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Live foraminiferal faunas from a 2800 m deep lower canyon station from the Bay of Biscay: Faunal response to focusing of refractory organic matter

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Abstract

A 2800 m deep station was sampled on three occasions, in January 1999, June 1999 and April 2000, in the lower part of Cap-Ferret Canyon (Bay of Biscay). This area is characterised by a rapid accumulation of fine-grained sediments and by important inputs of reworked organic matter in an intermediate state of decay. Diagenetic reactions within the sediment follow the well-established depth sequence resulting from the oxidation of organic deposits by different electron acceptors. At our station, live benthic foraminiferal faunas differ strongly from faunas previously collected at nearby open slope sites at a comparable water depth. Spectacularly high densities of deep infaunal species are observed in the deeper parts of the sediment for all three sampling periods. In our opinion, these high deep infaunal densities are a direct response to the massive flux of partially degraded organic matter, which is slowly introduced into the deeper parts of the sediment, where it induces a rather stable succession of redox gradients. *Melonis barleeanus* lives in the dysoxic part of the sediment whereas *Globobulimina affinis* appears preferentially close to the zero oxygen boundary. Both taxa occupy niches where the highest content of Mn (III, IV)-oxides and -oxihydroxides and Fe (III)-oxides are recorded. The fact that most of the geochemical reactions within the sediment are directly or indirectly catalysed by

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heterotrophic and chemolithoautotrophic bacterial consortia could suggest that deep infaunal foraminifera may be highly specialised protozoans able to feed on, or live in symbiosis with these prokaryotic communities.

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1. Introduction

In deep-sea environments, the exported organic matter flux and the oxygenation and redox conditions in the bottom and interstitial waters are generally considered to be the major parameters controlling the density, composition and microhabitat of benthic foraminiferal faunas (e.g. Altenbach, 1988; Altenbach and Sarnthein, 1989; Lutze and Thiel, 1989; Mackensen and Douglas, 1989; Rathburn and Corliss, 1994; Jorissen et al., 1995; Rathburn et al., 1996; Fariduddin and Loubere, 1997; Jorissen, 1999a; Schmiedl et al., 2000; Morigi et al., 2002). In a recent study on benthic foraminiferal faunas from a five-station (140–2000 m) open slope transect from the Bay of Biscay, Fontanier et al. (2002) showed that foraminiferal densities reflect the vertically exported organic matter flux and thus show a significant decrease with water depth. Foraminiferal standing stocks are high in the relatively eutrophic lower shelf and upper and middle slope environments. There, foraminifera are generally concentrated at the sediment–water interface. The first cms of the sediment, where some important redox boundaries are situated, may provide microhabitats for specific foraminiferal taxa (Fontanier et al., 2002). For example, *Melonis barleeanus* generally concentrates in the hypoxic parts of the sediment and still deeper, whereas *Globobulimina affinis* is generally distributed around the zero oxygen level (Fontanier et al., 2002). In the more oligotrophic lower slope environments, benthic foraminiferal density is much lower, and foraminifera are essentially limited to the sediment–water interface, where the scarce trophic resources are concentrated.

Furthermore, foraminiferal faunas respond to seasonal signals. Several field studies show that deep-sea foraminiferal taxa are capable of taking

rapid advantage of seasonal phytodetritus deposits on the sea floor and exhibit a density increase close to the sediment–water interface during more or less short eutrophic episodes (Gooday, 1988, 1993; Gooday and Lamshead, 1989; Jorissen et al., 1992; Barmawidjaja et al., 1992; Silva et al., 1996; Ohga and Kitazato, 1997; Jannink et al., 1998; Loubere, 1998; Gooday and Rathburn, 1999; Kitazato et al., 2000; Fontanier et al., 2003). Phytoplankton detritus is supposed to consist of easily hydrolysable organic matter, which could sustain metabolic activities of the most opportunistic foraminiferal taxa colonising and reproducing in these deposits once they reach the sea bottom (Gooday, 1988, 1993; Lamshead and Gooday, 1990; Turley et al., 1993). Such opportunistic behaviour was recently confirmed by laboratory experiments, which depict a clear reproductive foraminiferal response to artificial food enrichment of the sediment (Heinz et al., 2001). In a study on the seasonal and inter-annual variability of benthic foraminifera at a 550 m deep upper slope station in the Bay of Biscay, Fontanier et al. (2003) suggest that the input of vertically transported phytodetritus deposits provokes a rapid reproductive response of the more opportunistic foraminiferal taxa living in the uppermost sediments (e.g. *Epistominella exigua*). Intermediate and deep infaunal populations that are associated with the deeper redox fronts in the sediment are much more stable through time, and less affected by phytodetritus deposits (Fontanier et al., 2003).

Submarine canyons differ from surrounding open environments in terms of the sedimentary processes that determine the quantity and quality of inorganic and organic deposits. In open slope settings, the main organic matter fluxes correspond to seasonal inputs of labile phytodetritus, which are directly exported from surface waters to bottom sediments (McCave, 1975; Billett et al.,

1983; Lampitt, 1985; Bruland et al., 1989; Auffret et al., 1994; Newton et al., 1994). In contrast, organic supplies in submarine canyons are predominantly induced by downslope transport or lateral advection (Van Weering et al., 2002). Consequently, important amounts of reworked terrestrial or marine organic matter are found in the sediment in these particular areas (Gardner, 1989; Buscail et al., 1990; Gadel et al., 1993; Crémer et al., 1993, 1999; Etcheber et al., 1999; Heussner et al., 1999, Van Weering et al., 2002). Such differences have important consequences for both the quantitative and qualitative characteristics of the foraminiferal fauna. A recent study performed by Schmiedl et al. (2000) shows that foraminiferal faunas from a 920 m deep site in the Lacaze-Duthiers Canyon (NW Mediterranean Sea) differ strongly from faunas sampled at a 800 m deep open slope station in the nearby Gulf of Lyons. High lateral advective organic matter fluxes in the canyon axis induce high organic carbon contents and steep redox gradients within the sediments, resulting in abundant faunas characterised by rather important amounts of intermediate and deep infaunal taxa such as *M. barleeanus* and *Globobulimina* spp. At the open slope stations, in contrast, lower fluxes of more easily metabolisable organic matter restrict foraminiferal faunas to well-oxygenated shallow infaunal niches and limit the abundance of intermediate and deep infaunal taxa.

Benthic foraminiferal faunas in canyon environments are still very poorly known. More research is needed to unravel the complex relationship between the geomorphology of continental margins, the quantitative and qualitative characteristics of sedimentary deposits and organic supplies and the abundance, composition and vertical distribution of foraminiferal faunas. In the present paper, we address two specific questions:

(1) How do the benthic foraminiferal faunas respond to the peculiar setting of a site in the lower part of Cap-Ferret Canyon (Bay of Biscay)? More specifically, how do the canyon foraminiferal faunas differ from open-slope faunas from comparable water depths?

(2) Do the superficial and deeper infaunal assemblages respond to the same environmental controls? Are the temporal changes recorded for both groups similar, and simultaneous, or do they suggest that ecosystem changes in these two compartments are triggered by different sources of organic matter and operate on different time scales?

2. Materials and methods

2.1. Study area

Station I (44°49'N, 2°33'W, water depth 2800 m) is situated on a flat part of the northern flank of Cap-Ferret Canyon (Fig. 1). Cap-Ferret Canyon has been intensively studied in the framework of the ECOMARGE program (Monaco et al., 1999).

At this site, bottom water temperature and salinity are close to 3.0 °C and 34.95. This station is probably bathed by bottom waters composed of a mixture of Northeastern Atlantic Deep Water (NEADW, $T = 2.9$ °C, $S = 34.95$) and Antarctic Bottom Water (AABW, $T = 2.5$ °C, $S = 34.92$) (Durrieu de Madron et al., 1999). Durrieu de Madron et al. (1999) showed that the water flow at

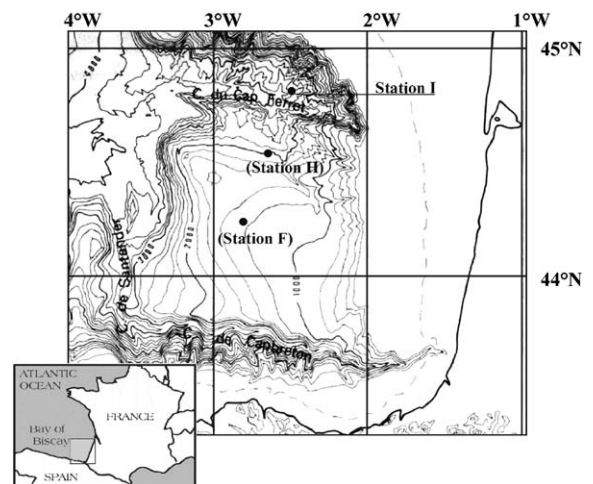


Fig. 1. Study area, bathymetry and geographical position of station I. Stations F and H, discussed in the text, are also presented (Fontanier et al., 2002).

a 3000 m deep station, only 5 km away from our site, is oriented westward along the canyon axis with a mean current velocity of only 6 cm s^{-1} . Bottom waters present low turbidity values ($< 30 \text{ m FTU}$), indicative of the absence of strong nepheloid layers in the lower canyon and of limited resuspension processes (Durrieu de Madron et al., 1999). The sediment consists of silty muds with less than 30% carbonate (Hyacinthe et al., 2001).

Station I was sampled in January 1999, June 1999, and April 2000. Cores with an undisturbed sediment–water interface, and with overlying bottom waters, were collected with a classical Barnett multi-tube corer (Barnett et al., 1984). Different cores were used for sedimentological, geochemical, biochemical and foraminiferal analyses.

2.2. Sedimentological analyses

One of the cores collected in April 2000 was radiographed with a Scopix system, which consists of an X-ray imaging system combined with image analysis software (Migeon et al., 1999). The aim of the X-ray radiography was to detect the presence of discrete sedimentary structures in the top 15 cm of the core. In order to evaluate changes visually, a photograph of the same core was also taken. Particle grain sizes were measured with a Malvern Laser Diffraction Particle Sizer (type 2600). This technique was applied to sediment samples belonging to the previously radiographed and photographed core, and allowed the calculation of mean grain sizes.

2.3. Geochemical analyses

During all cruises, overlying waters were immediately collected for dissolved O_2 measurements by the Winkler titration method (Strickland and Parsons, 1972). Profiles of pore water O_2 were measured on board with a cathode-type mini-electrode (Helder and Bakker, 1985; Revsbech and Jørgensen, 1986). Sediment temperature was kept constant with an insulating device. Sampling resolution for other chemical analyses was 0.5 cm from the sediment surface to a depth of 4 and 1 cm

in the lower part of the cores. Pore water was extracted by centrifugation at 5000 rpm for 20 min under inert atmosphere (N_2). The supernatant was filtered ($0.2 \mu\text{m}$, syringe filter SFCA NALGENE^R purged by N_2), acidified for dissolved metals analysis (HNO_3 ; s.p.), and frozen for nutrient analysis. Surface sediments from a second core were collected for ^{210}Pb and ^{234}Th analysis.

Porosity was determined from weight loss upon freeze-drying. The freeze-dried solid fraction was homogenised for solid-phase analysis. The maximum sedimentation rates and the thickness of the mixed layer of the sediment were estimated from vertical profiles of excess ^{210}Pb and excess ^{234}Th ($^{210}\text{Pb}_{\text{xs}}$, $^{234}\text{Th}_{\text{xs}}$). The activities of radiogenic isotopes ^{210}Pb (half-life = 22.4 years) and ^{234}Th (half-life = 24.1 days) were determined in freeze-dried samples of about 5 g each. They were sealed in a counting vial and measured by a high-resolution and low-background gamma spectrometer with a semi planar detector for at least 12 h (Jouanneau et al., 1988).

Dissolved nitrate ($\Sigma\text{NO}_3^- = \text{NO}_3^- + \text{NO}_2^-$) and ammonia (NH_4^+) were analysed by flow injection analysis (FIA) according to standard procedures (Anderson, 1979; Hall and Aller, 1992). Precisions are $\pm 0.5 \mu\text{mol l}^{-1}$ for ΣNO_3^- and $\pm 5\%$ for NH_4^+ . Dissolved manganese (Mn^{2+}) was measured by flame atomic absorption spectrometry (Perkin Elmer AA 300). Dissolved iron (Fe^{2+}) was analysed by the ferrozine procedure described by Stookey (1970). The precision for both methods is $\pm 10\%$.

In order to extract the most reactive part of Fe (III) phases and all Mn (III, IV) oxides and oxihydroxides, sediments were treated with an ascorbate solution (Kostka and Luther, 1994; Anschutz et al., 1998; Hyacinthe et al., 2001). About 1 g of wet sediment was leached for 24 h with 25 ml of an ascorbate reagent consisting of 50 g of NaHCO_3 , 50 g sodium citrate and 20 g ascorbic acid in one litre of water with a final pH of 8. In order to analyse Fe and Mn by flame atomic absorption spectrometry, aliquots of centrifuged solution were then diluted to obtain a 0.2 M HCl matrix. The precision estimated from replicates was $\pm 3\%$ for Mn and $\pm 7\%$ for Fe.

2.4. Biochemical analyses

Particulate organic carbon (C-org) and total carbon were measured on freeze-dried samples by combustion in an LECO C-S 125 analyzer. Particulate organic carbon was measured after removal of carbonates with 2 M HCl from 50 mg of powdered sample. The analyses were performed by direct combustion in an induction furnace. The newly formed CO₂ was determined quantitatively by infrared absorption. Inorganic carbon is the difference between total carbon and particulate organic carbon. Inorganic carbon was also measured by calcimetry, which gave almost identical results. The precision of these analyses was $\pm 3 \mu\text{mol g}^{-1}$.

During the January 1999 cruise both total hydrolysable amino acids (THAA) and enzymatically hydrolysable amino acids (EHAA) were assessed in the top cm of the sediment. A subsample of this layer was immediately sealed in a pre-weighed vial and frozen in nitrogen. Back at the laboratory, this sample was freeze-dried and stored at -20°C . It was then crushed and passed through a 200 μm mesh prior to analysis. All biochemical assays were performed three times.

In order to assess THAA, 15 mg DW of sediment were submitted to a strong acid hydrolysis (500 μl of 6 N HCl, 100°C , 24 h, under vacuum). 0.4-ml subsamples of the hydrolysates were neutralised with 0.4 ml of 6 N NaOH and buffered with 0.8 ml of H₃BO₃ (0.4 M, pH 8). Fluorescent derivatives were obtained by adding 6 μl of an orthophthaldialdehyde solution (125 mg in 2.5 ml of methanol and 0.125 ml of mercaptoethanol) and 400 μl of H₃BO₃ to 100 μl of those samples. THAA quantification was directly based on fluorescence measurements and was achieved through comparison with a standard containing 19 amino acids. Excitation wavelength was 335 nm and emission wavelength was 450 nm.

EHAA were extracted following the biomimetic approach proposed by Mayer et al. (1995). In total, 100 mg DW of sediment were poisoned with 1 ml of a solution containing 2 inhibitors of bacterial active transport systems (0.1 M sodium arsenate and 0.1 mM pentachlorophenol within a pH 8 sodium phosphate buffer). This mixture was

incubated for 1 h at room temperature. 100 μl of proteinase K solution (1 mg ml^{-1}) were then added and the samples were incubated for 6 h at 37°C . They were then centrifuged to remove the remaining particulate material. 75 μl of pure TCA were added to 750 μl of supernatant to precipitate macromolecules, which are considered to be unsuitable for absorption. In total, 750 μl of the supernatant were then hydrolyzed and processed as described for THAA. In addition, a blank accounting for possible degradation of the enzyme was carried out. EHAA were quantified by the same procedure as for THAA. The EHAA/THAA ratio was used as an index of POM lability (Medernach et al., 2001; Grémare et al., 2002; Rosenberg et al., 2003).

2.5. Foraminiferal fauna analyses

For faunal analysis, one entire 72 cm² core was sliced horizontally; usually every 0.25 cm for the first cm of the sediment, every half cm between 1 and 4 cm depth, and every cm between 4 and 10 cm. In April 2000, two replicate cores were taken from the same multi-tube corer deployment. On board the ship, sediments were stored in 500 cm³ bottles filled with 95% ethanol containing 1 g l^{-1} Rose Bengal stain. The samples were shaken for several minutes in order to get a homogeneous mixture. Several weeks after the campaign, samples were sieved through 63- and 150- μm mesh screens, and the sieve residues were stored in 95% ethanol. Foraminifera belonging to the >150- μm fraction were sorted from wet (about 50% ethanol) samples and stored in Chapman slides. Because of the extremely time consuming character, we limited this study of the 63–150 μm fraction to the first cm of the sediment. Our taxonomic framework is outlined in Appendix A. Pictures of the most common taxa are shown on webpage http://sciences.univ-angers.fr/geologie/atlas/Taxo_tophe.htm.

The use of the rose Bengal staining technique to distinguish live from dead foraminifera is an inexpensive and easy method (Walton, 1952; Bernhard, 1988, 2000). However, below the zero oxygen level within the sediment, the degradation of foraminiferal protoplasm may take a

considerable period of time after the death of the organism (Corliss and Emerson, 1990); as a consequence, in the deeper anoxic part of the sediment some dead taxa may present a doubtful staining (Bernhard, 1988, 2000; Corliss and Emerson, 1990). We applied our staining criteria (all chambers except the last one stained brightly pink) always very strictly, and compared doubtful individuals with perfectly stained specimens of the same species found in oxic superficial sediment layers, where the staining efficiency is unambiguous. For deep infaunal taxa that usually occupy the anoxic part of the sediment (e.g. *G. affinis*), the differentiation between live and dead foraminifera was based on the presence of a stained protoplasm body close to the aperture, and the absence of a mosaic-like veil of bacterial degradation in the interior of the test. Non-transparent agglutinated and porcellaneous taxa were crushed in order to investigate the test interior. *Glomospira* spp. (*Glomospira charoides* and *Glomospira gordialis*) were not included in the quantitative analyses, because the orange-reddish colour of their test makes it particularly difficult to determine whether the organism was alive or dead at the time of sampling. Also, fragments of the very fragile arborescent agglutinating foraminiferal fragments (such as *Hyperammina* spp., *Rhizammina* spp., *Bathysiphon* spp.) have not been included, since it is impossible to determine to how many individuals they correspond. Because samples were preserved and sorted in ethanol, many soft-shelled foraminiferal species may have shrunk and become unrecognisable during picking. Thus, our counting does not represent the soft-shelled foraminiferal group. Faunal counting results are listed in Appendices B and C for the 63–150 μm and >150 μm fractions, respectively.

