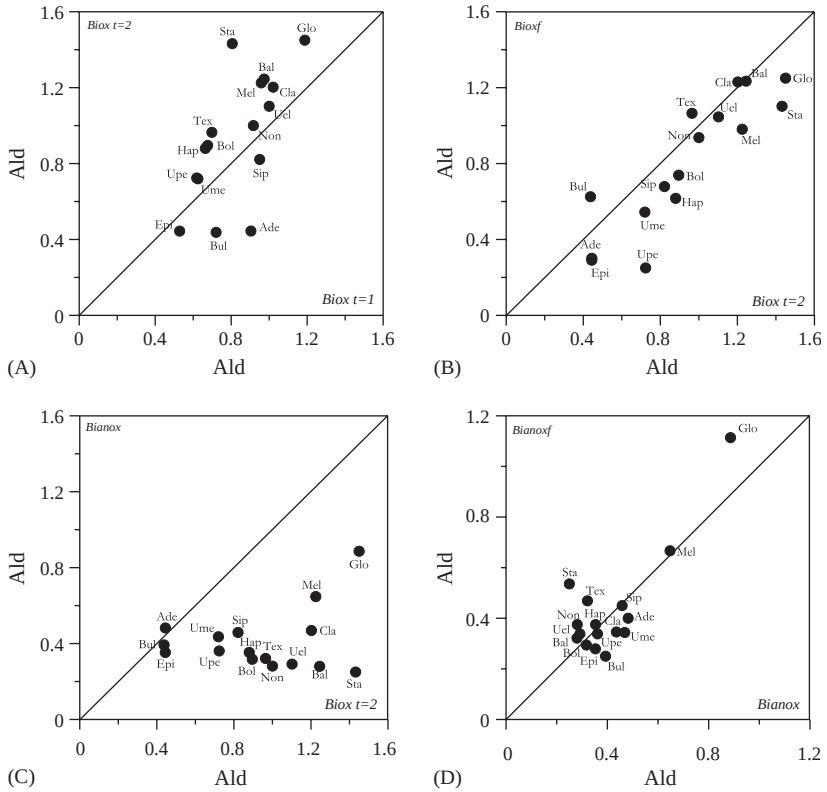

Fig. 8. Average ALD_2 of the selected species (all specimens >37 μm summed) compared between the treatments: (A) *Biox* $t = 2$ vs. *Biox* $t = 1$, (B)*Bioxf* vs. *Biox* $t = 2$, (C) *Bianox* vs. *Biox* $t = 2$, (D) *Bianoxf* vs. *Bianox*. (Ade = *Adercotryma glomerata*, Bal = *Bolivina alata*, Bol = *Bolivina* spp., Bul = *Bulimina marginata*, Cla = *Clavulina cylindrica*, Epi = *Epistominella exigua*, Glo = *Globobulimina* spp., Hap = *Haplophragmoides bradyi*, Mel = *Melonis barleeanus*, Non = *Nonionella* sp., Sip = *Siphogenerina columellaris*, Sta = *Stainforthia* sp., Tex = *Textularia* sp., Uel = *Uvigerina elongatastriata*, Ume = *Uvigerina mediterranea*, Upe = *Uvigerina peregrina*)

are even associated with anoxic conditions. From all species only *E. exigua* correlates well with the increased organic load. In general, the treatments change with *time*, except the *Bioxf* treatments. As expected, the treatments that received organic matter correlate with the variable *organic carbon flux*. The difference between the oxic and anoxic treatments, except for *Biox* $t = 2$, corresponds well with the variable *oxygen concentration*.

The results of the ANOVA analyses are presented in Table 2. The effects of adding food and oxygen depletion are compared with the control situations at $t = 0$ and 1. Most taxa did not respond significantly to the addition of food within the experimental period. *E. exigua* showed a significant increase in abundance comparing the abundance in *Bioxf* $t = 1$ vs. *Biox* $t = 1$. The effects of oxygen depletion were significant for almost all species; a higher abundance was found in the shallow sediment layers under anoxia. *Stainforthia* sp. was the only taxon with a significantly higher abundance under the anoxic conditions comparing both the control and the anoxic situation at $t = 1$. *A. glomerata*, *B. marginata*, *U. peregrina*, and *Globobulimina* spp. appeared to be left unaffected by the changed redox-conditions.

4. Discussion

4.1. Studied size fractions and samples

In this study, the smallest studied size class contained foraminifera larger than 37 μm.

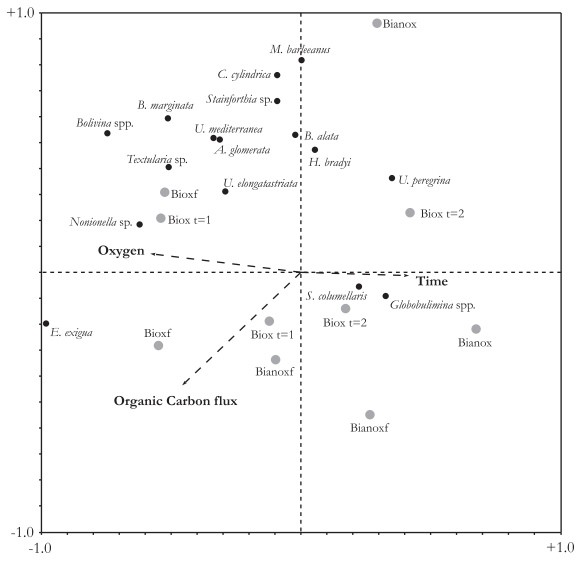

Fig. 9. Results of the PCA-analysis for the first two axes; species and treatments are ordinated including environmental parameters, such as organic flux and oxygen concentration. See text for discussion.

Identification in the smallest size fraction is far more difficult than it is in the $>63\,\mu m$ size fraction. Still, assignments at the genus level are well possible. The large number of foraminifera found in the smallest fraction indicates its importance, certainly for some taxa that are important in this size fraction (e.g. *Bolivina* spp. and *E. exigua*) or are even exclusively found in this size class (e.g. *Stainforthia* sp.).