In order to get a general idea about the microhabitat patterns, we calculated the Average Living Depth (ALD_x , Jorissen et al., 1995) of the total foraminifera fauna or of individual taxa. Following Buzas et al. (1993), we recognise only three different microhabitat categories: shallow, intermediate and deep infaunal taxa. Overall, weighted ALD_{10} values have been calculated for each taxon by integrating the results obtained in

the subsequent cores using

$$\overline{\text{ALD}}_{10} = \sum_{C=1,y} ((\text{ALD}_{10})_y \times n_y) / N,$$

where C is the total number of cores, N the total number of individuals in all cores, ALD_{10}^y the average living depth for the ten first cm of core y , n_y the number of specimens in core y .

2.6. Statistical analyses

We decided to use a statistical approach to compare the normalised densities of intermediate and deep infaunal foraminiferal taxa (>150 μm size fraction) with the concentration of redox elements (oxygen, nitrate/nitrite (ΣNO_3^-), ammonia (NH_4^+), dissolved metals (Mn^{2+} and Fe^{2+}) and metal-oxides and -oxihydroxides (Mn_{asc} and Fe_{asc}). For our statistical analyses, we considered all sediment layers where foraminiferal faunas were analysed. We based our analysis on standardised densities (number of individuals per 50 cc sediment volume) of three taxa (*M. barleeanus*, *Chilostomella oolina*, *G. affinis*). We deleted one core collected in April 2000 because the microhabitat patterns of foraminiferal faunas seemed to be affected by active deep macrofaunal bioturbation. We constrained our statistical analysis to all sediment intervals (and related mid-points) where we could associate a full data set of geochemical variables to foraminiferal densities. On six occasions, we were obliged to combine faunal data of two successive depth intervals to compare with the corresponding geochemical measurements. It should be kept in mind, however, that foraminiferal and geochemical analyses were performed on two different cores of the same multitube corer deployment. This may explain small discrepancies, especially in cases of active bioturbation. As there is a small amount of data (37 samples for our 3 cores), classical analyses such as mean comparison or ANOVA are not applicable. Therefore, we performed a normalised PCA (using the French software package ADDAD) and a common hierarchical clustering (Ward criterion) applied to the weighted factors of the PCA. This method allows us to interpret the potential relationship

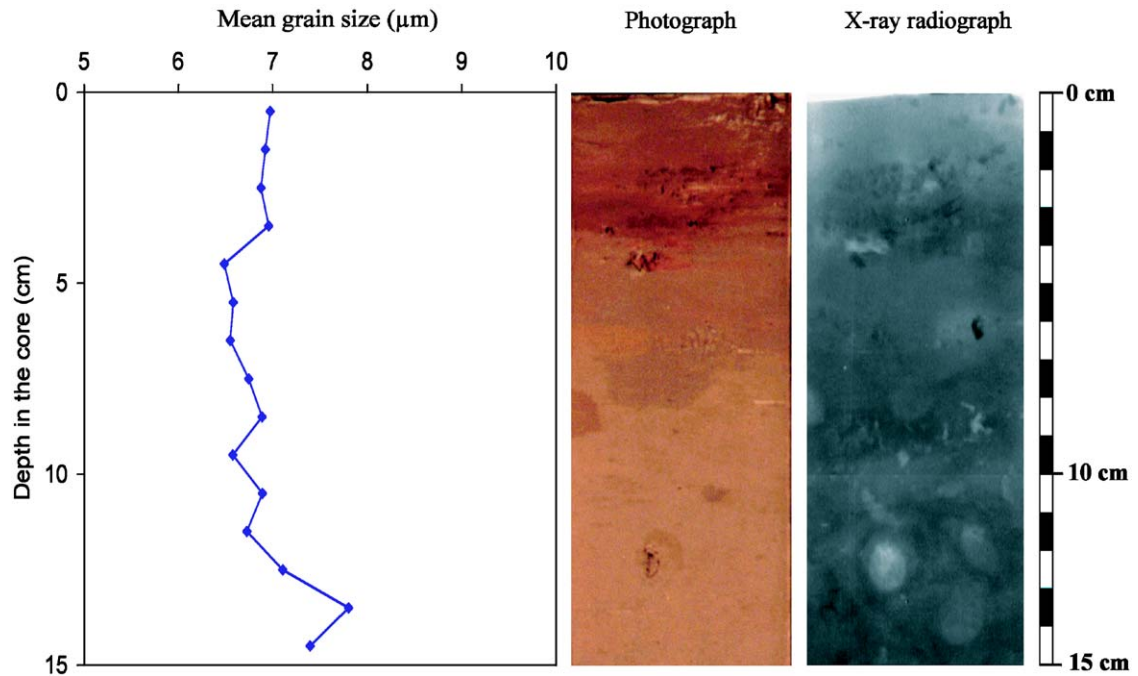


Fig. 2. Photograph and X-ray radiograph of a half core collected in April 2000 at station I. Mean grain size is indicated along the same 15 cm long half-core.

between foraminiferal microhabitat and redox zones.

3. Results

3.1. Sedimentary patterns

The photographic observation of a 15 cm long vertical section of the core collected in April 2000 allows us to distinguish a vertical succession of four sub-horizontal layers (Fig. 2). The topmost layer is olive-brown and extends down to 2 cm deep in the sediment. Below, an olive-brown 2 cm thick layer presents discontinuous dark brown sub-horizontal sedimentary micro-horizons. Down to about 7–8 cm depth, there is a greyish brown layer, which exhibits a rather disturbed lower boundary and some brown or brownish-yellow patches. Between 8 and 15 cm depth (the bottom of the core), the sediment is predominantly grey

with lighter ovoid or elongated sub-horizontal patches.

The X-ray radiograph of the same core shows neither a clear erosive surface, nor graded sediments (Fig. 2). From the sediment–water interface to about 2 cm depth, there is a bright layer with a disturbed lower limit. Below, darker layers incorporate lighter sediment horizons with more or less clearly defined limits (e.g. the white track at 4 cm depth or the grey patch at 6 cm depth.) and ovoid or sub-horizontal elongated patches.

These patches probably correspond to burrow infill. In a second core taken in April 2000, we recorded the presence of a live subsphaerical holothurian (about 3 cm in diameter) and a 4 cm long polychaete between 4 and 7 cm depth. The holothurian belonged to the genus *Molpadia*, an infaunal taxon able to dig large burrows within the sediment (M. Sibuet, pers. com.; 2002).

The grain size record for the upper 15 cm shows mean values ranging from 6.5 to 7.8 μm (Fig. 2). In the interval extending from 15 to 4 cm depth, a

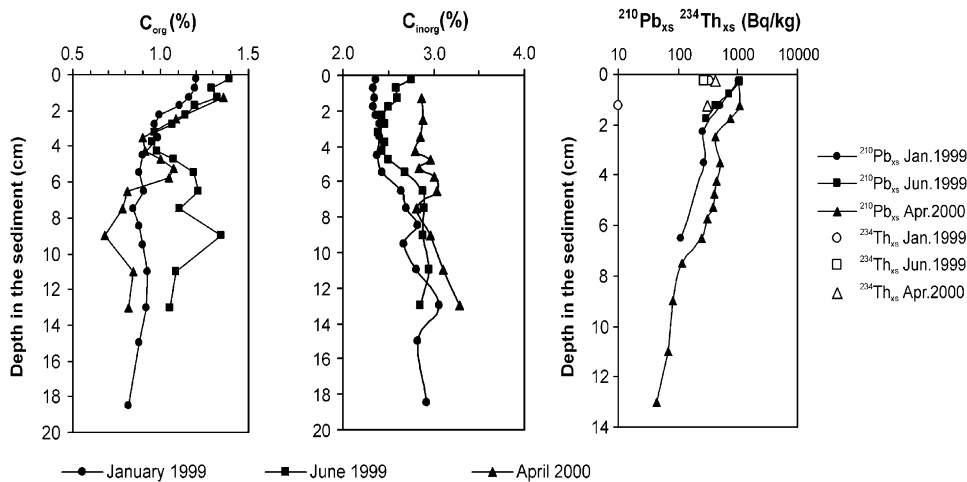


Fig. 3. $^{210}\text{Pb}_{\text{xs}}$, $^{234}\text{Th}_{\text{xs}}$, organic and inorganic carbon content (C-org): vertical profiles for the three sampling periods (January 1999, June 1999 and April 2000).

vague fining-up tendency can be distinguished. In the top 4 cm, mean grain size values are rather constant (about $7.0\ \mu\text{m}$).

3.2. Geochemical analyses

The absolute values of $^{234}\text{Th}_{\text{xs}}$ in the topmost sediment samples show only minor differences between the various sampling periods (January 1999, June 1999, and April 2000) (Fig. 3). In all cores, excess ^{234}Th activity decreases rapidly below the sediment–water interface and reaches the detection limit at about 1 cm depth. The ^{210}Pb excess activity decreases exponentially below the sediment–water interface in all three cores (Fig. 3). In the absence of macrofaunal bioturbation, downcore $^{210}\text{Pb}_{\text{xs}}$ profiles make it possible to estimate recent sediment accumulation rates. In the studied sediments, however, where particle mixing by macrofauna will occur, $^{210}\text{Pb}_{\text{xs}}$ profiles have probably been modified. In such a case, $^{210}\text{Pb}_{\text{xs}}$ profiles allow only a maximum estimate of accumulation rates (Silverberg et al., 1986; Thomson et al., 2000). For our cores, these maximum sediment accumulation rates range from 0.033 to $0.046\ \text{cm year}^{-1}$ (33 – $46\ \text{cm ka}^{-1}$). By combining sedimentation rates with porosity values and the density of particles, we have computed that

maximum mass accumulation rates range from 17 to $24\ \text{mg cm}^{-2}\ \text{year}^{-1}$.

Both the O_2 concentrations in bottom water and the vertical profiles in the sediment are rather similar in January and June 1999 (Figs. 4a and 5a). At the sediment–water interface, O_2 concentrations are about $200\ \mu\text{mol l}^{-1}$ ($5\ \text{ml l}^{-1}$) and the oxygen penetration ranges from 4.8 to $5.4\ \text{cm}$ depth, with the highest value recorded in January 1999. In April 2000, in contrast, the O_2 concentration at the sediment–water interface is only $123\ \mu\text{mol l}^{-1}$ ($2.7\ \text{ml l}^{-1}$) and the oxygen penetration depth is only $3.8\ \text{cm}$ (Fig. 6a).

For all cores, the nitrate concentration ($\Sigma\text{NO}_3^- = \text{NO}_3^- + \text{NO}_2^-$) of the bottom water is close to $20\ \mu\text{mol l}^{-1}$ (Figs. 4a–6a). In comparison to bottom waters, interstitial waters of the topmost part of the cores are enriched in ΣNO_3^- . Below the first two cms, the ΣNO_3^- concentrations decrease irregularly and reach zero values at 7 – $10\ \text{cm}$ depth. Whereas the concentrations of dissolved NH_4^+ in bottom waters are too low to be detected, they exhibit relatively constant and low values in the oxic topmost layers of all cores (Figs. 4a–6a). In January and June 1999, NH_4^+ concentrations increase rapidly below the oxic layer. In April 2000, in contrast, the NH_4^+ profile is irregular and shows only a slight increase below $4\ \text{cm}$ depth.

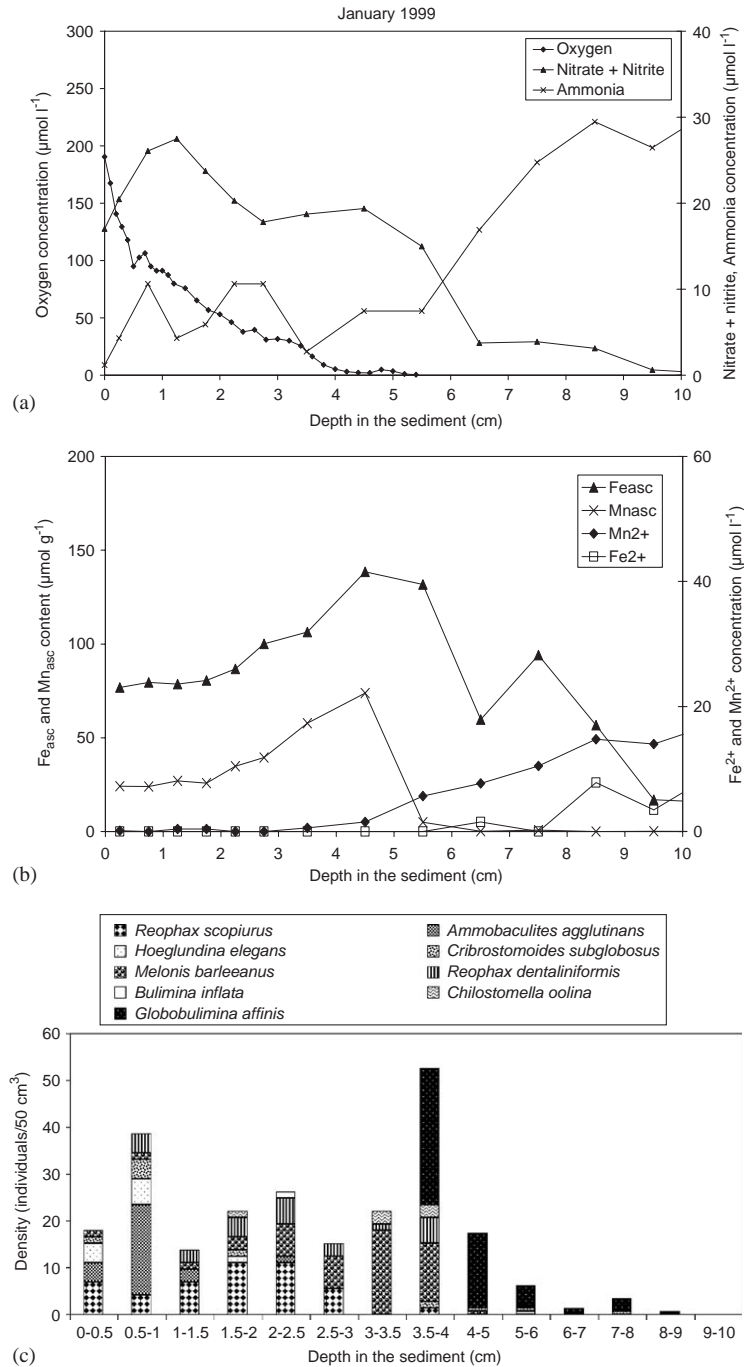


Fig. 4. (a) Dissolved oxygen, nitrate + nitrite and ammonia concentrations in a core collected in January 1999; (b) reduced iron (Fe^{2+} , Mn^{2+}) and iron and manganese oxide and oxihydroxide content (Fe_{asc} , Mn_{asc}) in the same core; (c) foraminiferal distribution (number of individuals $>150\mu\text{m}$ fraction found in each level, standardised for a 50cm^3 sediment volume). Only taxa with a higher than 5% (percentage abundance) in one of the cores are presented.

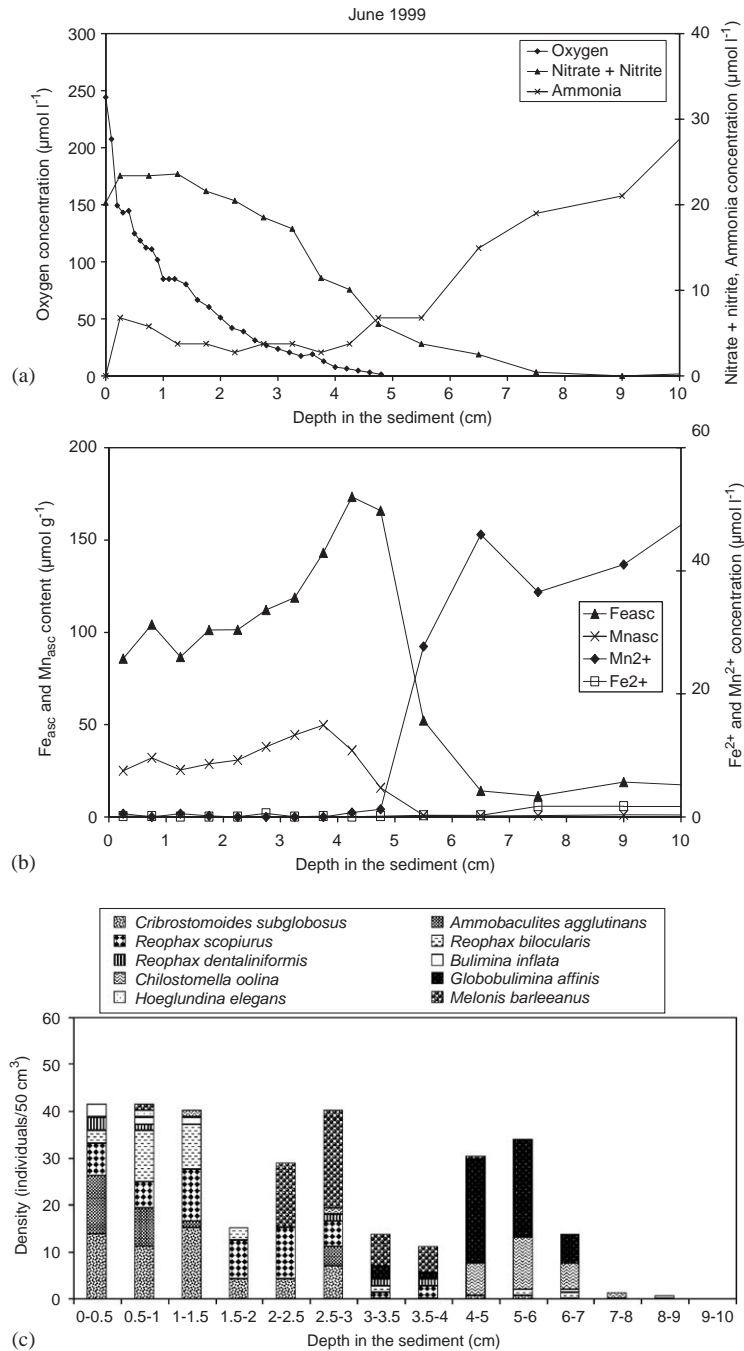


Fig. 5. (a) Dissolved oxygen, nitrate+nitrite and ammonia concentrations in a core collected in June 1999; (b) reduced iron and manganese (Fe^{2+} , Mn^{2+}) and iron and manganese oxide and oxihydroxide content (Fe_{asc} , Mn_{asc}) in the same core; (c) foraminiferal distribution (number of individuals $>150 \mu\text{m}$ fraction found in each level, standardised for a 50cm^3 sediment volume). Only taxa with a percentage higher than 5% (percentage abundance) in one of the cores are presented.

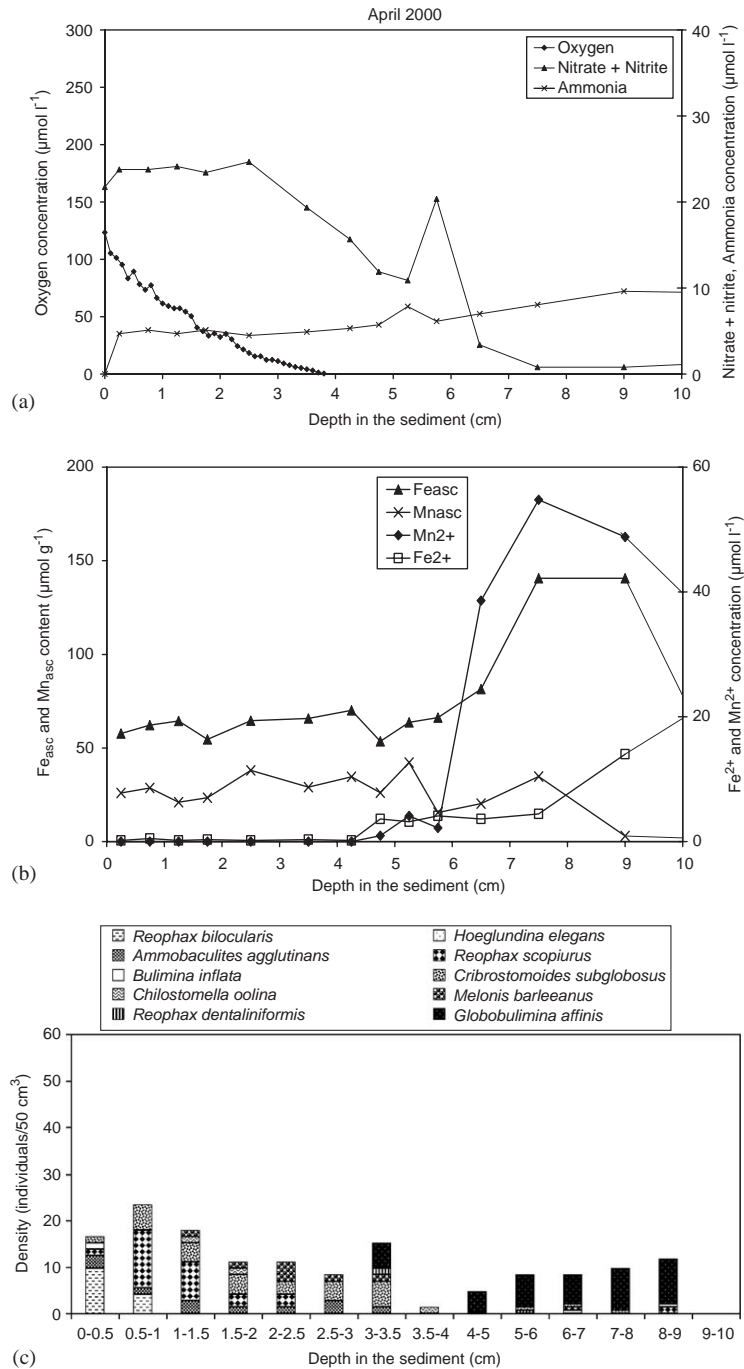


Fig. 6. (a) Dissolved oxygen, nitrate+nitrite and ammonia concentrations in core A collected in April 2000; (b) reduced iron and manganese (Fe^{2+} , Mn^{2+}) and iron and manganese oxide and oxihydroxide content (Fe_{asc} , Mn_{asc}) in the same core; (c) foraminiferal distribution (number of individuals $> 150 \mu\text{m}$ fraction found in each level, standardised for a 50 cm^3 sediment volume). Only taxa with a percentage higher than 5% (percentage abundance) in one of the cores are presented.

Dissolved manganese (Mn^{2+}) remains undetectable in the oxic part of the sediments (Figs. 4b–6b). In the anoxic sediment, the Mn^{2+} concentration increases gently with depth. However, it should be noticed that in April 2000 the Mn^{2+} values increase far below the zero redox boundary (at 6 cm depth) (Figs. 4b–6b). Dissolved iron (Fe^{2+}) appears directly below the zero oxygen boundary and increases gently downcore in the anoxic interval (Figs. 4b–6b).

In January and June 1999, the profiles of particulate manganese extractable by an ascorbate solution (Mn_{asc}) show subsurface maxima just above the zero oxygen boundary. Below the oxic front, the Mn_{asc} contents decrease sharply (Figs. 4b–6b). In April 2000, the Mn_{asc} profile does not exhibit a subsurface peak; the whole first 8 cm of the sediment are enriched in reactive Mn (mean concentration of $30 \mu\text{mol g}^{-1}$). Only below 8 cm depth does the Mn_{asc} content decrease to zero (Fig. 6b). In January and June 1999, the vertical distribution of extractable iron (Fe_{asc}) is almost similar to Mn_{asc} with a subsurface maximum at the zero oxygen boundary just below the Mn_{asc} peak and a downcore decrease into the anoxic sediment (Figs. 4b and 5b). In April 2000, the Fe_{asc} profile exhibits a peak between 7 and 10 cm (Fig. 6c).

3.3. Biochemical analyses

The organic carbon concentrations of surficial sediments are rather similar (between 1.20 and 1.50 wt%, Fig. 3) for the various sampling periods (January 1999, June 1999, and April 2000). In all cores, the C-org content decreases strongly below the sediment–water interface and reaches ~ 0.9 wt% at about 4 cm depth. Deeper in the sediment, the C-org content continues to decrease slowly. Exceptionally, in June 1999 the C-org profile shows a slight increase between 4 and 10 cm depth. In January 1999, THAA and EHAA concentrations of the top sediment are 35.4 and $8.5 \text{ nmol mg DW}^{-1}$, respectively, with an EHAA/THAA ratio of 23.9%.

3.4. Foraminiferal faunal analyses

In the $>150 \mu\text{m}$ fraction, live foraminiferal densities vary from about 550 (April 2000, core

B) to about 240 individuals per 10 cm deep, 72 cm^2 core (January 1999 and April 2000, core A) (Appendix C). In the 63– $150 \mu\text{m}$ fraction, densities vary from about 470 (April 2000, core B) to about 230 individuals in the topmost cm of a 72 cm^2 core (January 1999) (Appendix B).

In terms of vertical distribution, density profiles for the $>150 \mu\text{m}$ fraction show a gradual downcore decrease of foraminiferal density in all cores (Fig. 7). This decrease is particularly well marked in one of the two cores (B) sampled in April 2000, where the faunas in the upper cm are very rich. In the $>150 \mu\text{m}$ fraction, percentages of the perforate foraminiferal group range from 56% in January 1999 to 32% in April 2000 (core B). Percentages of non-fossilising agglutinated foraminifera range from 63% in April 2000 (core B) to 39% in January 1999. Porcellaneous and fossilising agglutinated foraminifera always show low percentages ($<10\%$) (Appendix C).

The faunal composition of the cores sampled in January 1999, June 1999 and April 2000 (core A) is rather similar (Table 1). The perforate taxa are dominated by *G. affinis* (18–24%), *M. barleeanus* (3–16%) and *C. oolina* (2–10%). The agglutinated part of the faunas is dominated by *Reophax scorpiurus* (9–14%), *Cribrostomoides subglobosus* (3–11%), *Ammobaculites agglutinans* (5–9%) and other *Reophax* species (4–8%). The second core (B) taken in April 2000, in which a holothurian individual was present in its burrow (4–7 cm depth), contains very low numbers of *G. affinis*, and *C. oolina*. This core shows, in contrast, strongly increased numbers of *Bulimina inflata* and *Hoeglundina elegans*. The agglutinated part of the fauna is rather similar to that found in the other three cores.

In the 63– $150 \mu\text{m}$ fraction of the top first cm, agglutinated non-fossilising foraminifera are the major group; their relative contribution varies from 68% in January 1999 to about 41% in April 2000 (core B) (Appendix B). Percentages of perforate foraminifera range from about 49% in April 2000 (both cores) to 28% in January 1999. Porcellaneous, fossilising agglutinated and soft-shelled foraminifera are minor groups. *Nuttallides pusillus*, *E. exigua* and *Cassidulina crassa* dominate the perforate group, whereas *Reophax guttiferus*,

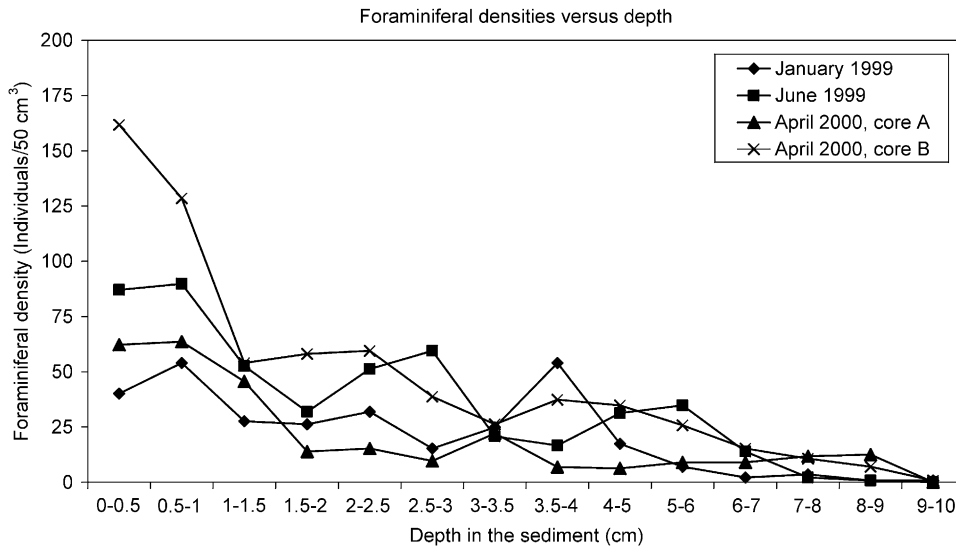


Fig. 7. Vertical profiles of foraminiferal density for the $>150\mu\text{m}$ fraction for all 4 cores. For each interval, density values are standardised for a 50cm^3 sediment volume.

Table 1
Relative abundance of dominant taxa in the $>150\mu\text{m}$ fraction for the four cores

Taxa ($>150\mu\text{m}$)	January 1999	June 1999	April 2000, core A	April 2000, core B
<i>Bulimina inflata</i>	0.82	1.20	0.82	4.60
<i>Chilostomella oolina</i>	3.29	9.16	2.06	0.00
<i>Globobulimina affinis</i>	23.87	17.83	23.46	2.02
<i>Hoeglundina elegans</i>	3.29	0.24	0.41	5.51
<i>Melonis barleeanus</i>	15.64	8.67	2.88	4.41
<i>Ammobaculites agglutinans</i>	8.23	4.57	4.52	9.37
<i>Cribrostomoides subglobosus</i>	2.47	10.12	9.64	12.50
<i>Reophax bilocularis</i>	0.00	6.02	4.11	4.60
<i>Reophax dentaliniformis</i>	7.82	1.45	0.41	0.92
<i>Reophax scorpiurus</i>	13.99	9.16	9.46	17.28

Reophax scorpiurus, *Hippocrepinella* sp., *Trochammina globigeriniformis* and *Reophax bilocularis* dominate the non-perforate group (Appendix B).

The vertical distribution of the dominant taxa of the $>150\mu\text{m}$ fraction is shown in Figs. 4c–6c. ALD_{10} values are represented in Table 2, in which for every taxon a mean weighed ALD_{10} is given which is based on all cores except core B of April 2000. In this core, the strongly modified vertical distribution of benthic foraminifera (Fig. 8) is probably caused by active macrofaunal bioturbation.

Among the perforate taxa, *G. affinis* (mean weighed $\text{ALD}_{10} = 5.4\text{cm}$) and *C. oolina* (mean weighed $\text{ALD}_{10} = 5.0\text{cm}$) can be considered as deep infaunal. *M. barleeanus* (mean weighed $\text{ALD}_{10} = 2.8\text{cm}$) and *Pullenia quinqueloba* (mean weighed $\text{ALD}_{10} = 2.7\text{cm}$) occupy intermediate infaunal microhabitats, whereas *Uvigerina peregriana* (mean weighed $\text{ALD}_{10} = 0.7\text{cm}$) and *H. elegans* (mean weighed $\text{ALD}_{10} = 0.7\text{cm}$) live close to the sediment–water interface. The vertical distribution of agglutinated taxa is much less

Table 2

Average living depth (ALD₁₀) of foraminiferal species and (between parentheses) the number of individuals on which the calculation is based

Taxa	Cores, ALD ₁₀			Average weighed ALD ₁₀	Microhabitat
	January 1999	June 1999	April 2000, core A		
<i>Chilostomella oolina</i>	3.68 (7)	5.37 (38)	4.15 (5)	5.01 (50)	DI
<i>Cibicides lobatulus</i>			0.66 (7)	0.66 (7)	SI
<i>Globobulimina affinis</i>	4.69 (58)	5.10 (74)	6.57 (57)	5.42 (189)	DI
<i>Hoeglundina elegans</i>	0.67 (8)			0.67 (8)	SI
<i>Melonis barleeanus</i>	2.93 (38)	2.79 (36)	2.25 (7)	2.81 (81)	II
<i>Pullenia quinqueloba</i>		2.69 (8)		2.69 (8)	II
<i>Uvigerina peregrina</i>	0.35 (12)	0.95 (13)		0.66 (25)	SI
<i>Quinqueloculina seminula</i>	0.68 (5)			0.67 (5)	SI
<i>Quinqueloculina</i> sp. 1	1.38 (5)		0.55 (8)	0.87 (13)	SI
<i>Ammobaculites agglutinans</i>	0.78 (20)	0.82 (7)	1.66 (10)	0.98 (49)	SI
<i>Cribrostomoides subglobosus</i>	0.80 (5)	1.37 (42)	1.89 (20)	1.48 (67)	SI/II
<i>Hormosina</i> sp.		0.65 (5)	1.04 (7)	0.88 (12)	SI
<i>Karrerulina</i> sp.		1.21 (9)	0.98 (8)	1.10 (17)	SI/II
<i>Psammosphaera</i> sp.		0.91 (13)	3.40 (5)	2.06 (29)	SI/II
<i>Recurvoides</i> sp.	1.06 (6)	1.26 (13)		1.48 (22)	II
<i>Reophax bilocularis</i>		1.67 (28)	0.35 (10)	1.32 (38)	SI/II
<i>Reophax dentaliniformis</i>	2.24 (19)	1.85 (6)		2.15 (25)	II
<i>Reophax guttiferus</i>		0.51 (9)		0.51 (9)	SI
<i>Reophax scorpiurus</i>	1.67 (34)	1.69 (38)	2.01 (23)	1.87 (189)	II
Total perforate	3.32 (136)	3.93 (191)	4.52 (103)	3.87 (430)	
Total porcellaneous	1.03 (13)	0.98 (8)	0.82 (22)	0.91 (43)	
Total non-fossilising agglutinated	1.57 (92)	1.49 (210)	1.80 (118)	1.59 (420)	
Total live foraminifera	2.57 (243)	2.61 (415)	2.87 (243)	2.67 (901)	
Oxygen penetration depth (cm)	5.4	4.8	3.80		

Only occurrences of ≥ 5 individuals are shown. The grey boxes represent dominant taxa with a relative abundance of $\geq 5\%$ at at least one of the stations. Microhabitat patterns are summarised as Shallow Infaunal (SI), Intermediate Infaunal (II) or Deep infaunal (DI) taxa.

distinct. *R. dentaliniformis* and *R. scorpiurus* tend to have infaunal maxima, but many other taxa combine slight surficial maxima with a persistent presence down to a significant depth in the sediment. This rather wide depth range makes it very difficult to assign microhabitat labels to these taxa.