Since in the experiment discussed here 75% of all specimens larger than 150 μm was found in the upper 2 cm depth interval, counting the samples to a depth of 5 cm seems to be a safe cut-off limit for the larger than 150 μm size fraction. In the field also few living foraminifera are encountered alive below 5 cm (Fontanier et al., 2003). For the smaller size fractions only the upper 2 cm of each mesocosm was feasible because of the time needed to count these samples. Still, these 2 cm give an indication of the microhabitat and distribution patterns of these smaller foraminifera in the upper 2 cm of the sediment, in which at least the oxic/anoxic boundary was located.

4.2. Experimental design

The disturbance that the species experienced during the initial set-up of the experiment, i.e. the sieving treatment and transport, certainly affected the foraminifera. However, this treatment is necessary to avoid initial patchiness in the mesocosms from the start of the experiment. Results from an earlier experiment with a shallow shelf assemblage (Adriatic Sea, 32 m water depth) by Duijnstee et al. (2003) revealed an initial increase in foraminiferal numbers. It was suggested that this was triggered by the stress during the onset of the experiment. Therefore, in this experiment the foraminifera were allowed to settle for 4 weeks.

Experiments like these are often questioned for their reproducibility, or especially the lack of it, in view of the limited number of (true) replicates. The practical difficulty of more than two replicates arises from the large amount of samples involved, which makes the study simply too time-consuming. Our replicates display fairly similar patterns and responses, and our results appear trustworthy awaiting further substantiation by repeated experiments.

The anoxic conditions encountered in this experiment by the foraminiferal assemblages are not representative of the conditions in the field, where throughout the year the oxygen penetration depth in the sediment is very constant and where anoxic conditions are never met (Fontanier et al., 2003). Nevertheless, we chose this extremity in order to trigger a strong response of the taxa, also in view of recent field and laboratory studies on the question whether there are amongst foraminifera species that can survive periods of severe anoxia (see also 4.5.1).

The mesocosms of the anoxic treatments were sealed in order to let oxygen consumption induce a slower decrease of oxygen levels than as accomplished by flushing with nitrogen, for example. Perhaps one drawback of this procedure is that we are not quite sure how fast anoxia was generated this way. Yet, anoxia in field situations would be generated in about the same period of time. In the mesocosm loaded with organic matter (*Bianoxf*) the process could have been more rapid than in the

Table 2
Results of the ANOVA analyses. The effect of the treatments on the individual species is calculated to identify significant ($P \leqslant 0.05$) changes in depth distribution and in total abundance of the total assemblage ($>37\,\mu m$) in the upper 2 cm

Effect on	Organic matter				Oxygen-depletion			
	Abundance Df = 1		Microhabitat Df = 3		Abundance (Df = 1)		Microhabitat (Df = 3)	
Compared to control	$t = 1$	$t = 2$	$t = 1$	$t = 2$	$t = 1$	$t = 2$	$t = 1$	$t = 2$
Adercotryma glomerata	*	*	*	*	*	*	*	*
Bolivina alata	*	*	*	*	*	*	*0.05 (3.94)*	*< 0.001 (1880.96)*
Bolivina spp.	*	*	*	*	*	*	*< 0.001 (37.82)*	*0.01 (6.75)*
Bulimina marginata	*	*	*	*	*	*	*	*
Clavulina cylindrica	*	*	*	*	*	*	*	*< 0.001 (84.35)*
Epistominella exigua	*	*0.05 (17.3)*	*0.002 (12.88)*	*	**0.04 (21.59)**	*	*0.01 (6.68)*	*
Globobulimina affinis	*	*	*	*	*	*	*	*
Haplophragmoides bradyi	*	*	*0.009 (7.75)*	*	*	*	*< 0.001 (328.08)*	*0.03 (4.95)*
Melonis barleeanus	*	*	*	*	*	*	*0.01 (6.77)*	*0.01 (6.78)*
Nonionella sp.	*	*	*	*0.01 (7.33)*	*	*	*	*< 0.001 (49.6)*
Siphogenerina columellaris	*	*	*	*	*	*	*	*0.02 (5.17)*
Stainforthia sp.	*	*	*	*	*	*0.04 (21.35)*	*0.004 (10.56)*	*< 0.001 (28)*
Textularia sp.	*	*	*	*	*	*	*< 0.001 (23.57)*	*0.02 (5.52)*
Uvigerina elongatastriata	*	*	*	*	*	*	*0.005 (9.48)*	*< 0.001 (84.32)*
Uvigerina mediterranea	*	*	*	*	*	*	*	*0.003 (11.45)*
Uvigerina peregrina	**0.04 (18.77)**	**0.006 (169)**	*0.017 (6.3)*	*0.049 (4.1)*	*	*	*	*

Responses are compared to the control mesocosms of $t = 1$ and 2. Nonsignificant responses are marked with an asterisk (*). Significant responses are marked in bold if they deal with a deepening of the habitat or a lowered abundance. Responses that showed a shallowing habitat or higher abundance is shown in italics. Resulting scores for the *p*-values are given, together with the F-values (in brackets). Degrees of freedom (Df) for both ANOVA analyses are given in the table as well.

mesocosms of the *Bianox* treatment. This probably was not a disadvantage except if the redox gradient migrated more rapidly than species could follow. Then species could have died, and the protoplasm could still stain with Rose Bengal if bacterial degradation processes were arrested or slowed down substantially. The latter, however, seems unlikely since the temperature during the experiment was rather high (10 °C), enhancing decay. Moreover, we included only vividly stained specimens in our counts.

4.3. Experiments: valid field analogues?

One of the important questions is whether the experiments can be used as field analogues. Field conditions are certainly not equal to the ones created in the laboratory; yet, species appear to display a similar behaviour in experiments as in the field (e.g. Ernst et al., 2000; Ernst et al. 2002; Heinz et al. 2002). Moreover, experiments such as the present one are the only option if one is interested in assessing the impact of a single environmental variable on foraminiferal distributions.