3.5. Statistical analyses

Our PCA approach shows that three axis explain more than 74% of the total variability of the data set (Table 3a). Nitrate + nitrite is opposed to dissolved manganese on the first axis (PCA1: 39% of inertia)

since these species show opposite trends in all cores ($R = 0.64$). The positive side of the second axis (PCA2: 22% of inertia) is dominated by *G. affinis* and *C. oolina* densities, which show maximum values in sediment intervals where Mn (III, IV)-oxides (and -oxihydroxides) and Fe (III)-oxides are recorded, and where oxygen concentration are very low. The third axis, although not very strong (PCA3: 13% of inertia) reveals an opposition of the concentration of dissolved iron against the *C. oolina* density. Since *C. oolina* and dissolved iron have the highest coefficient of variation (respectively, 212% and 210%) this opposition should be considered as weak. The use of a hierarchical clustering (Ward criterion) applied to

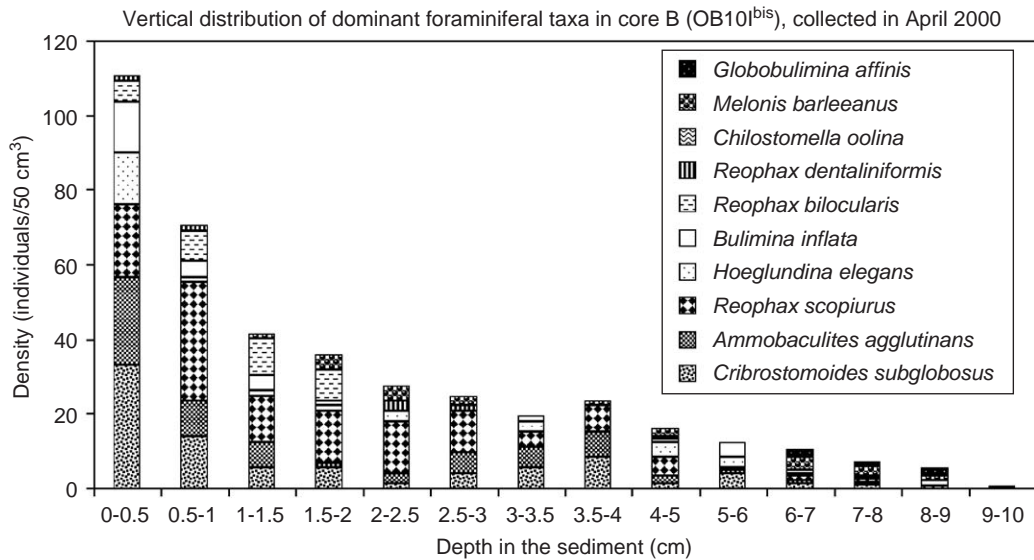


Fig. 8. Foraminiferal distribution (number of individuals $>150\ \mu\text{m}$ fraction found in each level, standardised for a $50\ \text{cm}^3$ sediment volume) in core B collected in April 2000. Only taxa with a percentage higher than 5% (percentage abundance) in one of the cores are presented.

the weighted factors of the PCA regroup in the same cluster *M. barleeanus*, *G. affinis*, iron and manganese oxides and oxihydroxides (cluster 1). There is a clear separation with two other clusters regrouping, respectively, nitrate + nitrite and oxygen concentrations (cluster 2) and dissolved iron, dissolved manganese and ammonia (cluster 3). The calculation of Pearson's correlation coefficient (bilateral test) yields a positive correlation between the vertical distribution of *M. barleeanus* and the profiles of particulate manganese extractable by an ascorbate solution (Mn_{asc}) ($r = 0.47$), whereas the vertical distributions of *G. affinis* is correlated with the vertical distribution of extractable iron (Fe_{asc} , $r = 0.33$) and of free oxygen ($r = -0.41$) (Table 3b). The significance level of these correlation coefficients is over 95%.

4. Discussion

4.1. Sediment transport and mixing

An important question is whether station I is under the influence of erosional or turbiditic

currents. Such disturbing agents may induce a strong modification of the redox conditions in the underlying or remobilised sediments layers (Mulder et al., 2001). Furthermore, recent data for the active Capbreton Canyon suggest that sediment instability exerts a strong impact on the benthic foraminiferal faunas (Anschutz et al., 2002). Several successive stages of recolonisation can be recognised and foraminiferal faunas only rarely arrive at a stage of maturity corresponding to a complete ecosystem recovery (Jorissen et al., 1994; Mulder et al., 2001).

The vertical succession of four distinct sedimentary facies found in one of the cores collected in April 2000 is identical to the patterns described for lower canyon cores by Crémer et al. (1999) and Gerino et al. (1999). The lack of graded sediments (X-ray analysis and photograph) and the rather constant grain size (silty clay, mean between 6.5 and $7.8\ \mu\text{m}$; Fig. 2) confirm the absence of turbidite in the top of the sediment. The $^{234}\text{Th}_{\text{xs}}$ and $^{210}\text{Pb}_{\text{xs}}$ profiles lead to the same conclusions. In all our cores, these two radioactive species show a rapid downcore decrease. Moreover, there are no deeper secondary peaks such as those found in a

Table 3

Results of normalised principal component analysis based on the densities of *Melonis barleeanus*, *Globobulimina affinis*, *Chilostomella oolina* and the concentration of redox elements in the sediment

	PCA1	PCA2	PCA3						
(a)									
Eigenvalues column	3.9	2.2	1.3						
Percent of trace	39.1	21.8	13.5						
Cumulative percent of trace	39.1	61.0	74.4						
Variables									
<i>Globobulimina affinis</i>	−0.07	0.62	−0.18						
<i>Melonis barleeanus</i>	0.23	0.17	0.28						
<i>Chilostomella oolina</i>	−0.13	0.47	−0.50						
Oxygen	0.32	−0.31	−0.22						
Nitrate + nitrite	0.47	−0.15	−0.13						
Mn _{asc}	0.39	0.23	0.26						
Fe _{asc}	0.20	0.36	0.47						
Dissolved Mn	−0.42	0.09	0.13						
Dissolved Fe	−0.31	−0.06	0.52						
Ammonia	−0.38	−0.23	−0.01						
<i>C. oolina</i> <i>G. affinis</i> <i>M. barleeanus</i> Nitrate + nitrite Ammonia Dissolved Mn Dissolved Fe Fe _{asc} Mn _{asc} Oxygen									
(b)									
<i>C. oolina</i>	0.75	−0.03	−0.28	−0.07	0.24	−0.16	−0.03	−0.21	−0.25
<i>G. affinis</i>		−0.03	−0.28	−0.14	0.16	−0.07	0.33	0.19	−0.41
<i>M. barleeanus</i>			0.25	−0.31	−0.30	−0.22	0.29	0.47	0.00
Nitrate + nitrite				−0.67	−0.80	−0.54	0.16	0.58	0.71
Ammonia					0.42	0.36	−0.47	−0.65	−0.38
Dissolved Mn						0.58	−0.20	−0.50	−0.47
Dissolved Fe							0.06	−0.36	−0.35
Fe _{asc}								0.54	0.01
Mn _{asc}									0.20
Oxygen									

(a) Eigenvalues and variables loadings of the three significant axes. (b) Pearson's correlation coefficients between the densities of *Melonis barleeanus*, *Globobulimina affinis*, *Chilostomella oolina* (standardised for a 50 cm³ sediment volume) and redox species concentrations (ΣNO_3^- , NH_4^+ , Mn^{2+} , Fe^{2+} , Mn_{asc} , Fe_{asc} and dissolved oxygen). Bold values are significant at the 0.05 threshold level (bilateral test).

core of the Capbreton Canyon with recent turbiditic deposition (Mulder et al., 2001). Only the ²¹⁰Pb_{xs} profile obtained in April 2000 reveals an anomaly, between 2.5 and 7.5 cm depth, with relatively constant activity (~400 Bq kg^{−1}). However, this anomaly could be the result of active downmixing of superficial sediment by macrofauna (see below).

Since ²³⁴Th_{xs} has a short half-life (24.1 days) with respect to the burial rate resulting from continuous sediment input, the high ²³⁴Th_{xs} values

found at the sediment–water interface of all cores imply freshly deposited sediments with a total absence of erosional events. This suggests that the bottom current velocity in our study area (about 6 cm s^{−1} according to Durrieu de Madron et al., 1999) is too weak to cause erosion of the sediment–water interface. The different ²³⁴Th_{xs} values in the topmost sediments of the successive cores further suggest short-term variability of sediment supply or mixing intensity. The maximum sedimentation rates of 0.033 and

0.046 cm year⁻¹, based on the ²¹⁰Pb_{xs} profiles, are close to the value of 0.060 cm year⁻¹ found by Radakovitch and Heussner (1999) at a site close to station I. This very high sedimentation rate suggests a continuous succession of fine-grained, non-eroded sediments, caused by continuous deposits of suspended material. The 10 cm long core will probably represent only a few centuries of sedimentation history in the rather passive Cap-Ferret Canyon.

The centimetre-scale ovoid structures visible in the core collected in April 2000 are interpreted as cross-sections of macrofaunal burrows. Numerous cores sampled in Cap-Ferret Canyon exhibit similar structures resulting from bioturbation (Gerino et al., 1999). Abandoned burrows are very abundant in subsurface layers (between 5 and 20 cm depth). According to Gerino et al. (1999), this intense bioturbation, linked to a high macrofaunal density, reflects the high organic matter supply that characterise non-active (or passive) canyon environments. According to the same authors, intensive bioturbating activity would create a rather homogeneous mixed layer where burrows are permanently created and reworked (Young et al., 1985; Berger et al., 1979; Mullins et al., 1985; Gerino et al., 1999).

4.2. Biochemical characteristics of sedimentary organic matter

The organic carbon contents recorded during the present study are consistent with the data obtained by Etcheber et al. (1999) in the lower part of Cap-Ferret Canyon (an average of 1.35% at 2500–3000 m water depth). They confirm the organic enrichment of Cap-Ferret Canyon compared to other open slope sedimentary environments in the Bay of Biscay (e.g. sites F and H located at 1300 and 2000 m deep, respectively, average $C_{org} = 0.70\%$; unpublished data, Fig. 1).

The comparison of THAA and EHAA between our canyon station I and the open slope stations H and F is complicated by the fact that the stations were not sampled at the same time. Based on the concentrations measured at 5 stations sampled on 7 different occasions, it nevertheless appears that seasonal fluctuations in both THAA and EHAA

are relatively limited in comparison to spatial variability in the superficial sediments of the Bay of Biscay (Grémare, unpublished data). On the basis of similar evidence, Etcheber et al. (1999) already suggested that the quality and quantity of organic carbon in surface sediments of Cap-Ferret Canyon do not exhibit important seasonal changes. The comparison of THAA and EHAA concentrations supports the observations made for organic carbon. Concentrations of THAA and EHAA are lower at station F (20.0 and 5.6 nmol mg DW⁻¹, respectively) and higher at stations H and I (between 32.6 and 35.5 and between 8.3 and 8.5 nmol mg DW⁻¹, respectively). These concentrations are much higher than those reported earlier for the superficial sediments of the more oligotrophic Gulf of Lions (THAA between 7.5 and 24.1; EHAA between 1.6 and 5.9 nmol mg DW⁻¹, Grémare et al., 2002). However, THAA concentrations recorded during the present study are much lower than those available for superficial sediments of more productive areas (i.e., up to 57.5 and 135.0 nmol mg DW⁻¹ in the North Sea and the upwelling area off central Chile, respectively; Dauwe et al., 1999; Grémare, unpublished data).

EHAA/THAA ratios range from 27.8% at station F to 24.0% at station I with an intermediate value of 25.6% at station H. EHAA/THAA ratios are indicative of the nutritional value of sedimentary organic matter for primary consumers (Mayer et al., 1995). Based on a survey carried out on North Sea sediments, Dauwe et al. (1999) concluded that EHAA/THAA ratios of superficial sediments were between 14% in the final deposition area of particulate matter and 50% in the production area. This last figure is consistent with the average EHAA/THAA ratio of 41% measured at 6 stations located in the upwelling area off Central Chile (Grémare, unpublished). According to Dauwe et al. (1999) EHAA/THAA ratios between 21% and 28% are typical of transitional deposition areas. Similarly, Grémare et al. (2002) reported EHAA/THAA ratios between 16.9% and 29.6% in the superficial sediments of 19 stations located in the Gulf of Lions and interpreted these results as indicative of organic matter in an intermediate state of decay.

The presence of organic matter in an intermediate state of decay in Cap Ferret Canyon is in agreement with our knowledge about particle transfers in this area. Cap Ferret Canyon is located too far away from the continent to be directly fed by riverine sedimentary discharge (Ruch et al., 1993; Castaing et al., 1999). As discussed by Heussner et al. (1999) and Durrieu de Madron et al. (1999), lateral along-slope advection appears to be the dominant particle transport mechanism in this canyon, whereas sedimentary remobilisation by gravity, mass or turbidity flows is believed to be limited (Crémer et al., 1993, 1999). In the upper and lower parts of the canyon, particulate matter transport is mainly northward and due to along-slope bottom currents. Suspended particles feeding the canyon preferentially originate from a homogeneous source located on the shelf and upper slope (<380 m) south of Cap-Ferret Canyon. A secondary southern source (<1000 m depth) may provide supplementary sediment input to the upper part of the canyon (Radakovitch and Heussner, 1999; Heussner et al., 1999). In the canyon channels, high concentrations of suspended particles move downward along- or cross-slope, following a horizontal downstream-decreasing gradient (Heussner et al., 1999). In comparison with the adjacent open slope, organic matter concentrates in the Cap-Ferret depression (Crémer et al., 1999; Etcheber et al., 1999).

Both our sedimentological and biochemical data (C_{org} values two times higher without a notable change in the EHAA/THAA ratio) suggest that Cap-Ferret Canyon constitutes a depocenter for large quantities of reworked, intermediate quality organic matter.

4.3. Sediment biogeochemistry

It is commonly accepted that the input of organic matter to the sea floor controls the distribution of diagenetic species in the sediment. In all cores, we observe that dissolved O_2 concentrations decrease gradually below the sediment–water interface. Nitrate increases in the top of the oxic layer and then decreases below. It disappears completely in the upper part of the anoxic zone. In relation to the abrupt decrease of

Mn- and Fe-oxide and oxihydroxide levels around the zero oxygen boundary, dissolved Mn (Mn^{2+}) and Fe (Fe^{2+}) show remarkable increases in anoxic sediments. This pattern follows the well-established depth sequence (Froelich et al., 1979; Postma and Jakobsen, 1996). All these diagenetic reactions are accelerated by an order of magnitude through enzymatic catalysis by living organisms, particularly by prokaryote micro-organisms that use the chemical energy of organic and inorganic compounds for their cell functions (e.g. growth and division, movement, etc.). Whereas many heterotrophic bacteria that directly use the carbon from the organic matter (both aerobic and anaerobic organisms, such as denitrifying bacteria, Mn- or Fe-reducing bacteria, sulfate-reducing bacteria) are essential for remineralisation, chemolithoautotrophic bacteria play also an important role in mineral cycling, and particularly in the cycles of N- and S-species (Fenchel et al., 1998; Jørgensen, 2000). These autotrophic organisms, which gain their energy by chemical oxidation and do not depend on pre-existing organic matter, produce new bacterial biomass that becomes available for the fauna. Such chemolithoautotrophic metabolism has been observed for iron bacteria (*Ferrobacillus* sp., *Shewanella* sp.), which can oxidise Mn^{2+} and Fe^{2+} diffusing from anoxic sediments to the more superficial oxic layers (Fenchel et al., 1998; Jørgensen, 2000).

Concerning the distribution of the diagenetic species, most geochemical profiles (of the N-, Mn- and Fe-species) show perturbations, particularly between 4 and 8 cm, just as the $^{210}Pb_{\text{xs}}$ -profile (see above). The presence of a deep infaunal living holothurian (*Molpadia* sp.) in the 4–6 cm depth interval in one of the cores collected during April 2000 suggests a strong potential macrofaunal sediment disturbance at this depth in the sediment.

4.4. Faunal characteristics

4.4.1. Foraminiferal response to focusing of refractory organic matter

The benthic foraminiferal faunas of this 2800 m deep station located in Cap Ferret Canyon exhibit higher densities and species richness, when compared with deep open-slope faunas (Fontanier

et al., 2002). Two 72 cm² cores sampled at the open slope stations F (~1300 m) and H (~2000 m) contain 122 and 179 specimens (>150 µm fraction), respectively, whereas the four cores described in this paper yield between 242 and 554 specimens. Similarly, in summer 2003, a 2430 m deep open slope station (FP1) was sampled north of our study area (46°20'N–5°00'W). At this very comparable water depth, foraminiferal density is only about 70 individuals per 72 cm² (Appendix D).

Also, the faunal composition is very different between station I and the open slope stations. The relatively poor faunas from stations H and F contain about 80% of perforate taxa, and only about 10% of agglutinated taxa. The faunas, which are essentially restricted to the topmost two cm of sediment, are dominated by the surface dwelling taxa *U. peregrina* and *H. elegans*. These taxa represent more than 40% of total fauna at each station. Intermediate and deep infaunal taxa (e.g. *M. barleeanus*, *C. oolina* and *G. affinis*) are rare at station F (less than 8% of total fauna with only some specimens of *M. barleeanus*) and almost totally absent at station H (less than 5% of total fauna; Fontanier et al., 2002). Also at station FP1, the perforate group dominates the foraminiferal fauna (~65%), and shallow infaunal *H. elegans* and *Bulimina alazanensis* are the most abundant taxa (respectively, 11.3% and 10% of total fauna). At station FP1, *M. barleeanus*, the only deep infaunal taxon, represents only 1.3% of total fauna. These low percentages of intermediate and deep infaunal taxa are in accordance with the oligotrophic nature of these sites (Jorissen et al., 1995; Jorissen 1999a).

The foraminiferal faunas of our lower slope canyon station “I”, in contrast, are strongly dominated by agglutinated taxa (39–64%). The cores sampled in January 1999, June 1999 and April 2000 (core A) all show a significant presence of live foraminifera down to 9 cm in the sediment, and the absence of a conspicuous maximum at the top of the sediment. The perforate component of the fauna shows uncommonly high densities of intermediate (*M. barleeanus*) and deep infaunal species (*C. oolina* and *G. affinis*). With the exception of the second

core (B) taken in April 2000, *M. barleeanus*, *G. affinis* and *C. oolina* account for 28–48% of the total fauna, and even 67–77% of the perforate calcareous group. These observations agree with the results of a comparative study carried out by Schmiedl et al. (2000) on foraminiferal faunas from upper slope environments in the NW Mediterranean. In the axis of the Lacaze-Duthiers Canyon, foraminiferal density and species richness values recorded for a 900 m depth station are higher than those recorded at an open slope station at an equivalent water depth. Intermediate and deep infaunal taxa (e.g. *M. barleeanus*, *Reophax* spp., *C. oolina*, *G. affinis* and *Globobulimina pseudospinescens*) dominate the “canyon” faunas and constitute rather stable populations which seem to be adapted to live in the organic-rich sediments of canyon environments (Schmiedl et al., 2000).

Increased percentages of deep infaunal taxa are usually interpreted as indicative of increased organic input or low oxygen conditions (Corliss, 1985; Mackensen and Douglas, 1989; Sen Gupta and Machain-Castillo, 1993; Bernhard and Sen Gupta, 1999; De Rijk et al., 2000). Therefore, in paleoceanographical studies, fossil assemblages dominated by such taxa are assumed to point out severe dysoxia or anoxia in bottom water of deep-sea paleoenvironments (e.g. Ross and Kennett, 1984; Kaiho, 1994; Baas et al., 1998; Jorissen, 1999b). At station I, however, where bottom water oxygenations are always greater than 123 µmol l⁻¹ (2.7 ml l⁻¹), and where the vertical downward flux of labile organic matter should be relatively small, the apparently eutrophicated aspect of the benthic foraminiferal faunas may be explained by lateral or down-canyon advection of important amounts of partially reworked organic matter. This interpretation is supported by the elevated percentages of organic matter found in the superficial and downcore sediments, which have also been recorded in the Lacaze-Duthiers Canyon (Schmiedl et al., 2000). As previously discussed, this already partially degraded organic matter will largely bypass the oxic niches at the sediment–water interface, and will be bioturbated into the deeper dysoxic and anoxic sediment layers (Carney, 1989). There, it will be

subject to further degradation by dysaerobic and anaerobic organoheterotrophic bacterial stocks (Fenchel and Finlay, 1995). Also, in the Hellenic and Pliny Trenches, bacterial biomass and activities are higher than in the surrounding open-slope areas (Boetius et al., 1996), showing an accumulation of metabolisable organic material in depressional areas. The conversion of more or less refractory organic matter into bacterial biomass in these confined environments may open ecological niches for consistent intermediate or deep infaunal foraminiferal populations living in symbiosis with bacteria or feeding directly on the bacterial stocks or on their breakup products (Bernhard and Reimers, 1991; Bernhard, 1993, 1996, 2003; Bernhard and Sen Gupta, 1999). Chemolithoautotrophic bacterial consortia, such as iron or manganese oxidising and nitrifying bacteria, may also take advantage of a particular redox energetic background by converting newly reduced species (Fe^{2+} and Mn^{2+}) into oxidised compounds.

As already shown by Corliss (1985), Corliss and Emerson (1990), Jorissen et al. (1995, 1998, 1999a) and Fontanier et al. (2002, 2003), *M. barleeanus* lives mainly in the dysoxic part of the sediment. In our three unbioturbated cores without active burrows, it settles between 2 and 4 cm depth, exactly where oxygen values decrease from about $50\text{--}5\ \mu\text{mol l}^{-1}$ and where bacterially mediated manganese (and iron) precipitation preferentially takes place (Figs. 4a–6c; Table 3a and b). These observations support the suggestion of Jorissen et al. (1998) of a relationship between the microhabitat of *M. barleeanus* and the presence of bacterial consortia. *M. barleeanus* may use bacterial stocks as a direct food source, or entertain symbiotic relationships with chemolithoautotrophic bacteria. Such life strategies have been envisaged by other authors (e.g. Bernhard and Reimers, 1991; Bernhard, 1993, 1996, 2003; Bernhard and Sen Gupta, 1999; Bernhard et al., 2000). Symbiosis between chemosynthetic bacteria and marine benthic organisms is well known (Fisher, 1990; Vacelet et al., 1996; Dubilier et al., 2001). By chemosynthesis, bacteria can fix inorganic carbon and nutrients from interstitial waters or from metabolic waste pro-

duced by their host. They produce bacteriogenic organic compounds, which can subsequently be used as food by their host (Fisher and Childress, 1986). A foraminiferal host would therefore no longer need to take up organic matter from its sedimentary biotope and could use dissolved oxygen from interstitial waters to degrade bacteriogenic and internal organic compounds. Conversely, bacterial consortia could benefit by obtaining a stable environment for growth and reproduction. *M. barleeanus* is obviously not directly dependent on a supply of freshly deposited labile organic matter and should therefore not show a strong response to seasonal input of phytodetritus to the ocean floor (Jorissen et al., 1998; Fontanier et al., 2003).

G. affinis lives in deep infaunal dysoxic and anoxic microhabitats, close to and below the zero oxygen level. Such a deep infaunal microhabitat is well known for *Globobulimina* spp. (e.g. Corliss, 1985, 1991; Mackensen and Douglas, 1989; Jorissen et al., 1995, 1998; Schmiedl et al., 2000; Fontanier et al., 2002, 2003). In our study, the varying position with respect to the zero oxygen level may be real, but can also be an artefact due to the fact that different cores were used for faunal and chemical analysis. Nevertheless, there is strong evidence that this species is able to live in totally anoxic sediment and must therefore be a facultative anaerobe (Bernhard, 1993, 1996). In all our cores the density maximum of *G. affinis* coincides with anoxic/dysoxic zones where Fe^{2+} oxidation occurs, suggesting a possible trophic relation with chemolithoautotrophic bacteria involved in this reaction (Figs. 4a–6c; Table 3a and b). It may also be envisaged that *G. affinis* lives in symbiosis with these prokaryotic and chemoautotrophic organisms capable of using reduced iron and manganese as energy sources. All available data show that *M. barleeanus* and *G. affinis* behave as highly specialised deep infaunal species that might require rather strict and stable bio-redox environments where predation and competition are strongly limited (e.g. Mackensen and Douglas, 1989; Van der Zwaan et al., 1999). We think that they depend on the presence of large quantities of low and intermediate quality organic matter, suggest-

ing a more or less complete decoupling between the seasonal labile organic matter flux to the sediment–water interface and the behaviour of these deep infaunal taxa.

We are aware that most of our ecological interpretations are based on a comparison between in situ faunistic data (density, microhabitat, composition) and geochemical measurements (redox elements and organic matter). There is still limited evidence for deep-sea foraminifera–bacteria trophic and symbiotic interaction (Bernhard and Reimers, 1991; Bernhard, 1993, 2003; Bernhard et al., 2000). To improve our knowledge about the controversial ecology of intermediate and deep infaunal taxa (e.g. *Melonis*, *Globobulimina* and *Chilostomella*), TEM observations on “in situ” or cultured deep-sea foraminifera are necessary. The identification of free symbionts within foraminiferal protoplasm would be a first step to confirm the assumed symbiotic linkage between chemolithoautotrophic bacteria and infaunal foraminiferal taxa. Moreover, laboratory experiments can help to discriminate the impact of biotic and abiotic parameters on deep-sea foraminifera (Gross, 2000; Heinz et al., 2001, 2002; Ernst and van der Zwaan, 2004; Langezaal et al., 2004).

4.4.2. Foraminiferal response to export of labile organic matter

As discussed before, the benthic foraminiferal faunas seem to be strongly adapted to profit maximally from important supplies of reworked organic matter by downslope or lateral advection, possibly facilitated by an intermediate step of bacterial activity. One may ask whether the input and temporal variability of probably much less important quantities of fresh phytodetritus provokes nevertheless a recognisable response of the foraminifera living close to the sediment surface. An important phytoplankton bloom generally occurs in the surface waters of the Bay of Biscay between March and May (Tréguer et al., 1979; Laborde et al., 1999; Fontanier et al., 2003). Therefore, our cores sampled in April and, in a lesser degree, in June, could represent conditions of increased supply of labile organic matter to the sea floor.

The presence of a phytodetritus deposit in the weeks before sampling could be corroborated by the oxygen concentrations in the core sampled in April 2000. Bottom water oxygen concentration was only $123 \mu\text{mol l}^{-1}$ (2.7 ml l^{-1}), and the zero oxygen level was already encountered at 3.8 cm, suggesting a period of strongly increased benthic respiration rates immediately prior to sampling.

In general, the foraminiferal faunas belonging to the $>150 \mu\text{m}$ fraction are surprisingly poor in the top sediment. The usual maximum close to the sediment–water interface is even absent in the cores sampled in January 1999, June 1999 and April 2000 (core A). Only the core with an active burrow sampled in April 2000 (core B) exhibits a clear superficial density maximum (Fig. 8). The latter core has by far the richest fauna, which suggests that the surface maximum could indeed be a response to the recent input of labile organic matter. However, the large differences between the surface faunas found in the two cores sampled in April 2000 may suggest important small scale patchiness related to putative spatially heterogeneous phytodetritus deposits, but can also be explained as the result of a marked “gardening” effect in core B, related to the presence of a holothurian.

In the $63\text{--}150 \mu\text{m}$ fraction, the highest foraminiferal density was found in the top first cm of the bioturbated core sampled in April 2000 (core B). In this core, the fauna shows elevated percentages of *N. pusillus*, *T. globigeriniformis*, *Hippocrepinella* sp. and *E. exigua*. For several of these taxa, a marked opportunistic life style has been described or suggested (e.g. Gooday, 1988; Gooday and Lamshead, 1989; Jorissen et al., 1992; Silva et al., 1996; Ohga and Kitazato, 1997; Jannink et al., 1998; Loubere, 1998; Jorissen, 1999b; Heinz et al., 2001; Gooday and Hughes, 2002; Fontanier et al., 2003). Nevertheless, the absolute densities of these taxa are not excessively higher than foraminiferal densities recorded for the three other cores sampled at station I, and they are relatively low in comparison with the huge peaks of *E. exigua* observed at a 550 m depth open slope station during the 2000 spring bloom (Fontanier et al., 2003).

We conclude that in neither of the two size fractions is a clear foraminiferal response to putative phytodetritus deposits related to the beginning of the 2000 spring bloom is perceptible.

5. Conclusions

The sedimentary environment of our 2800 m deep lower station in Cap Ferret Canyon is characterised by the rapid accumulation of fine-grained sediments with an important component of reworked, partially degraded organic matter. The vertical flux of labile organic matter from the overlying surface waters seems to represent only a minor part of the total organic input. Benthic foraminiferal faunas show a dual response to these particular conditions:

- (1) At the sediment–water interface, the flux of labile organic matter is usually too low to sustain important epifaunal/shallow infaunal foraminiferal standing stocks.
- (2) The continuous input of large amounts of partially degraded organic matter, characteristic of Cap Ferret Canyon, causes an enrichment in the deeper sediment layers, where the ongoing decay of the organic matter results in a particularly well-established succession of redox zones. Benthic foraminiferal faunas seem to respond to this system with a very strong dominance of intermediate and deep infaunal taxa. The vertical zonation of the two principal taxa concerned shows a strong similarity with the exact location of major biogeochemical species. *M. barleeanus* is systematically found in the dysoxic part of the sediment ($<50 \mu\text{mol l}^{-1}$) whereas *G. affinis* lives around as well as below the zero oxygen boundary. Both taxa thrive in sediment layers where bacterially mediated manganese and iron precipitation occurs. The population dynamics of both species appears to be more

or less independent of the limited vertical flux of labile organic matter to the seafloor.

- (3) The peculiar fauna found at this lower canyon station, with its uncommonly high proportions of deep infaunal species complicates the use of these taxa for paleoceanographic reconstructions. Very often, fossil assemblages dominated by these taxa are interpreted as characteristic of highly eutrophic (important input of labile organic matter) or severely dysoxic bottom water conditions. The formation of such an assemblage in a well-oxygenated environment with important focusing of partially degraded organic matter shows that such fossil assemblages can also be formed in rather well-oxygenated settings without a strong vertical flux of labile organic matter.

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Appendix A

Species of benthic foraminifera recognised at station I from the Bay of Biscay, with references to plates and figures in the literature on Atlantic and Mediterranean foraminifera.

Species	References
<i>Adercotryma glomerata</i> (Brady), 1878	Jones (1994), pl. 34, Figs. 15–18
<i>Ammobaculites agglutinans</i> (d'Orbigny), 1846	Hess (1998), pl. 4, Fig. 4
<i>Bolivina pseudoplicata</i> Heron-Allen & Earland 1930	Schiebel (1992), pl. 8, Fig. 8a–b
<i>Bulimina alazanensis</i> Cushman, 1927	Schiebel (1992), pl. 2, Fig. 5
<i>Bulimina inflata</i> Seguenza, 1862	Van Leeuwen (1989), pl. 8, Fig. 4
<i>Bulimina marginata</i> d'Orbigny, 1826	Hess (1998), pl. 10, Fig. 7
<i>Cassidulina carinata</i> Silvestri, 1896	Phleger et al. (1953), pl. 9, Figs. 32–37
<i>Cassidulina crassa</i> d'Orbigny, 1839	Jones (1994), pl. 54, Fig. 4 and 5
<i>Chilostomella oolina</i> Schwager, 1878	Jones (1994), pl. 55, Figs. 12–14
<i>Cibicides lobatulus</i> Walker & Jacob, 1798	Jones (1994), pl. 92, Fig. 10
<i>Cibicides wuellerstorfi</i> (Schwager), 1866	Van Leeuwen (1989), pl. 10, Figs. 1–9
<i>Cibicidoides pachydermus</i> (Rzehac), 1886	Jones (1994), pl. 94, Fig. 9
<i>Cibicidoides robertsonianus</i> (Brady), 1881	Van Leeuwen (1989), pl. 9, Figs. 1–3
<i>Cornuspira involvens</i> (Reuss), 1950	Jones (1994), pl. 11, Figs. 1–3
<i>Cribostromoides subglobosus</i> (Cushman), 1910	Jones (1994), pl. 34, Figs. 8–10
<i>Cribostromoides wiesneri</i> (Parr), 1950	Jones (1994), pl. 40, Fig. 14 and 15
<i>Eggerella bradyi</i> (Cushman), 1911	Jones (1994), pl. 47, Figs. 4–7
<i>Eggerella scabra</i> (Williamson), 1858	Jones (1994), pl. 47, Figs. 15–17
<i>Epistominella exigua</i> (Brady), 1884	Schiebel (1992), pl. 5, Fig. 9
<i>Globobulimina affinis</i> (d'Orbigny), 1839	Phleger et al. (1953), pl. 6, Fig. 32
<i>Globocassidulina subglobosa</i> (Brady), 1881	Jones (1994), pl. 54, Fig. 17
<i>Glomospira charoides</i> Jones & Parker, 1860	Phleger et al. (1953), pl. 5, Fig. 1
<i>Glomospira gordialis</i> Jones & Parker, 1860	Phleger et al. (1953), pl. 5, Fig. 2
<i>Gyroidina altiformis</i> Stewart & Stewart, 1930	Jorissen (1987), pl. 1, Fig. 11
<i>Gyroidina orbicularis</i> (sensu Parker, Jones and Brady), 1865	Jones (1994), pl. 115, Fig. 6
<i>Gyroidina umbonata</i> (Silvestri), 1898	Parker (1958), pl. 3, Fig. 19 and 20
<i>Gyroidinoides soldanii</i> (d'Orbigny), 1826	Jones (1994), pl. 107, Fig. 6 and 7
<i>Hoeglundina elegans</i> (d'Orbigny), 1826	Phleger et al. (1953), pl. 9, Fig. 24 and 25
<i>Lagenammmina tubulata</i> (Rhumbler), 1931	Hess (1998), pl. 2, Fig. 10
<i>Lenticulina gibba</i> (d'Orbigny), 1839	Hess (1998), pl. 13, Fig. 1
<i>Melonis barieeanus</i> (Williamson), 1858	Van Leeuwen (1989), pl. 13, Fig. 1 and 2
<i>Melonis pompilioides</i> (Fichtel and Moll), 1798	Jones (1994), pl. 109, Fig. 10 and 11
<i>Nonionella turgida</i> (Williamson), 1858	Jones (1994), pl. 109, Figs. 17–19
<i>Nuttallides pusillus</i> (Parr), 1950	Phleger et al. (1953), pl. 9, Fig. 5 and 6
<i>Nuttallides umboniferus</i> (Cushman), 1933	Van Leeuwen (1989), pl. 15, Figs. 11–13; pl. 16, Figs. 1–7
<i>Parafissurina lateralis</i> (Cushman), 1913	Jones (1994), pl. 56, Fig. 17 and 18

<i>Pullenia bulloides</i> (d'Orbigny), 1826	Phleger et al. (1953), pl. 10, Fig. 19
<i>Pullenia quinqueloba</i> (Reuss), 1851	Jones (1994), pl. 84, Fig. 14 and 15
<i>Pyrgo depressa</i> (d'Orbigny), 1826	Jones (1994), pl. 2, Figs. 12, 16 and 17
<i>Pyrgo elongata</i> (d'Orbigny), 1826	Hess (1998), pl. 9, Fig. 5
<i>Pyrgo murrhina</i> (Schwager), 1866	Hess (1998), pl. 9, Fig. 1
<i>Pyrgo subsphaerica</i> d'Orbigny, 1839	Cushman (1929), pl. 18, Fig 1 and 2
<i>Quinqueloculina seminula</i> (Linné), 1758	Jones (1994), pl. 5, Fig. 6
<i>Reophax bilocularis</i> Flint, 1899	Hess (1998), pl. 2, Fig. 13 and 14
<i>Reophax calcareus</i> (Cushman), 1947	Timm (1992), pl. 2, Fig.2a–b
<i>Reophax dentiliniiformis</i> Brady, 1881	Jones (1994), pl. 30, Fig. 21 and 22
<i>Reophax gausisicus</i> (Rhumbler), 1913	Jones (1994), pl. 31, Fig. 1 and 2, ?5
<i>Reophax guttiferus</i> Brady, 1881	Jones (1994), pl. 31, Fig. 10–15
<i>Reophax micaceus</i> Eerland 1934	Schiebel (1992), pl. 8, Fig. 7
<i>Reophax nodulosus</i> Brady, 1879	Jones (1994), pl. 31, Figs. 6–9
<i>Reophax scorpiurus</i> Montfort, 1808	Loeblich and Tappan (1988a, b), pl. 44, Figs. 1–3
<i>Reophax spiculifer</i> Brady, 1879	Jones (1994), pl. 31, Fig. 16 and 17
<i>Reophax subfusiformis</i> Eerland, 1933	Schiebel (1992), pl. 8, Fig. 8
<i>Sphaeroidina bulloides</i> Deshayes, 1832	Jones (1994), pl. 84, Figs 1–5, ?6–7
<i>Sigmoilopsis schlumbergeri</i> Silvestri, 1904	Jones (1994), pl. 8, Figs. 1–4
<i>Technitella legumen</i> Norman, 1878	Jones (1994), pl. 25, Figs. 8–10
<i>Technitella melo</i> Norman, 1978	Jones (1994), pl. 25, Fig. 7
<i>Thurammia albicans</i> Brady, 1879	Jones (1994), pl. 37, Fig. 2–7
<i>Trifarina angulosa</i> (Williamson), 1858	Jones (1994), pl, 74, Fig. 17 and 18
<i>Triloculina trigonula</i> (Lamarck), 1804	Jones (1994), pl.3, Fig. 15 and 16
<i>Trochammina globigenniformis</i> (Parker & Jones), 1865	Timm (1992), pl. 4, Fig. 2a–b
<i>Uvigerina peregrina</i> Cushman, 1923	Van der Zwaan et al. (1986), pl. 1, Figs.1–6

Appendix B

Census data for live benthic foraminifera in the 63–150 µm size fraction in the first cm of all 4 cores.