Fontanier et al. (2003) compare the foraminiferal abundances at station B with the chlorophyll-a concentration in the surface waters over the years 1997–2000. The foraminiferal abundances appear to change out of phase (4–6 weeks) with the amount of chlorophyll produced in the surface waters. The resolution of the field samples, however, appears to be too low for substantiating such a correlation, and these data show the difficulties encountered during the study of the effects of such environmental parameters in field data. The TSS (specimens >150 μm) in the upper 2 cm in the field at the time of sampling (see Fontanier et al., 2003) were higher than the average TSS of the experimental (*Biox*) samples. Although the abundances in the experiment were lower, they are not unnaturally low since the TSS of some field samples (e.g. July 1998, April 1999 in Fontanier et al., 2003) are in the same order. The taxa in the experiment and field samples can only be compared for the >150 μm size fraction since data from the field from the smaller size-classes is only available for surface samples (i.e., the 63–150 μm size fraction has only been studied in the shallowest 0.5 cm). As in the field, *U. mediterranea* was the most dominant taxon in the >150 μm size fraction (21.5%, in the field 17.9–39.9%). In this size-fraction, all other taxa had ranges in their relative abundance in the field that were very comparable with the composition of the experimental assemblage.

Further comparison is difficult with field data because of the discrepancy in studied size classes and sample depths. The effects of fresh organic matter in the experimental situation are seen mainly in the smallest size fraction within the first weeks after addition. The period of 4–6 weeks as seen in the field is not so strange since these are the specimens larger than 150 μm, which need more time to grow. What is clear is that the smaller size fraction yield important information, which is lost when only the >150 μm fraction is studied.

4.4. Food source: composition and amount of organic matter flux

Lee (1980) and Lipps (1983) give an overview of what little is known about nutrition and trophic dynamics of foraminifera. Most foraminifera display omnivorous feeding and collect their food in several ways. In a number of studies food was supplied to foraminifera. For instance, Muller and Lee (1969) and Lee et al. (1977) used a diverse collection of algae species (among them *Dunaliella salina*, *Phaeodactylum tricornutum*, several *Navicula* and *Nitzschia* species, *Amphiprora paludosa* and many more), which proved to be good food for salt-marsh foraminifera. Heinz et al. (2002) showed that supply of various diatom and algal species (e.g. *Pyramimonas* sp., *Dunaliella tertiolecta* and *Amphiprora* sp.) led to an increase of foraminiferal numbers. Gross (2000) showed that deep-sea foraminifera used (freeze-dried) *Chlorella* sp. as a food source. The phytoplankton blooms in the Bay of Biscay are composed of diatoms (predominantly of the genera *Chaetoceros* and *Nitzschia*, several unidentified pennate taxa: Tréguer et al., 1979; Fernandez et al., 1995), coccolithophorids (*Emiliania huxleyi*, *Gephyrocapsa oceanica*: Fernandez et al., 1995). In the present study a mixture of heat-killed algae (*Dunaliella salina*) and diatoms (*Amphiprora* sp., *Phaeodactylum*

sp., and some unidentified diatom species) was used to simulate organic flux. These cultures originate from ones that are already used for years in successful foraminiferal cultures (Maria Holzmann, personal communication). Therefore, we expect that this mixture indeed was exploitable as food for the foraminiferal species in our assemblage, and a good alternative for the field flux in the Bay of Biscay. However, no actual observations of foraminifera feeding on the offered mixture were made.

Since the material used in this study was sampled during a more eutrophic period in the field after the spring bloom, it could be that the effects of an organic matter pulse would have been more pronounced if sampling was done during a more oligotrophic period in the year. However, during the initial 4 weeks of the experiment more or less 'oligotrophic' conditions were created since no organic matter or food was added. This 'oligotrophic' period without fresh organic matter could have enhanced the effects of the availability of fresh organic matter in the mesocosms at $t = 1$. However, the response of certain taxa, e.g. *E. exigua,* shows that it is not excluded to respond again to a fresh pulse of organic matter.

The amount of organic flux used in this experiment ($0.054\,mg\,C/cm^2$) is important since it is over 20 times higher than the average daily total amount of organic carbon flux ($\sim 0.0025\,mg\,C/cm^2$) arriving at the sea floor at this depth (Heusner et al., 1999; Fontanier et al., 2002). As Etcheber et al. (1999) point out, the actual amount of organic matter arriving at the sea floor in this region appears to be highly variable and difficult to measure precisely, depending on a wide variety of variables such as current circulation and transport/resuspension processes. The observed fluxes are therefore merely an indication of the maximum amount of organic carbon arriving at the seafloor. Finally, competition for the available organic matter was lower by the absence of macrofauna and therefore potentially a larger amount of food was in this experiment available for the foraminifera compared with the natural situation, although this is not quantifiable.

4.5. Results of the experiments

All our results support a rough subdivision of the studied taxa on the basis of their microhabitat preference: a shallow infaunal, an intermediate infaunal, and an intermediate to deep infaunal group. The group of shallow infaunal species resided preferably in the upper sediment regions. Two of them (*E. exigua* and *A. glomerata*) were found only in the smaller than 150 μm size fraction and are known to be opportunistic species (e.g. Gooday and Rathburn, 1999; Heinz et al, 2002). The shallow infaunal group was able to survive and thrive in deeper regions in the sediment, but was found at shallower depths when food (fresh diatoms/algae) was deposited on the surface. Deeper infaunal species were the ones that appear to be continuous inhabitants of the deeper regions, near or even below the oxic/anoxic boundary. Some species displayed a remarkably narrow depth-zone in which they seem to thrive. *B. alata* is a clear example, mostly found in a single depth interval between 1 and 1.5 cm deep, just above the oxic/anoxic boundary. Also *M. barleeanus* and *U. elongatastriata* displayed clear preferences for a specific depth-zone, which is also observed in the field (Fontanier et al., 2002, Fontanier et al., 2003).