Taxa	January 1999		June 1999		April 2000, core A		April 2000, core B	
	Total	%	Total	%	Total	%	Total	%
Perforate								
Indet.	2	0.87	1	0.40	6	2.12	1	0.22
<i>Anomalinoidea</i> sp.					16	5.65	3	0.65
<i>Bolivina</i> sp.			4	1.58	1	0.35	2	0.43
<i>Bolivina</i> sp.1							1	0.22
<i>Bolivina pseudoplicata</i>	1	0.43	7	2.77	4	1.41	13	2.80
<i>Bulimina</i> sp.1	2	0.87	3	1.19	1	0.35	12	2.59
<i>Bulimina alazanensis</i>	2	0.67	2	0.79	2	0.71	3	0.65
<i>Bulimina inflata</i>	1	0.43	5	1.98	2	0.71	6	1.30

<i>Bulimina marginata</i>			1	0.40	1	0.35	3	0.65
<i>Cassidulina carinata</i>	1	0.43	2	0.79	2	0.71	1	0.22
<i>Cassidulina crassa</i>	2	0.87	7	2.77	19	6.71	26	5.60
<i>Ceratobulimina</i> sp.	2	0.87			7	2.47	1	0.22
<i>Cibicides</i> sp.					3	1.06	1	0.22
<i>Cibicides lobatulus</i>	1	0.43					1	0.22
<i>Cibicidoides robertsonianus</i>							1	0.22
<i>Epistominella exigua</i>	12	5.19	16	6.32	15	5.30	31	6.68
<i>Fissurina</i> sp.			1	0.40				
<i>Globocassidulina subglobosa</i>	3	1.30	3	1.19	18	6.36	5	1.08
<i>Gyroidina</i> sp.	1	0.43	1	0.40			2	0.43
<i>Gyroidina</i> sp.1	1	0.43	2	0.79				
<i>Gyroidina orbicularis</i>			3	1.19	2	0.71	2	0.43
<i>Gyroidina umbonata</i>	7	3.03	8	3.16	6	2.12	24	5.17
<i>Hoeglundina elegans</i>			4	1.58			3	0.65
<i>Lagena</i> sp.					1	0.35	1	0.22
<i>Nonionella</i> sp.	1	0.43			4	1.41	2	0.43
<i>Nuttallides pusillus</i>	6	2.60	27	10.67	11	3.89	47	10.13
<i>Nuttallides umboniferus</i>							2	0.43
<i>Oridorsalis umbonatus</i>					1	0.35		
<i>Parafissurina</i> sp.	2	0.87			1	0.35	3	0.65
<i>Pullenia</i> sp.	3	1.30						
<i>Pullenia</i> sp.1	10	4.33	1	0.40	11	3.89	3	0.65
<i>Pullenia bulloides</i>	1	0.43	1	0.40			1	0.22
<i>Pullenia quinqueloba</i>							1	0.22
<i>Robertinoides</i> sp.			2	0.79				
<i>Stainforthia</i> sp.					1	0.35	2	0.43
<i>Trifarina angulosa</i>			6	2.37			16	3.45
<i>Uvigerina</i> sp.	1	0.43					1	0.22
<i>Uvigerina</i> sp.1							1	0.22
<i>Uvigerina peregrina</i>	3	1.30	1	0.40	4	1.41	5	1.08
Porcellaneous								
Indet.	3	1.30			1	0.35	2	0.43
<i>Cornuspira</i> sp.	2	0.87	1	0.40	1	0.35		
<i>Miliolinella</i> sp.					1	0.35	1	0.22
<i>Ophtalmidium</i> sp.	3	1.30					1	0.22
<i>Pyrgo</i> sp.							1	0.22
<i>Pyrgo elongata</i>							2	0.43
<i>Quinqueloculina</i> sp.	1	0.43	4	1.58	4	1.41	33	7.11
<i>Sigmoilina</i> sp.			1	0.40			1	0.22
<i>Triloculina</i> sp.							1	0.22
Non-fossilising agglutinated								
Indet.			1	0.40			1	0.22
<i>Adercotryma glomerata</i>	15	6.49	4	1.58	4	1.41	10	2.16
<i>Ammobaculites</i> sp.	1	0.43	1	0.40			4	0.86
<i>Cribrostomoides</i> sp.							1	0.22
<i>Cribrostomoides subglobosus</i>			7	2.77	22	7.77	13	2.80

<i>Eggerella scabra</i>					1	0.35	2	0.43
<i>Hippocrepinella</i> sp.	12	5.19	34	13.44	10	3.53	43	9.27
<i>Karrerulina</i> sp.			1	0.40	2	0.71		
<i>Psammosphaera</i> sp.	2	0.87	5	1.98	3	1.06	1	0.22
<i>Pseudotextularia</i> sp.					1	0.35	1	0.22
<i>Recurvoides</i> sp.					2	0.71		
<i>Reophax</i> sp.	2	0.87	4	1.58	1	0.35		
<i>Reophax</i> sp.3			1	0.40	1	0.35		
<i>Reophax bilocularis</i>	28	12.12	9	3.56	4	1.41	18	3.88
<i>Reophax calcareous</i>	2	0.87						
<i>Reophax dentaliniformis</i>							2	0.43
<i>Reophax guttiferus</i>	55	23.81	28	11.07	15	5.30	26	5.60
<i>Reophax scorpiurus</i>	19	8.23	16	6.32	45	15.90	16	3.45
<i>Spiroplectammina</i> sp.	3	1.30			8	2.83	4	0.86
<i>Technitella melo</i>							1	0.22
<i>Trochammina</i> sp.			2	0.79				
<i>Trochammina</i> sp.1	2	0.87	2	0.79	3	1.06	2	0.43
<i>Trochammina globigeriniformis</i>	16	6.93	24	9.49	13	4.59	47	10.13
Fossilising agglutinated								
<i>Eggerella bradyi</i>			3	1.19	1	0.35		
<i>Sigmoilopsis schlumbergeri</i>							1	0.22
Soft-shelled								
Indet.					1	0.35	2	0.43
Total live foraminifera	231	100.00	253	100.00	283	100.00	464	100.00
Nbr species	36		42		43		57	
Ostracoda	6		4		5		2	
Arborescent indet.					2			
<i>Glomospira</i> spp.	3				4		5	

N.B.: numbers are not standardised for sediment volume.

Appendix C

Census data for live benthic foraminifera in the >150 µm size fraction for all 4 cores.

January 1999																		
Depth	0–0.25	0.25–0.5	0.5–0.75	0.75–1	1–1.5	1.5–2	2–2.5	2.5–3	3–3.5	3.5–4	4–5	5–7	6–7	7–8	8–9	9–10	Total	%
Perforate																		
Indet.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
<i>Bulmina inflata</i>	0	0	0	0	0	0	1	0	0	0	0	(1)	0	0	0	0	2	0.83
<i>Chilostomella oolina</i>	0	0	0	0	0	1	0	0	2	2	1	1	0	(1)	0	0	8	3.31
<i>Cibicides wuellerstorfi</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
<i>Globobulimina affinis</i>	0	0	0	0	0	0	0	0	0	21	23	7	2	4	1	0	58	23.97
<i>Gyroidina orbicularis</i>	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	3	1.24
<i>Hoeglundina elegans</i>	1	2	3	1	0	1	0	0	0	0	0	0	0	0	0	0	8	3.31
<i>Melonis barleanus</i>	0	1	0	1	1	2	5	5	13	9	1	0	0	0	0	0	38	15.70
<i>Nonionella</i> sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
<i>Parafissurina lateralis</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.41
<i>Pullenia quinqueloba</i>	0	0	0	0	1	0	0	0	0	(1)	0	0	0	0	0	0	2	0.83
<i>Uvigerina</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0.41
<i>Uvigerina peregrina</i>	4	5	3	0	0	0	0	0	0	0	0	0	0	0	0	0	12	4.96
Porcellaneous																		
<i>Quinqueloculina seminula</i>	0	1	2	2	0	0	0	0	0	0	0	0	0	0	0	0	5	2.07
<i>Quinqueloculina</i> sp.1	0	0	0	1	3	0	1	0	0	0	0	0	0	0	0	0	5	2.07
<i>Quinqueloculina</i> sp.2	0	0	0	0	1	1		0	0	0	0	0	0	0	0	0	2	0.83
<i>Triloculina trigonula</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
Non-fossilising agglutinated																		
Indet.	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	3	1.24
Agglut. indet sp.B	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.41
<i>Adercotryma glomerata</i>	0	0	0	0	0	0	0	0	0		1	0	0	0	0	0	1	0.41
<i>Ammobaculites agglutinans</i>	2	1	8	6	2	0	1	0	0	0	0	0	0	0	0	0	20	8.26
<i>Cribrostomoides subglobosus</i>	1	0	2	1	0	1	0	0	0	(1)	0	0	0	0	0	0	6	2.48
<i>Haplophragmoides</i> sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.41
<i>Recurvoides</i> sp.	0	2	0	1	1	2	0	0	0	0	0	0	0	0	0	0	6	2.48
<i>Reophax</i> sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.41
<i>Reophax dentaliniformis</i>	0	0	2	1	2	3	4	2	1	4	0	0	0	0	0	0	19	7.85
<i>Reophax nodulosus</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.41
<i>Reophax scorpiurus</i>	1	4	2	1	5	8	8	4	0	1	0	0	0	0	0	0	34	14.05
<i>Reophax suhfusiformis</i>	0	0	0	0	n	0	0	0	0	0	0	0	0	0	0	1	1	0.41

Total live foraminifera	11	18	23	16	20	19	23	11	18	39	25	10	3	5	1	1	242	100.00
Nbr species	6	9	8	9	11	8	7	3	5	7	3	4	1	2	1	1	27	
Ostracoda	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	
Arborescent indet.	6	15	10	16	14	10	7	3	8	0	3	0	3	0	0	0	95	
June 1999																		
Perforate																		
Indet.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
<i>Bulimina inflata</i>	1	1	1	0	1	0	0	0	0	0	0	0	(1)	0	0	0	5	1.21
<i>Chilostomella oolina</i>	0	0	0	0	1	0	0	1	0	0	10	16	8	2	0	0	38	9.20
<i>Cibicides lobatulus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
<i>Globobulimina affinis</i>	0	0	0	0	0	0	0	0	2	1	32	30	9	0	0	0	74	17.92
<i>Gyroidina</i> sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.24
<i>Gyroidina orbicularis</i>	0	0	1	0	0	0	0	(1)	0	0	0	0	0	0	0	0	2	0.48
<i>Gyroidinoides soldanii</i>	1	0	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	2	0.48
<i>Hoaglundina elegans</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
<i>Melonis barleeanus</i>	0	0	0	1	0	0	10	15	5	4	1	0	0	0	0	0	36	8.62
<i>Nonionella atlantica</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
<i>Parafissurina lateralis</i>	1	0	0	0	0	0	0	(1)	0	0	0	0	0	0	0	0	2	0.48
<i>Pullenia bulloides</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.24
<i>Pullenia quinqueloba</i>	0	0	0	0	0	0	2	5	1	0	0	0	0	0	0	0	8	1.94
<i>Robertina</i> sp.	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	4	0.97
<i>Robertinoides</i> sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
<i>Uvigerina peregrina</i>	2	1	3	1	4	1	1	0	0	0	0	0	0	0	0	0	13	3.15
Porcellaneous																		
<i>Cornuspira involvens</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0.24
<i>Pyrgo depressa</i>	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0.48
<i>Pyrgo elongata</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.24
<i>Pyrgo murrhina</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
<i>Quinqueloculina seminula</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
<i>Quinqueloculina</i> sp.1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
<i>Triloculina</i> sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
<i>Triloculina trigonula</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Non-fossilising agglutinated																		
Indet.	2	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	5	1.21
Agglut. sp.C	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	4	0.97
<i>Adercotryma glomerata</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.24
<i>Ammobaculites agglutinans</i>	6	3	4	2	1	0	0	3	0	0	0	0	0	0	0	0	19	4.60
<i>Cribrostomoides subglobosus</i>	6	4	5	3	11	3	3	5	0	0	1	1	0	0	0	0	42	10.17
<i>Cribrostomoides wiesneri</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.24

<i>Cystamina</i> sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0.24	
<i>Haplophragmoides</i> sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0.24	
<i>Hippocrepinella</i> sp.	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0.48	
<i>Hormosina</i> sp.	1	0	3	0	1	0	0	0	0	0	0	0	0	0	0	5	1.21	
<i>Karrerulina</i> sp.	0	2	2	1	0	2	2	0	0	(1)	0	0	0	0	0	10	2.42	
<i>Psammosphaera</i> sp.	6	4	1	1	0	2	1	1	1	0	0	(1)	0	(1)	0	19	4.60	
<i>Recurvoides</i> sp.	0	1	1	5	1	3	2	0	0	0	0	0	0	0	0	13	3.15	
<i>Reophax</i> sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24	
<i>Reophax</i> sp.3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.24	
<i>Reophax bilocularis</i>	2	0	0	8	7	2	0	0	1	0	0	2	2	0	(1)	0	25	6.05
<i>Reophax calcareus</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24	
<i>Reophax dentaliniformis</i>	1	1	0	1	0	0	0	1	1	1	0	0	0	0	0	6	1.45	
<i>Reophax gaussicus</i>	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	3	0.73	
<i>Reophax guttiferus</i>	2	1	5	1	0	0	0	0	0	0	0	0	0	0	0	9	2.18	
<i>Reophax micaceus</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.24	
<i>Reophax scorpiurus</i>	2	3	3	1	8	6	8	4	1	2	0	0	0	0	0	38	9.20	
<i>Technitella legumen</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24	
<i>Technitella melo</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24	
Fossilising agglutinated																		
<i>Eggerella bradyi</i>	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	4	0.97	
<i>Sigmoilopsis schlumbergeri</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.24	
Total live foraminifera	37	26	36	29	38	23	37	43	15	12	45	50	20	3	1	0	413	100.00
Nbr species	16	14	18	14	12	9	15	13	9	7	5	5	4	2	1	0	49	
<i>Glomospira</i> spp.	0	1	0	1	1	2	1	4	3	2	4	4	3	3	1	0	30	
Ostracoda	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	3	
Arborescent indet.	1	10	27	19	18	12	13	5	11	0	0	0	0	0	0	116		
April 2000, core A																		
Perforate																		
<i>Bulimina alazanensis</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41	
<i>Bulimina inflata</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	(1)	0	2	0.82
<i>Chilostomella oolina</i>	0	0	0	0	1	1	0	0	0	1	0	0	1	1	0	0	5	2.06
<i>Cibicides lobatulus</i>	2	0	0	5	0	0	0	0	0	0	0	0	0	0	0	7	2.88	
<i>Cibicides wuellerstorti</i>	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1.23	
<i>Cibicidoides robertsonianus</i>	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0.82	
<i>Fissurina</i> sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41	
<i>Fissurina</i> sp.1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0.41	
<i>Globobulimina affinis</i>	0	0	0	0	0	0	0	0	4	0	7	10	9	13	14	0	57	23.46
<i>Gyroidina altiformis</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41	
<i>Gyroidina orbicularis</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.41	

<i>Gyroidinoides soldanii</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.41
<i>Hoeglundina elegans</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0.41
<i>Lagena</i> sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
<i>Melonis barleeanus</i>	0	0	0	0	1	1	3	1	1	0	0	0	0	0	0	7	2.88
<i>Melonis pompilioides</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
<i>Nonionella atlantica</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0.82
<i>Parafissurina lateralis</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0.41
<i>Pullenia quinqueloba</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0.41
<i>Pullenia</i> sp.1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.82
<i>Robertinoides</i> sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.41
<i>Sphaeroidina bulloides</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.41
<i>Uvigerina</i> sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0.41
<i>Uvigerina peregrina</i>	0	0	0	0	0	0	1	0	0	0	0	0	(1)	0	0	2	0.82
Porcellaneous																	
<i>Comuspira involvens</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0.41
<i>Pyrgo</i> sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.41
<i>Pyrgo depressa</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.82
<i>Pyrgo elongata</i>	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	3	1.23
<i>Pyrgo subsphaerica</i>	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	4	1.65
<i>Quinqueloculina seminula</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
<i>Quinqueloculina</i> sp.1	2	3	0	2	1	0	0	0	0	0	0	0	0	0	0	8	3.29
<i>Quinqueloculina</i> sp.2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2	0.82
Non-fossilising agglutinated																	
Indet.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.41
Agglut. sp.C	2	0	1	1	3	0	0	0	0	0	0	0	0	1	0	8	3.29
<i>Adercotryma glomerata</i>	0	0	0	0	1	0	0	0	3	0	0	0	0	0	0	4	1.65
<i>Ammobaculites agglutinans</i>	0	2	1	0	2	1	1	2	1	0	0	(1)	0	0	0	11	4.53
<i>Cribrostomoides</i> sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.41
<i>Cribrostomoides subglobosus</i>	1	0	2	2	3	3	2	3	4	0	0	(1)	0	0	0	21	8.64
<i>Haplophragmoides</i> sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0.41
<i>Hippocrepinella</i> sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
<i>Hormosina</i> sp.	1	0	0	1	5	0	0	0	(1)	0	0	0	0	0	0	8	3.29
<i>Karrerulina</i> sp.	0	1	3	1	2	0	1	0	0	0	0	0	0	0	0	8	3.29
<i>Psammosphaera</i> sp.	1	0	1	0	1	0	0	0	0	0	0	0	0	2	0	5	2.06
<i>Recurvoides</i> sp.	0	0	0	2	1	1	0	0	0	0	0	0	0	0	0	4	1.65
<i>Reophax</i> sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	(1)	0	2	0.82
<i>Reophax</i> sp.3	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0.82
<i>Reophax bilocularis</i>	5	2	2	1	0	0	0	0	0	0	0	0	0	0	0	10	4.12
<i>Reophax dentaliniformis</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0.41
<i>Reophax gausisicus</i>	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2	0.82

<i>Reophax guttiferus</i>	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	3	1.23
<i>Reophax nodulosus</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.41
<i>Reophax scorpiurus</i>	1	0	3	6	6	2	2	0	0	0	0	0	1	0	2	23	9.47
<i>Reophax spiculifer</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
<i>Trochammina</i> sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0.41
Total live foraminifera	24	21	20	26	33	10	11	7	16	5	9	13	13	17	18	243	100.00
Nbr species	16	17	13	14	18	7	7	4	7	4	2	5	4	4	4	53	
<i>Glomospira</i> spp.	0	0	3	2	7	4	11	8	10	3	4	7	3	4	0	66	
Ostracoda	3	1	2	1		1	0	0	0	0	0	0	0	0	0	8	
Arborescent indet.	4	11	28	62	84	41	8	33	14	3	0	1	0	0	0	289	
April 2000, core B																	
Perforate																	
<i>Bulimina alazanensis</i>	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0.37
<i>Bulimina inflata</i>	8	2	3	0	3	1	0	0	0	0	1	6	1	0	0	25	4.60
<i>Cibicides wuellerstorti</i>	1	0	4	0	0	0	0	2	0	0	0	0	(1)	0	0	8	1.47
<i>Cibicidoides robertsonianus</i>	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	3	0.55
<i>Fissurina</i> sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0.18
<i>Globobulimina affinis</i>	0	0	0	0	0	0	0	0	0	0	0	0	3	4	3	11	2.02
<i>Gyroidina</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0.18
<i>Gyroidina altiformis</i>	1	0	0	0	0	0	0	0	0	0	(1)	0	0	0	0	2	0.37
<i>Gyroidina orbicularis</i>	0	0	0	1	0	1	1	0	0	0	(1)	0	0	0	0	4	0.74
<i>Gyroidinoides soldanil</i>	0	1	0	0	2	0	0	0	0	0	0	(1)	0	0	0	4	0.74
<i>Hoeglundina elegans</i>	6	4	0	1	1	1	2	0	2	0	6	4	1	0	2	30	5.51
<i>Lenticulina gibba</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0.18
<i>Melonis barleeanus</i>	0	0	0	0	1	3	3	2	0	1	3	0	5	4	2	24	4.41
<i>Malonis pompilioides</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0.18
<i>Nonionella atlantica</i>	1	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	2	0.37
<i>Pullenia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0.18
<i>Pullenia bulloides</i>	3	1	1	0	0	(1)	0	0	0	0	0	0	0	(1)	0	7	1.29
<i>Pullenia quinqueloba</i>	0	1	0	0	0	0	6	0	0	1	3	5	0	0	0	16	2.94
<i>Pullenia</i> sp.1	0	0	1	0	0	1	0	2	0	1	4	2	0	0	0	11	2.02
<i>Robertina</i> sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.18
<i>Uvigerina peregrina</i>	4	4	2	1	0	0	1	1	0	1	1	2	1	0	0	18	3.31
Porcellaneous																	
Indet	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0.18
<i>Comuspira</i> sp.	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	0.37
<i>Comuspira involvens</i>	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	2	0.37
<i>Ophtalmidium</i> sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.18
<i>Pyrgo elongata</i>	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	2	0.37

<i>Pyrgo murrhina</i>	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	3	0.55	
<i>Pyrgo subsphaerica</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.18	
<i>Quinqueloculina seminula</i>	0	1	0	3	0	0	0	0	0	0	0	2	0	0	0	6	1.10	
<i>Quinqueloculina</i> sp.1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	2	0.37	
<i>Quinqueloculina</i> sp.2	1	0	1	3	0	0	0	0	0	0	0	0	0	0	0	5	0.92	
Non-fossilising agglutinated																		
Indet.	1	1	0	1	0	1	0	0	0	0	0	1	0	0	0	5	0.92	
Agglut. sp.C	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3	0.55	
<i>Ammobaculites agglutinans</i>	14	3	5	2	5	1	2	4	4	5	3	1	1	1	0	51	9.38	
<i>Cribrostomoides</i> sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0.18	
<i>Cribrostomoides subglobosus</i>	14	10	5	5	4	4	1	3	4	6	2	6	2	1	1	68	12.50	
<i>Cribrostomoides wiesneri</i>	0	0	0	0	0	0	0	1	0	1	2	0	0	1	0	5	0.92	
<i>Haplophragmoides</i> sp.	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	3	0.55	
<i>Hippocrepinella</i> sp.	3	0	1	2	1	0	0	0	0	0	0	0	0	0	0	7	1.29	
<i>Hormosina</i> sp.	0	1	1	0	1	7	4	0	1	1	3	0	0	0	0	19	3.49	
<i>Karrerulina</i> sp.	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	3	0.55	
<i>Lagenamina tubulata</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.18	
<i>Psammosphaera</i> sp.	0	0	0	0	0	1	0	1	0	1	3	1	0	1	0	8	1.47	
<i>Recurvoides</i> sp.	1	2	0	2	1	1	0	1	1	2	0	0	0	0	2	13	2.39	
<i>Reophax</i> sp.	2	1	3	0	0	0	2	0	0	0	1	1	0	0	0	10	1.84	
<i>Reophax bilocularis</i>	1	3	4	2	7	6	0	0	1	0	1	0	0	0	0	25	4.60	
<i>Reophax dentaliniformis</i>	1	0	0	1	0	0	2	1	0	0	0	0	0	0	0	5	0.92	
<i>Reophax guttiferus</i>	1	1	1	4	2	0	0	2	0	0	1	0	0	0	0	12	2.21	
<i>Reophax scorpiurus</i>	10	4	15	8	9	10	10	8	3	5	7	1	2	2	0	94	17.28	
<i>Thuramina albicans</i>	0	0	0	0	0	0	1	0	1	1	0	0	!	0	0	3	0.55	
<i>Trochammina</i> sp.	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	4	0.74	
Fossilising agglutinated																		
<i>Eggerella bradyi</i>	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	2	0.37	
<i>Sigmoilopsis schlumbergeri</i>	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	4	0.74	
Total live foraminifera	76	41	54	39	39	42	43	28	19	27	50	37	22	16	10	1	544	100.00
Nbr species	20	16	19	16	14	13	15	9	8	10	18	14	11	5	4	1	51	
<i>Glomospira</i> spp.	3	3	3	1	6	3	10	8	9	12	13	15	15	19	6	0	126	
Ostracoda	1	1	2	1	3	1	1	0	0	0	0	0	0	0	0	0	10	
Arborescent indet.	3	5	6	8	22	50	49	8	7	8	0	5	2	1	0	0	174	

N.B. Numbers are not standardised for sediment volume.

Porcellaneous												
<i>Biloculinella</i> sp.	2	1	0	0	0	0	0	0	0	3	3.8	
<i>Biloculinella irregularis</i>	1	0	0	0	0	0	0	0	0	1	1.3	
<i>Pyrgo depressa</i>	2	0	0	0	0	0	0	0	0	2	2.5	
<i>Pyrgoella sphaera</i>	0	1	1	0	0	0	0	0	0	2	1.3	
Non-fossilising agglutinated												
<i>Ammobaculites agglutinans</i>	0	0	1	0	0	0	0	0	0	1	1.3	
<i>Ammodiscus</i> sp.	2	0	1	0	0	0	0	0	0	3	3.8	
<i>Cribrostomoides</i> sp.	1	0	0	0	0	0	0	0	0	1	1.3	
<i>Cribrostomoides subglobosus</i>	0	1	1	1	1	0	0	0	0	4	5.0	
<i>Eggerella scabra</i>	0	3	0	0	0	0	0	0	0	3	3.8	
<i>Haplophragmoides</i> sp.	2	1	0	0	0	0	0	0	0	3	3.8	
<i>Recurvoides</i> sp.	0	1	0	0	0	0	0	0	0	1	1.3	
<i>Reophax dentaliniformis</i>	1	1	0	0	0	0	0	0	0	2	2.5	
<i>Reophax scorpiurus</i>	1	0	0	0	0	0	0	0	0	1	1.3	
<i>Spiroplectammina</i> sp.	1	0	0	0	0	0	0	0	0	1	1.3	
<i>Techmitella melo</i>	1	0	0	0	0	0	0	0	0	1	1.3	
Total live foraminifera	40	24	8	3	1	1	1	0	1	80	100.00	
Nbr species	23	14	7	3	1	1	1	0	1	34		
Arborescent indet.	1	4	0	1	0	0	0	0	0	5		

N.B.: numbers are not standardised for sediment volume and correspond to foraminifera picked in a set of 3 multi-tube cores collected from the same multi-tube corer deployment. The cumulative surface area of the three cores is about 82 cm².

References

- Altenbach, A.V., 1988. Deep sea benthic foraminifera and flux rate of organic carbon. *Revue de Paléobiologie* (special vol.) 2, 719–720.
- Altenbach, A.V., Sarnthein, M., 1989. Productivity record in benthic foraminifera. In: Berger, W.H., Smetacek, V.S., Wefer, G. (Eds.), *Productivity of the Ocean: Present and Past*. Wiley, Chichester, pp. 255–269.
- Anderson, L., 1979. Simultaneous spectrophotometric determination of nitrite and nitrate by flow injection analysis. *Analytica Chimica Acta* 110, 123–128.
- Anschutz, P., Zhong, S., Sundby, B., Mucci, A., Gobeil, C., 1998. Burial efficiency of phosphorus and the geochemistry of iron in continental margin sediments. *Limnology and Oceanography* 43, 53–64.
- Anschutz, P., Jorissen, F.J., Chaillou, G., Abu-Zied, R., Fontanier, C., 2002. Recent turbidite deposition in the eastern Atlantic: diagenesis and biotic recovery. *Journal of Marine Research* 60, 835–854.
- Auffret, G., Khrifounoff, A., Vangriesheim, A., 1994. Rapid post-bloom resuspension in the northeastern Atlantic. *Deep-Sea Research I* 41, 925–939.
- Baas, J.H., Schönfeld, J., Zahn, R., 1998. Mid-depth oxygen drawdown during Heinrich events: evidence from benthic foraminiferal community structure, trace-fossil tiering, and benthic $\delta^{13}\text{C}$ at the Portuguese Margin. *Marine Geology* 152, 25–55.
- Barmawidjaja, D.M., Jorissen, F.J., Puskarić, S., Van der Zwaan, G.J., 1992. Microhabitat selection by benthic foraminifera in the northern Adriatic Sea. *Journal of Foraminiferal Research* 22, 297–317.
- Barnett, P.R.O., Watson, J., Connely, D., 1984. A multiple corer for taking virtually undisturbed sample from shelf, bathyal and abyssal sediments. *Oceanologica Acta* 7, 399–408.
- Berger, W.H., Ekdale, A.A., Bryant, P.P., 1979. Selective preservation of burrows in deep-sea carbonates. *Marine Geology* 32, 205–230.
- Bernhard, J.M., 1988. Postmortem vital staining in benthic foraminifera: duration and importance in population and distributional studies. *Journal of Foraminiferal Research* 18, 143–146.
- Bernhard, J.M., 1993. Experimental and field evidence of Antarctic foraminiferal tolerance to anoxia and hydrogen sulfide. *Marine Micropaleontology* 20, 203–213.
- Bernhard, J.M., 1996. Microaerophilic and facultative anaerobic benthic foraminifera: a review of experimental and ultrastructural evidence. *Revue de Paléobiologie* 15, 261–275.
- Bernhard, J.M., 2000. Distinguishing live from dead foraminifera: methods review and proper applications. *Micropaleontology* 46 (1), 38–46.
- Bernhard, J.M., 2003. Potential symbionts in bathyal foraminifera. *Science (Washington)* 299 (5608), 861.
- Bernhard, J.M., Reimers, C.E., 1991. Benthic foraminiferal population fluctuations related to anoxia: Santa Barbara Basin. *Biogeochemistry* 15, 127–149.
- Bernhard, J.M., Sen Gupta, B., 1999. Foraminifera of oxygen-depleted environments. In: Sen Gupta, B.K. (Ed.), *Modern Foraminifera*. Kluwer Academic Press, Dordrecht, pp. 201–216.
- Bernhard, J.M., Buck, K.R., Farmer, M.A., Bowser, S.S., 2000. The Santa Barbara Basin is a symbiosis oasis. *Nature* 403, 77–80.
- Billett, D.S.M., Lampitt, R.S., Rice, A.L., Mantoura, R.F.C., 1983. Seasonal sedimentation of phytodetritus to the deep sea benthos. *Nature* 302, 520–522.
- Boetius, A., Scheibe, S., Tselepidis, A., Thiel, H., 1996. Microbial biomass and activities in deep-sea sediments of the Eastern Mediterranean: trenches are benthic hotspots. *Deep-Sea Research I* 43, 1439–1460.
- Bruland, K.W., Beifang, P.K., Bishop, J.K., Eglinton, G., Ittekkot, V.A.W., Lampitt, R., Sarnthein, M., Theide, J., Walsh, J.J., Wefer, G., 1989. Flux to the sea floor. In: Berger, W.H., Smetacek, V.S., Wefer, G. (Eds.), *Productivity of the Ocean: Present and Past*. Wiley, Chichester, pp. 193–215.
- Buscail, R., Pocklington, R., Daumas, R., Guidi, L., 1990. Flux and budget of organic matter in the benthic boundary layer over the Northwestern Mediterranean Margin. *Continental Shelf Research* 10, 1089–1122.
- Buzas, M., Culver, S.J., Jorissen, F.J., 1993. A statistical evaluation of the microhabitats of living (stained) infaunal benthic foraminifera. *Marine Micropaleontology* 20, 3–4.
- Carney, R.S., 1989. Examining relationship between organic carbon flux and deep-sea deposit feeding. In: Lopez, G., Taghon, G., Levinton, J. (Eds.), *Ecology of Marine Deposit Feeders, Lecture Notes on Coastal and Estuarine Studies*, vol. 31. Springer, Berlin, pp. 24–58.
- Castaing, P., Froidefond, J.-M., Lazure, P., Weber, O., Prud'homme, R., Jouanneau, J.-M., 1999. Relationship between hydrology and seasonal distribution of suspended sediments on the continental shelf of the Bay of Biscay. *Deep-Sea Research II* 46, 1979–2001.
- Corliss, B.H., 1985. Microhabitats of benthic foraminifera within deep-sea sediments. *Nature* 314, 435–438.
- Corliss, B.H., 1991. Morphology and microhabitat preferences of benthic foraminifera from the northwest Atlantic Ocean. *Marine Micropaleontology* 17, 195–236.
- Corliss, B.H., Emerson, S., 1990. Distribution of Rose Bengal stained deep-sea benthic foraminifera from the Nova Scotia continental margin and Gulf of Maine. *Deep-Sea Research* 37, 381–400.
- Crémer, M., Weber, O., Jouanneau, J.-M., 1993. Les sédiments de l'interface dans la région du canyon de Cap-ferret (Golfe de Gascogne). *Actes du III^{ème} Colloque international «Océanographie du Golfe de Gascogne»*, pp. 153–157.