4.5.1. Oxygen

The cellular process through which foraminifera apparently survive prolonged anoxic periods is not clear. Bernhard and Sen Gupta (1999) review the effect of anoxia on benthic foraminifera. The main conclusion is that a number of foraminifera are able to survive anoxia for considerable periods of time, although species that are obligate anaerobes have not been discovered. Moodley et al. (1997) demonstrated in an experiment the ability of foraminifera to survive a period of over two months of anoxia. Examples of such apparently facultative anaerobes are *Nonionella stella*, *Stainforthia fusiformis*, *Chilostomella* and *Globobulimina* species (see for overview Bernhard and Sen Gupta, 1999, and Van der Zwaan et al., 1999). That benthic foraminifera are able to thrive in anoxic layers is also demonstrated in field studies: below the oxic-anoxic redox front often large numbers of foraminifera occur (e.g. Rathburn and

Corliss, 1994; Jannink et al., 1998; Gooday et al., 2000). Alve and Bernhard (1995) and Duijnstee et al. (2003) observed upward migration of deep living foraminifera upon onset of anoxia. In their view these migrations suggest tracking of the shifting redox front as earlier surmised by Van der Zwaan and Jorissen (1991). This is also the case for most taxa in this experiment. Taxa survived the anoxic conditions during a period of several weeks, and migrated towards the sediment-water interface. Only some apparently specialized taxa (e.g. *Globobulimina* spp. and *M. barleeanus*) appear to be almost exclusively restricted to the deeper and anoxic parts of the sediment and did not migrate to surface layers when the whole sediment column turned anoxic. Whether these taxa are obligate anaerobes is not yet clear: research is needed to answer this question.

4.5.2. Organic flux

A large number of processes are initiated at the moment when food/organic matter arrives at the sea floor. For example, increase in abundance and biomass of taxa, change in dominance or diversity of the community, increase in life-processes such as reproduction and growth. A number of studies addressed the impact of organic flux on benthic communities, and especially the response of deep-sea benthos received considerable attention (e.g. Linke and Lutze 1993; Schmiedl et al., 2000; Pfannkuche et al., 2000; Gooday, 1996; De Rijk et al., 2000). Amongst foraminifera especially opportunistic taxa are adapted to fluctuating nutrient supply and when food reaches the sea bottom, they are able to grow and reproduce rapidly (e.g. Ohga and Kitazato, 1997; Kitazato et al., 2000; Gooday, 1993). Deep infaunal species (*G. affinis*, *Chilostomella ovoidea*) appear to lack such a response when organic flux events take place (e.g. Ohga and Kitazato, 1997). Experiments further seem to suggest that responses to food supply are not always straightforward. Widbom and Elmgren (1988) described the effects of long-term eutrophication on the benthic meiofauna. Phytoplankton abundance and macrofaunal biomass increased, but the benthic meiofauna did not change in biomass and abundance. The authors explained the lack of meiofaunal response by assuming the biotic interaction of macrofauna to be limiting. Other experiments (Altenbach, 1992; Moodley et al., 2000) showed the rapid uptake of fresh organic matter by foraminifera. Foraminifera from deep-sea environments seem to respond as quickly as species from shallow depth (Altenbach, 1992). Heinz et al. (2002) demonstrated that an organic matter flux caused an increase in abundance 7 to 21 days after supply of fresh algae.

Although our material was collected just after the spring bloom, certain taxa responded to the experimentally initiated organic matter pulse. *E. exigua* was the species most clearly reacting to the supply of fresh labile organic matter. This taxon and related species in this genus are already well known for their opportunistic response to seasonal fluxes in field and experimental studies (e.g. Gooday and Turley, 1999; Heinz et al. 2001, 2002). Without addition of organic matter its abundance decreased (*Biox* $t = 2$), as if the lack of fresh food affected the survival. In the oxic treatments an ANOVA demonstrated that its population increased significantly in the 37–63 μm size fraction ($p = 0.03$, $F = 32.4$) when food was added. With similar food conditions but without oxygen (*Bianoxf*) the specimens display a higher survival compared to the anoxic treatment without food (*Bianox*). The shallow infaunal taxon *A. glomerata* seemed to benefit from the food input as well but the increase appeared not statistically significant. In an experimental study of Heinz et al. (2002) this taxon responded very rapidly to freshly added food. The infaunal taxa did not react at all. This lack of response might be understood if one realizes that these taxa thrive under conditions depleted in labile or fresh organic matter, suggesting they could be more dependent on degraded material. Another option is that they specialize on labile matter produced by bacteria associated with the various redox zones. This could be an explanation for the specific depth-distribution of various species (e.g. Jorissen et al., 1998; Van der Zwaan et al., 1999). Finally, the lack of bioturbation of, for instance, larger metazoans because of their removal by the sieving treatment at the start of the experiment could have affected the transport of nutrients downwards towards the deeper regions of the sediment.

4.5.3. The TROX-model

The TROX-model (Jorissen et al., 1995) has proved to be very successful in describing and predicting foraminiferal distributions and occurrences in sediments. Fontanier et al. (2002) conclude that the TROX-model is in agreement with the results they obtained in their study of live foraminifera along a depth transect in the Bay of Biscay. Their main conclusion was that (porewater) oxygen concentration is less a structuring parameter than organic flux, especially concerning the vertical distribution (and composition) of taxa. In the range of environments (eutrophic to oligotrophic) they studied, deep infaunal taxa seemed to live at shallower depth when organic flux levels decreased. They conclude that in general the annually available amount of organic flux at a site determines the species composition and abundance of an assemblage. However, long-term field studies in different environments (Barmawidjaja et al., 1992; Kitazato et al., 2000; Murray and Alve, 2000; Duijnstee, 2001; Jannink, 2001) have shown that interannually a large variability in abundance, vertical distribution and sometimes even composition of taxa exists. These patterns could not just be explained by variations in organic flux.

The temporal and spatial distribution of the data used in foraminiferal studies is very important. Fontanier et al. (2002) compared five single cores from the Bay of Biscay, from different water depths, but the samples were not collected at the same time. The resulting data-set excludes information about the seasonal variation in taxa and environmental parameters at the sites, and merely reflects the situation at the different sites at a single moment in time. In our experiment we have subjected a single assemblage to various environmental conditions and this allows us to monitor in detail the difference in effect of various factors.

Our study shows that the impact of the environmental variables is not so straightforward. On the other hand, the results we obtained suggest that organic flux did not significantly affect the microhabitat structure of most foraminiferal taxa (Table 2). On the other hand, anoxic conditions were shown to have a strong impact on the vertical distribution. We compared our results for the different treatments with the TROX-model (Fig. 10), together with the average TSS and the vertical distribution of microhabitat groups (based upon the ALD data, Figs. 7 and 8). The figure shows again that adding organic flux did not alter the vertical distribution, although the TSS increased. But upon changing redox conditions to anoxic in the surface layers, the microhabitat structure of the community changed completely (Fig. 10). Under these conditions, all species were found exclusively in the upper 5 mm of the sediment except for deep infauna (e.g. *Globobulimina* sp.). Adding organic flux under anoxic conditions did not make any difference to these deep infaunal taxa. Their distribution patterns are perhaps dependant upon other trophic resources (e.g. bacteria), as already suggested in Jorissen et al. (1998). Only a small number of epifaunal and opportunistic taxa (e.g. *E. exigua*) responded to fresh labile organic matter on the time scale of weeks or days. One could question whether the experimental period is too short for most taxa to see already a response in this period. Fontanier et al. (2003) studied the same sample area and they observed that after a surface plankton bloom, several to 6 weeks may pass before a response is seen in the foraminifera. Their explanation for this time lag, besides the time involved in the transport of the nutrients to the seabed, is that the response of foraminiferal taxa depends on increases in heterotrophic bacterial stocks that increase their abundance after the arrival of organic matter at the seabed. If this is the case, a longer experimental period than 19 days might be necessary to see any response in, for instance, foraminiferal reproduction for most taxa. On the other hand, a number of studies have shown the rapid uptake of fresh organic matter by foraminifera (Altenbach, 1992; Moodley et al., 2000) and in the experiment presented here the organic matter was directly available for the benthic faunas.

The TROX-model does not specify the differential temporal impact of changes in oxygen and organic flux, and in the model these factors are regarded equally important. Our results suggest that there is a distinction on a temporal scale between the effects of these two parameters.

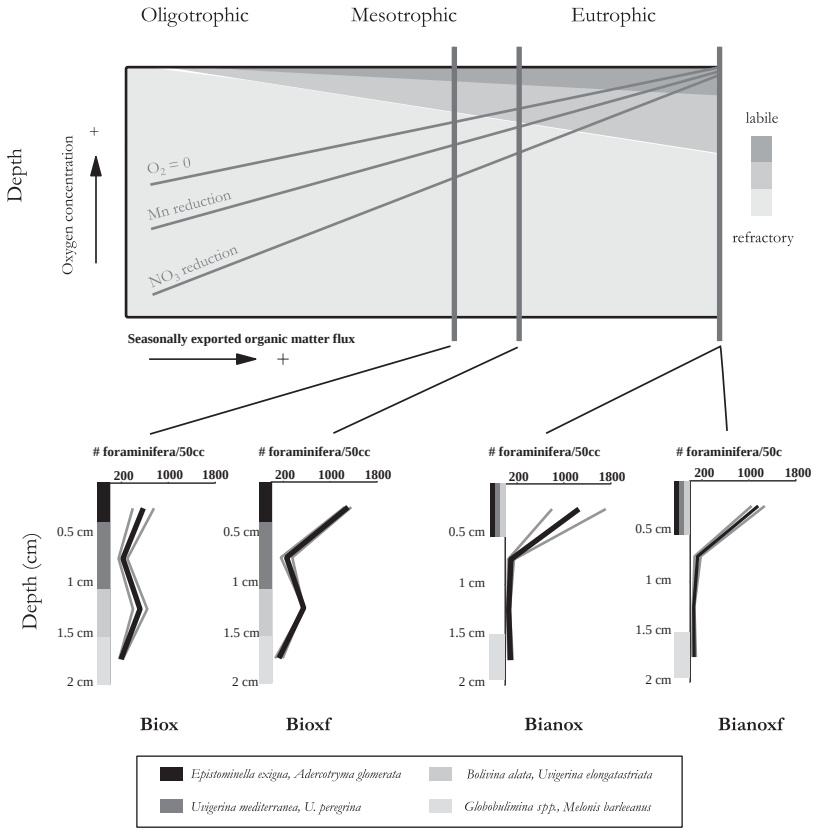

Fig. 10. The results of the experimental treatments interpreted and summarized by placing them in the TROX-model based on Jorissen et al. (1995). Total standing stocks of the upper 2 cm and the vertical distribution of four microhabitat groups (based upon their ALD_5 and ALD_2 data of Figs. 7 and 8 respectively) in the experimental treatments are shown.

Oxygen variations appear to control the composition and abundances of taxa on short time scales, together with their vertical distribution in the sediment. At longer time scales the amount of organic matter or food that is arriving at the seafloor becomes important.

In the future, experiments need to be carried out with controlled levels of oxygen and food supply over prolonged periods of time with assemblages from various environments. This will result in detailed knowledge of the individual response of benthic foraminifera to environmental change. It becomes clear that this detailed ecological information on individual species and assemblages is essential in resolving the problems encountered in paleoenvironmental reconstructions and the development of proxies (e.g. Murray, 2001).

5. Conclusions

The results of our experiment suggest that the variation in the environmental variables, oxygen and organic flux, had a differential temporal impact on the foraminiferal assemblages. Oxygen appeared to induce strong changes in the vertical distribution of the foraminifera within short periods of time. When subjected to anoxic conditions most species, except some deep infaunal taxa (*M. barleeanus*, *Globobulimina* spp.), migrated towards the sediment water interface, probably trying to escape the hostile conditions. These anoxic conditions appear to be limiting in the end to many specimens, shown by lowered abundances within 19 days. Adding organic flux affected only some shallow living, opportunistic

taxa (*E. exigua*, *A. glomerata*). All other species did not responded significantly to the addition of fresh organic matter, either under oxic or anoxic conditions. Clearly, the studied assemblage is on short time scales more strongly influenced by oxygen variation than by changes in available organic matter or food. The latter appears to be more important over a longer period of time. The outcome of our study forms an important supplement to the TROX-model, in which no distinction is made for the time scales on which the effects of variation of these two parameters operate.

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Appendix A:. Taxonomic notes

The selection of species identified at species level discussed in this paper are listed here, other taxa identified in the samples are listed in Appendix C. Taxonomic references that were used are Van der Zwaan et al. (1986), Jorissen (1988) and Jones (1994).

A. glomerata (Brady) = *Lituola glomerata* Brady 1878. (Plate II, Fig. A–C).
B. alata (Seguenza) = *Vulvulina alata* Seguenza 1862 (Plate I, Fig. A, B)
B. spathulata (Williamson) = *Textularia variablis* var. *spathulata* Williamson 1858. (Plate I, Fig. D,E).
B. striatula Cushman = *Bolivina striatula* Cushman 1922 (Plate I, Fig. C)
B. marginata d'Orbigny = *Bulimina marginata* d'Orbigny 1826 (Plate I, Fig. K)
C. Clavulina cylindrica d'Orbigny = *Clavulina cylindrica* d'Orbigny 1825 (Plate II, Fig. H)
E. exigua (Brady) = *Pulvinulina exigua* Brady 1884 (Plate I, Fig. H,I)
Globobulimina affinis d'Orbigny = *Globobulimina affinis* d'Orbigny 1839 (Plate I, Fig. N)
Globobulimina pyrula (Brady) = *Bulimina pyrula* var. *spinescens* Brady 1884 (Plate I, Fig. M), could be synonomous with *Globobulimina affinis* var. *pseudospinescens* (Emiliani), see Verhallen (1991), Plate 27, Fig. 1.
Haplophragmoides bradyi (Robertson) = *Trochammina bradyi* Robertson 1891 (Plate II, Fig. D, E)
Melonis barleeanus (Williamson) = *Nonionina barleeana* Williamson 1858 (Plate I, Fig. F, G)
Siphogenerina columellaris (Brady) = Sagrina columellaris Brady 1884 (Plate I, Fig. L)
Uvigerina elongatastriata (Colom) = Angulogerina elongatastriata Colom 1952 (Plate I, Fig. O)
Uvigerina mediterranea Hofker = Uvigerina mediterranea Hofker 1932 (Plate I, Fig. P, Q)
Uvigerina peregrina Cushman = *Uvigerina peregrina* Cushman 1923 (Plate I, Fig. R, S)
The scale bars represent 100 μm, but for some figures the scale bar represents 50 μm. If this is the case, it is noted in the plate.

Appendix B

Census data, in total number of foraminifera per sample, of all mesocosms differentiated per size

fraction; 37–63 μm, 63–150 μm, and >150 μm. Volume of the samples of 0.5 cm thick is 14.1 cm^3, the deeper 1 cm thick sample intervals have a volume of 28.2 cm^3

Appendix B, size fraction >150 μm

Biox t=1

Species	A 0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	2-3cm	3-4cm	4-5cm
Bolivina alata		11	2				
Bulimina marginata							
Clavulina cylindrica	1	8	2	1	1	1	
Globobulimina spp.		1			1	4	2
Haplophragmoides bradyi		1				1	
Melonis barleeanus		1	2	1	1	1	
Siphogenerina columellaris	1	4					
Uvigerina elongatastriata		1	3				
Uvigerina peregrina	4	1					
Uvigerina mediterranea	21	4		3	5	3	
Rest	3	5	2	2	2	1	

Species	B 0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	2-3cm	3-4cm	4-5cm
Bolivina alata							
Bulimina marginata							
Clavulina cylindrica			11			1	
Globobulimina spp.			7			2	1
Haplophragmoides bradyi	2		1		1		
Melonis barleeanus			1			3	
Siphogenerina columellaris	1						
Uvigerina elongatastriata		1	5				
Uvigerina peregrina	1					1	
Uvigerina mediterranea	6	4	2	2	2	1	
Rest	3	1	1		2	4	11

Biox t=2

Species	A 0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	2-3cm	3-4cm	4-5cm
Bolivina alata			18	1			1
Bulimina marginata	1	1					1
Clavulina cylindrica			8				1
Globobulimina spp.			2	2	3	1	2
Haplophragmoides bradyi			1				1
Melonis barleeanus		1	3	1	2	5	
Siphogenerina columellaris	2	2			2		
Uvigerina elongatastriata	7	3	2	2	1	2	2
Uvigerina peregrina	6	1					1
Uvigerina mediterranea							
Rest	5	2	9	1	4		

Species	B 0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	2-3cm	3-4cm	4-5cm
Bolivina alata			16			1	2
Bulimina marginata			1				
Clavulina cylindrica		1	9		1	1	
Globobulimina spp.			1		1	4	4
Haplophragmoides bradyi		1					1
Melonis barleeanus		2	4	4	3	2	1
Siphogenerina columellaris		2				2	
Uvigerina elongatastriata	1	2	11			1	
Uvigerina peregrina	1	1		1	2	2	1
Uvigerina mediterranea	5	9		2		3	2
Rest	5	2	1	5	1	4	

BioxF

Species	A 0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	2-3cm	3-4cm	4-5cm
Bolivina alata		3	11				
Bulimina marginata	2			1			1
Clavulina cylindrica		1	5	1		2	
Globobulimina spp.				1	1	4	2
Haplophragmoides bradyi		1					
Melonis barleeanus		2	2	1	2	1	1
Siphogenerina columellaris	1				1	2	
Uvigerina elongatastriata	1	12	9				
Uvigerina peregrina	2						
Uvigerina mediterranea	14	1	1	2	2	6	2
Rest	9		4	3	1	1	

Species	B 0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	2-3cm	3-4cm	4-5cm
Bolivina alata			19				
Bulimina marginata							
Clavulina cylindrica		2	1	1			
Globobulimina spp.		1	2		3	1	
Haplophragmoides bradyi							1
Melonis barleeanus				1	1	2	1
Siphogenerina columellaris	2			1			1
Uvigerina elongatastriata		1	12				
Uvigerina peregrina	1						
Uvigerina mediterranea	7	4	2	1	2	3	
Rest	8	2	2	1	1		1

Bianox

Species	A 0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	2-3cm	3-4cm	4-5cm
Bolivina alata	2						
Bulimina marginata		1					1
Clavulina cylindrica	13	3	2	2	1		
Globobulimina spp.		2	2		2	2	2
Haplophragmoides bradyi				1			
Melonis barleeanus	4	1	1		8	1	3
Siphogenerina columellaris	1	1	1		1		1
Uvigerina elongatastriata	13	3					
Uvigerina peregrina	8				1	2	1
Uvigerina mediterranea	23	5	1	2	4	8	6
Rest	11	1	1	5	1	1	3

Species	B 0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	2-3cm	3-4cm	4-5cm
Bolivina alata	16						
Bulimina marginata	1						
Clavulina cylindrica	6	1					1
Globobulimina spp.		2			3	2	
Haplophragmoides bradyi				1			
Melonis barleeanus	2			2	2	2	2
Siphogenerina columellaris	5		1		1		1
Uvigerina elongatastriata	9						
Uvigerina peregrina	6				1		
Uvigerina mediterranea	1					2	2
Rest	6			1		1	

BianoxF

Species	A 0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	2-3cm	3-4cm	4-5cm
Bolivina alata	9						
Bulimina marginata	1						
Clavulina cylindrica	6						
Globobulimina spp.		2	3		2	2	1
Haplophragmoides bradyi							
Melonis barleeanus	2			1			
Siphogenerina columellaris	2				2		
Uvigerina elongatastriata	12	1		1		1	
Uvigerina peregrina	3	1					
Uvigerina mediterranea	18	1		1	1	3	1
Rest	4					2	1

Species	B 0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	2-3cm	3-4cm	4-5cm
Bolivina alata	9	1	1	1			
Bulimina marginata							
Clavulina cylindrica	4	3			3		1
Globobulimina spp.		3	1	1	5		1
Haplophragmoides bradyi							
Melonis barleeanus			1	1	2	1	2
Siphogenerina columellaris					1		
Uvigerina elongatastriata	12	2					
Uvigerina peregrina	3	1					
Uvigerina mediterranea	22	2		1	2	2	
Rest	2	1	1	4	5	5	7

Appendix B, size fraction 63-150 μm

Species	Biox t=1 A				Biox t=2 A			
	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm
Adercotryma glomerata	1	2		5	2			
Bolivina alata	6	19				1	36	
Bolivina spp.	20	10	9	5	8	1	4	2
Bulimina marginata	7	2	2	2	1			
Clavulina cylindrica								
Epistominella exigua	40	2	13	2	15			2
Globobulimina spp.								
Haplophragmoides bradyi								
Melonis barleeanus	4	6				8		6
Nonionella sp.	5	2		1	1	1	2	
Siphogenerina columellaris						2	2	2
Textularia sp.	3	3		2	3	1		4
Uvigerina elongatastriata							4	
Uvigerina peregrina	4	1	1		1		2	
Uvigerina mediterranea						1		
Rest	37	21	11	14	15	10	12	4

	B				B			
	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm
Adercotryma glomerata	1				3			2
Bolivina alata			23			1	31	
Bolivina spp.	4	7	7	5	7		13	9
Bulimina marginata			1					
Clavulina cylindrica						1	2	
Epistominella exigua	11		1	3	6			1
Globobulimina spp.								
Haplophragmoides bradyi		10			1	19	3	2
Melonis barleeanus		4	1	4		2	9	
Nonionella sp.		1	11				2	
Siphogenerina columellaris				1				
Textularia sp.					1	3	2	
Uvigerina elongatastriata								
Uvigerina peregrina	2		5		1	2	2	1
Uvigerina mediterranea	1	1	4		1		1	
Rest	14	16	19	19	16	14	18	10

	Bioxf A				Bianox A			
	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm
Adercotryma glomerata	6	3		1	19	1		2
Bolivina alata			20		40	5		
Bolivina spp.	9	8	8	4	62	2	2	3
Bulimina marginata				2	10	1		
Clavulina cylindrica			2		4			
Epistominella exigua	11	1	2		20	1		2
Globobulimina spp.						2	1	
Haplophragmoides bradyi	8	8			17			
Melonis barleeanus	1	16	4	4	18		1	4
Nonionella sp.	1	2	18		11	1		
Siphogenerina columellaris		1	1		2			
Textularia sp.	2	8	3		2		1	
Uvigerina elongatastriata		4	3		4			
Uvigerina peregrina	1				2		2	
Uvigerina mediterranea	1				3			
Rest	18	6	22	10	78	5	6	7

	B				B			
	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm
Adercotryma glomerata	4							2
Bolivina alata			42		18	1		
Bolivina spp.	10	3	3		10	3		1
Bulimina marginata	1	1	1				1	
Clavulina cylindrica			3		1			
Epistominella exigua	26		2		1			
Globobulimina spp.					2			
Haplophragmoides bradyi	6	3	2	2	10			
Melonis barleeanus	2	4	1	1	3		1	2
Nonionella sp.	3		16		1			
Siphogenerina columellaris	1				1			
Textularia sp.					1			
Uvigerina elongatastriata		1	6		7			
Uvigerina peregrina	2							
Uvigerina mediterranea	1							
Rest	25	2	8		10	1	4	2

	Bianoxf			
A	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm
Adercotryma glomerata	4			
Bolivina alata	12	1		
Bolivina spp.	22	1		
Bulimina marginata	4			
Clavulina cylindrica				
Epistominella exigua	21		2	
Globobulimina spp.				
Haplophragmoides bradyi	15		1	
Melonis barleeanus	4	2		2
Nonionella sp.	6			
Siphogenerina columellaris	1	2		
Textularia sp.	2		2	
Uvigerina elongatastriata	2			
Uvigerina peregrina	4			
Uvigerina mediterranea	1			
Rest	26	2	1	5

B	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm
Adercotryma glomerata	4			2
Bolivina alata	21	1		
Bolivina spp.	22	3		
Bulimina marginata				
Clavulina cylindrica	1			
Epistominella exigua	34	1		1
Globobulimina spp.				1
Haplophragmoides bradyi	3			1
Melonis barleeanus	4	1		1
Nonionella sp.	3	2		
Siphogenerina columellaris	4		1	
Textularia sp.	1			
Uvigerina elongatastriata	4			
Uvigerina peregrina	4	1		
Uvigerina mediterranea	1			
Rest	25	7	3	2

Appendix B, size fraction 37-63μm

Species	Biox t=1				Biox t=2			
A	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm
Adercotryma glomerata					20			
Bolivina spp.	47	38	6	12	48		8	14
Bulimina marginata					4			
Epistominella exigua	36	6	6	6	36			6
Melonis barleeanus								
Nonionella sp.	4	4						
Siphogenerina columellaris								
Stainforthia sp.	6	8	2	2				
Textularia sp.	5	2						
Uvigerina spp.	4							
Rest	45	8	20	4	40	8		16
B	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm
Adercotryma glomerata	4				5		4	
Bolivina spp.	50	16	10	4	14	6	24	14
Bulimina marginata	2							
Epistominella exigua	54	2	6	4	13	6		
Melonis barleeanus								
Nonionella sp.	2	2	8	2		6	4	
Siphogenerina columellaris					2			
Stainforthia sp.	6	2	10		1	2		4
Textularia sp.	4	4		2	2	4	8	
Uvigerina spp.	2				1			
Rest	92	12	20	10	26		16	

	Bioxf				Bianox			
A	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm
Adercotryma glomerata	37				2			
Bolivina spp.	43	24	12	8	44		1	
Bulimina marginata	4							
Epistominella exigua	92		2	2	2			
Melonis barleeanus								
Nonionella sp.	9		4		10	1		
Siphogenerina columellaris								
Stainforthia sp.	3		6	10	24			
Textularia sp.	8		1		8			
Uvigerina spp.	4							
Rest	99		16	4	30	6		8
B	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm
Adercotryma glomerata	8				2			
Bolivina spp.	48	6	10	8	56	2		
Bulimina marginata	4							
Epistominella exigua	96				8			
Melonis barleeanus								
Nonionella sp.	12		18		8			
Siphogenerina columellaris								
Stainforthia sp.	4	4			18			
Textularia sp.	4	6			2			
Uvigerina spp.	4							
Rest	76	6	6	2	16	4	4	4

Bianoxf				
A	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm
Adercotryma glomerata	4			
Bolivina spp.	49			
Bulimina marginata				
Epistominella exigua	31			
Melonis barleeanus				
Nonionella sp.	3	2		
Siphogenerina columellaris				
Stainforthia sp.	6			
Textularia sp.				
Uvigerina **spp.**				
Rest	23	6	4	

B	0-0,5cm	0,5-1cm	1-1,5cm	1,5-2cm
Adercotryma glomerata	6			
Bolivina spp.	66	3	4	
Bulimina marginata	2			
Epistominella exigua	48			
Melonis barleeanus	4			
Nonionella sp.				
Siphogenerina columellaris				
Stainforthia sp.	4		4	
Textularia sp.	8	3		
Uvigerina **spp.**	2			
Rest	38	16	4	12

Appendix C

List of all taxa (including the rest group) identified in the samples.

Appendix C

Adercotryma glomerata (Brady) 1878
Ammolagena sp.
Ammoscalaria sp.
Amphycoryna scalaris (Batsch) 1791
Bigenerina nodosaria d'Orbigny 1826
Bolivina alata (Seguenza) 1862
Bolivina spathulata (Williamson) 1858
Bolivina striatula Cushman 1922
Bolivina subaenariensis Cushman 1922
Bolivinita quadrilatera Schwager 1866
Bulimina costata d'Orbigny 1826
Bulimina marginata d'Orbigny 1826
Cancris sp.
Cassidulina carinata Silvestri 1896
Chilostomella oolina Schwager 1878
Cibicides lobatulus Walker & Jacob 1798
Cibicidoides pachydermus (Rhezac) 1886
Cibicidoides ungerianus (d'Orbigny) 1846
Clavulina cylindrica d'Orbigny 1825
Cornuspira carinata (Costa) 1856
Cribrostomoides subglobosum (M. Sars) 1868
Cruciloculina sp.
Cyclammina cancellata Brady 1879
Dentalina sp.
Eggerella scabra (Wiliamson) 1858
Epistominella exigua (Brady) 1884
Fissurina sp.
Glandulina ovula d'Orbigny 1846
Globobulimina affinis d'Orbigny 1839
Globobulimina pyrula (Brady) 1884
Glomospira sp.
Gyroidina altiformis Stewart & Stewart 1930
Gyroidina orbicularis
Gyroidina umbonata (Silvestrii) 1898
*Hanzawaia boueana (*d'Orbigny) 1846
Haplophragmoides bradyi (Robertson) 1891

Haplophragmoides sp.
Hoeglundina elegans (d'Orbigny) 1826
Hyalinea balthica Schroeter 1783
Lagena sp.
Lenticulina peregrina (Schwager) 1866
Lenticulina sp.
Melonis barleeanus (Williamson) 1858
Nonionella sp.
Nuttallides umboniferus (Cushman) 1933
Pseudoclavulina crustata Cushman 1936
Pullenia quinqueloba (Reuss) 1851
Pyrgo depressa (d'Orbigny) 1826
Pyrgo subsphaerica d'Orbigny 1839
Quinqueloculina seminula (Linne) 1758
Reophax dentaliniformis Brady 1881
Reophax fusiformis (Williamson) 1858
Reophax guttifera (Brady) 1881
Reophax scorpiurus Montfort 1808
Reophax spiculifer Brady 1879
Saccammina sp.
Siphogenerina columellaris (Brady) 1884
Siphotextularia concava (Karrer) 1868
Spiroplectinella sp.
Stainforthia sp.
Textularia sp.
Trifarina angulosa (Williamson) 1858
Trifarina sp.
Trochammina inflata (Montagu)1808
Uvigerina elongatastriata (Colom) 1952
Uvigerina mediterranea Hofker 1932
Uvigerina peregrina Cushman 1923
Uvigerina proboscidea Schwager 1866

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