- Crémer, M., Weber, O., Jouanneau, J.-M., 1999. Sedimentology of box cores from the Cap-Ferret Canyon area (Bay of Biscay). *Deep-Sea Research II* 46, 221–2247.
- Cushman, J.A., 1929. The Foraminifera of the Atlantic Ocean. Part 6. *Miliolidae*, *Ophthalmidiidae* and *Fischerinidae*. Smithsonian Institution. United States National Museum, Bulletin 104.
- Dauwe, B., Middelburg, J.J., Van Rijswijk, P., Sinke, J., Herman, P.M.J., Heip, C.H.R., 1999. Enzymatically hydrolyzable amino acids in North Sea sediments and their possible implication for sediment nutritional values. *Journal of Marine Research* 57, 109–134.
- De Rijk, S., Jorissen, F.J., Rohling, E.J., Troelstra, S.R., 2000. Organic flux control on bathymetric zonation of Mediterranean benthic foraminifera. *Marine Micropaleontology* 40, 151–166.
- Dubilier, N., Mülders, C., Ferdelman, T., de Beer, D., Pernthaler, A.D., Klein, M., Wagner, M., Erséus, C., Thiermann, F., Krieger, J., Giere, O., Amann, R., 2001. Endosymbiotic sulfate-reducing and sulfide-oxidizing bacteria in an oligochaete worm. *Nature* 411, 298–302.
- Durrieu de Madron, X., Castaing, P., Nyffeler, F., Courp, T., 1999. Slope transport of resuspended particulate matter on the Aquitanian margin of the Bay of Biscay. *Deep-Sea Research II* 46, 2003–2027.
- Ernst, S.R., van der Zwaan, G.J., 2004. Effects of experimentally induced raised levels of organic flux and oxygen depletion on a continental slope benthic foraminiferal community. *Deep-Sea Research I* 51, 1709–1739.
- Etcheber, H., Relexans, J.-C., Béliard, M., Weber, O., Buscail, R., Heussner, S., 1999. Distribution and quality of sedimentary organic matter on the Aquitanian margin (Bay of Biscay). *Deep-Sea Research II* 46, 2249–2288.
- Fariduddin, M., Loubere, P., 1997. The surface ocean productivity response of deeper water benthic foraminifera in the Atlantic Ocean. *Marine Micropaleontology* 32, 289–310.
- Fenchel, T.M., Finlay, B.J., 1995. *Ecology and Evolution in Anoxic Worlds*. Oxford University Press, Oxford (276pp.).
- Fenchel, T., King, G.M., Blackburn, T.H., 1998. *Bacterial Biogeochemistry: The Ecophysiology of Mineral Cycling*. Academic Press, London (307pp.).
- Fisher, C.R., 1990. Chemoautotrophic and methanotrophic symbiosis in marine invertebrates. *Reviews in Aquatic Sciences* 2, 399–436.
- Fisher, C.R., Childress, J.J., 1986. Translocation of fixed carbon from the symbiotic bacteria to host tissues in the gutless bivalve, *Solemya reidi*. *Marine Biology* 93, 59–68.
- Fontanier, C., Jorissen, F.J., Licari, L., Alexandre, A., Anschutz, P., Carbonel, P., 2002. Live benthic foraminiferal faunas from the Bay of Biscay: faunal density, composition, and microhabitats. *Deep-Sea Research I* 49, 751–785.
- Fontanier, C., Jorissen, F.J., Chaillou, G., David, C., Anschutz, P., Lafon, V., 2003. Seasonal and interannual variability of benthic foraminiferal faunas at 550 m depth in the Bay of Biscay. *Deep-Sea Research I* 50, 457–494.
- Froelich, P.N., Klinkhammer, G.P., Bender, M.L., Luedke, N.A., Heath, G.R., Cullen, D., Dauphin, P., Hammond, D., Hartman, B., Maynard, V., 1979. Early oxidation of organic matter in pelagic sediments of the Eastern Equatorial Atlantic: suboxic diagenesis. *Geochimica et Cosmochimica Acta* 43, 1075–1090.
- Gadel, F., Charrière, B., Serve, L., 1993. Behaviour of suspended and sedimentary organic matter in the deltaic areas of the Gulf of Lions (Mediterranean Sea). *Netherlands Journal of Aquatic Ecology* 27 (2–4), 437–447.
- Gardner, W.D., 1989. Baltimore canyon as a modern conduit of sediment to the deep sea. *Deep-Sea Research* 56, 323–338.
- Gerino, M., Stora, G., Weber, O., 1999. Evidence of bioturbation in the Cap-Ferret Canyon in the deep northeastern Atlantic. *Deep-Sea Research II* 46, 2289–2307.
- Gooday, A.J., 1988. A response by benthic Foraminifera to the deposition of phytodetritus in the deep-sea. *Nature London* 332, 70–73.
- Gooday, A., 1993. Deep-sea benthic foraminifera species which exploit phytodetritus: characteristic features and controls on distribution. *Marine Micropaleontology* 22, 187–205.
- Gooday, A.J., Hughes, J.A., 2002. Foraminifera associated with phytodetritus deposits at a bathyal site in the northern Rockall Trough (NE Atlantic): seasonal contrasts and a comparison of stained and dead assemblages. *Marine Micropaleontology* 46, 83–110.
- Gooday, A.J., Lamshead, P.J.D., 1989. Influence of seasonally deposited phytodetritus on benthic foraminiferal populations in the bathyal northeast Atlantic: the species response. *Marine Ecology-Progress Series* 5, 53–67.
- Gooday, A.J., Rathburn, A.E., 1999. Temporal variability in living deep-sea foraminifera: a review. *Earth Sciences Reviews* 46, 187–212.
- Grémare, A., Medernach, L., deBovée, F., Amouroux, J.M., Vétion, G., Albert, P., 2002. Relationships between sedimentary organics and benthic meiofauna on the continental shelf and the upper slope of the Gulf of Lions (NW Mediterranean). *Marine Ecology-Progress Series* 234, 85–94.
- Gross, O., 2000. Influence of temperature, oxygen and food availability on the migrational activity of bathyal benthic foraminifera: evidence by microcosm experiments. *Hydrobiologia* 426, 123–137.
- Hall, P.O.J., Aller, R.C., 1992. Rapid, small-volume flow injection analysis for CO₂ and NH₄⁺ in marine and freshwaters. *Limnology Oceanography* 37, 1113–1119.
- Heinz, P., Schmiedl, G., Kitazato, H., Hemleben, C., 2001. Response of deep-sea benthic foraminifera from the Mediterranean Sea to simulated phytoplankton pulses under laboratory conditions. *Journal of Foraminiferal Research* 31, 210–227.
- Heinz, P., Hemleben, C., Kitazato, H., 2002. Time-response of cultured deep-sea benthic foraminifera to different algal diets. *Deep-Sea Research I* 49, 517–537.

- Helder, W., Bakker, J.F., 1985. Shipboard comparison of micro- and mini electrodes for measuring oxygen in marine sediments. *Limnology and Oceanography* 30, 1106–1109.
- Hess, S., 1998. Verteilungsmuster rezenter benthischer Foraminiferen im Südchinesischen Meer. Reports, Geologisch-Paläontologisches Institut und Museum Christian-Albrechts-Universität Kiel, Deutschland, 59, 155pp.
- Heussner, S., Durrieu de Madron, X., Radakovitch, O., Beaufort, L., Biscaye, P.E., Carbonne, J., Delsaut, N., Etcheber, H., Monaco, A., 1999. Spatial and temporal patterns of downward particle fluxes on the continental slope of the Bay of Biscay (northeastern Atlantic). *Deep-Sea Research II* 46, 2101–2146.
- Hyacinthe, C., Anschutz, P., Carbonel, P., Jouanneau, J.M., Jorissen, F.J., 2001. Early diagenetic processes in the muddy sediments of the Bay of Biscay. *Marine Geology* 177, 111–128.
- Jannink, N.T., Zachariasse, W.J., Van der Zwaan, G.J., 1998. Living (Rose Bengal stained) benthic foraminifera from the Pakistan continental margin (northern Arabian Sea). *Deep-Sea Research I* 45, 1483–1513.
- Jones, R.W., 1994. *The Challenger Foraminifera*. Oxford Science Publications—The Natural History Museum, 149pp.
- Jørgensen, B.B., 2000. Bacteria and marine biochemistry. In: Shultz, H.D., Zabel, M. (Eds.), *Marine Geochemistry*. Springer, Berlin, pp. 173–207.
- Jorissen, F.J., 1987. The distribution of benthic foraminifera in the Adriatic Sea. *Marine Micropaleontology* 12, 21–48.
- Jorissen, F.J., 1999a. Benthic foraminiferal microhabitats. In: Sen Gupta, B.K. (Ed.), *Foraminifera*. Kluwer Academic Publishers, Dordrecht, pp. 161–179.
- Jorissen, F.J., 1999b. Benthic foraminiferal successions across late Quaternary Mediterranean sapropels. In: Rohling, E.J. (Ed.), *Fifth Decade of Mediterranean Paleoclimate and Sapropel Studies*, *Marine Geology*, vol. 153 (1–4), pp. 91–101.
- Jorissen, F.J., Barmawidjaja, D.M., Puskaric, S., van der Zwaan, G.J., 1992. Vertical distribution of benthic Foraminifera in the Northern Adriatic Sea. The relation with high organic flux. *Marine Micropaleontology* 19, 131–146.
- Jorissen, F.J., Buzas, M., Culver, S., Kuehl, S., 1994. Vertical distribution of living benthic Foraminifera in submarine canyons off New Jersey. *Journal of Foraminiferal Research* 24, 28–36.
- Jorissen, F.J., De Stigter, H.C., Widmark, J.G.V., 1995. A conceptual model explaining benthic foraminiferal microhabitats. *Marine Micropaleontology* 22, 3–15.
- Jorissen, F.J., Wittling, I., Peypouquet, J.P., Rabouille, C., Relexans, J.C., 1998. Live benthic foraminiferal faunas off Cap Blanc, NW Africa: community structure and microhabitats. *Deep-Sea Research I* 45, 2157–2188.
- Jouanneau, J.M., Garcia, C., Oliveira, A., Rodrigues, A., Dias, J.A., Weber, O., 1988. Dispersal and deposition of suspended sediment on the shelf off the Tagus and Sado estuaries, SW Portugal. *Progress in Oceanography* 42, 233–257.
- Kaiho, K., 1994. Benthic foraminiferal dissolved-oxygen index and dissolved-oxygen levels in the modern ocean. *Geology* 22, 719–722.
- Kitazato, H., Shirayama, Y., Nakatsuka, T., Fujiwara, S., Shimanaga, M., Kato, Y., Okada, Y., Kanda, J., Yamaoka, A., Masukawa, T., Suzuki, K., 2000. Seasonal phytodetritus deposition and responses of bathyal benthic foraminiferal populations in Sagami Bay, Japan: preliminary results from “Project Sagami 1996–1999”. *Marine Micropaleontology* 40, 135–149.
- Kostka, J.E., Luther III, G.W., 1994. Portioning and speciation of solid phase iron in saltmarsh sediments. *Geochimica et Cosmochimica Acta* 58, 1701–1710.
- Laborde, P., Urrutia, J., Valencia, V., 1999. Seasonal variability of primary production in the Cap-Ferret Canyon area (Bay of Biscay) during the ECOFER cruises. *Deep-Sea Research II* 46, 2057–2079.
- Lambhead, P.J.D., Gooday, A.J., 1990. The impact of seasonally deposited phytodetritus on epifaunal and shallow infaunal benthic foraminiferal populations in the bathyal northeast Atlantic: the assemblage response. *Deep-Sea Research* 37, 1263–1283.
- Lampitt, R.S., 1985. Evidence for seasonal deposition of detritus to deep sea floor and its subsequent resuspension. *Deep-Sea Research* 32, 885–897.
- Langezaal, A.M., van Bergen, P.M., van der Zwaan, G.J., 2004. The recovery of benthic of foraminifera and bacteria after disturbance: experimental evidence. *Journal of Experimental Biology and Ecology* 312, 137–170.
- Loeblich, A.R., Tappan, H., 1988a. *Foraminifera Genera and their Classification*. Van Nostrand Reinhold, New York (970pp.).
- Loeblich, A.R., Tappan, H., 1988b. *Foraminifera genera and their classification—plates*. Van Nostrand Reinhold, New York (212pp.).
- Loubere, P., 1998. The impact of seasonality on the benthos as reflected in the assemblages of deep-sea foraminifera. *Deep-Sea Research I* 45, 409–432.
- Lutze, G.F., Thiel, H., 1989. *Cibicidoides wuellerstorfi* and *Planulina ariminensis*, elevated epibenthic Foraminifera. In: Altenbach, A.V., Lutze, G.F., Weinholz, P. (Eds.), *Beobachtungen an Benthos-Foraminiferen*. 6. Ber. Sonderforschungsbereich 313. Kiel University, pp. 17–30.
- Mackensen, A., Douglas, R.G., 1989. Down-core distribution of live and dead deep-water benthic foraminifera in box cores from the Weddell Sea and the California continental borderland. *Deep-Sea Research* 36, 879–900.
- Mayer, L.M., Schick, L.L., Sawyer, T., Plante, C.J., Jumars, P.A., Self, R.F.L., 1995. Bioavailable amino acids in sediments: a biomimetic, kinetics-based approach. *Limnology Oceanography* 40, 511–520.
- McCave, I.N., 1975. Vertical flux of particles in the ocean. *Deep-Sea Research* 22, 491–502.
- Medernach, L., Grémare, A., Amouroux, J.M., Colomines, J.C., Vétion, G., 2001. Temporal changes in the amino acid contents of particulate organic matter sedimenting in the

- Bay of Banyuls-sur-Mer (northwestern Mediterranean). *Marine Ecology-Progress Series* 214, 55–65.
- Migeon, S., Weber, O., Faugère, J.-C., Saint-Paul, J., 1999. SCOPIX: a new X-ray imaging system for core analysis. *Geo-Marine Letters* 18, 251–255.
- Monaco, A., Biscaye, P.E., Laborde, P., 1999. The ECOFER (ECOsystème du canyon du cap-FERret) experiment in the Bay of Biscay: introduction, objectives and major results. *Deep-Sea Research II* 46, 1967–1978.
- Morigi, C., Jorissen, F.J., Gervais, A., Guichard, S., Borsetti, A.M., 2002. Benthic foraminiferal faunas in surface sediments off NW Africa: relationship with the organic flux to the ocean floor. *Journal of Foraminiferal Research* 31, 350–368.
- Mulder, T., Weber, O., Anschutz, P., Jorissen, F.J., Jouanneau, J.M., 2001. A few months-old storm-generated turbidite deposited in the Capbreton Canyon (Bay of Biscay, SW France). *Geo-Marine Letters* 21, 149–156.
- Mullins, H.T., Thompson, J.B., McDougall, K., Vercoutere, T.L., 1985. Oxygen minimum zone edge effects: evidence from the central California coastal upwelling system. *Geology* 13, 491–494.
- Newton, P.P., Lampitt, R.S., Jickells, T.D., King, P., Boutle, C., 1994. Temporal and spatial variability of biogenic particle fluxes during the JGOFS northeast Atlantic process studies at 47°N, 20°W. *Deep-Sea Research I* 41, 1617–1642.
- Ohga, T., Kitazato, H., 1997. Seasonal changes in bathyal foraminiferal populations in response to the flux of organic matter (Sagami Bay, Japan). *Terra Nova* 9, 33–37.
- Parker, F.L., 1958. Eastern Mediterranean Foraminifera. Reports of the Swedish Deep-sea Expedition 1947–1948, vol. VIII: Sediment Cores from the Mediterranean and the Red Sea, vol. 4. 283pp.
- Pfleger, F.B., Parker, F.L., Peirson, J.F., 1953. North Atlantic Foraminifera. Reports of the Swedish Deep-sea Expedition 1947–1948, vol. VII: Sediment Cores from the North Atlantic, vol. 1. 122pp.
- Postma, D., Jakobsen, R., 1996. Redox zonation: equilibrium contains on the Fe(III)/SO₄²⁻ reduction interface. *Geochimica et Cosmochimica Acta* 60, 3169–3175.
- Radakovitch, O., Heussner, S., 1999. Fluxes and Budget of 210Pb on the continental margin of the Bay of Biscay (northeastern Atlantic). *Deep-Sea Research II* 46, 2175–2203.
- Rathburn, A.E., Corliss, B.H., 1994. The ecology of living (stained) deep-sea benthic foraminifera from the Sulu Sea. *Paleoceanography* 9, 87–150.
- Rathburn, A.E., Corliss, B.H., Tappa, K.D., Lohmann, K.C., 1996. Comparison of the ecology and stable isotopic compositions of living (stained) benthic foraminifera from the Sulu and South China Seas. *Deep-Sea Research I* 43, 1617–1646.
- Revsbech, N.P., Jørgensen, B.B., 1986. Microelectrodes: their use in microbial ecology. *Advances in Microbial Ecology* 9, 293–352.
- Rosenberg, R., Grémare, A., Amouroux, J.M., Nilsson, H.C., 2003. Benthic habitats in the northwest Mediterranean characterised by sedimentary organics, benthic macrofauna and sediment profile images. *Estuarine Coastal Shelf Science* 57, 297–311.
- Ross, C.R., Kennett, J.P., 1984. Late Quaternary paleoceanography as recorded by benthonic foraminifera in Strait of Sicily sediment sequences. *Marine Micropaleontology* 8, 315–336.
- Ruch, P., Mirmann, M., Jouanneau, J.-M., Latouche, C., 1993. Sediment budget and transfer of suspended sediment from the Gironde Estuary to Cap-Ferret canyon. *Marine Geology* 111, 109–119.
- Schiebel, R., 1992. Rezente benthische Foraminiferen in Sedimenten des Schelfes und oberen Kontinentalhanges im Golf von Guinea (Westafrika). *Berichte—Reports, Geologisch-Paläontologisches Institut und Museum Christian-Albrechts-Universität Kiel, Deutschland*, vol. 51. 126pp.
- Schmiedl, G., de Bovée, F., Buscail, R., Charrière, B., Hemleben, C., Medernach, L., Picon, P., 2000. Trophic control of benthic foraminiferal abundance and microhabitat in the bathyal Gulf of Lions, western Mediterranean Sea. *Marine Micropaleontology* 40, 167–188.
- Sen Gupta, B.K., Machain-Castillo, M.L., 1993. Benthic foraminifera in oxygen-poor habitats. *Marine Micropaleontology* 20, 3–4.
- Silva, K.A., Corliss, B.C., Rathburn, A.E., Thunnell, R.C., 1996. Seasonality of living benthic foraminifera from the San Pedro Basin, California Borderland. *Journal of Foraminiferal Research* 26, 71–93.
- Silverberg, N., Nguyen, H.V., Delibrias, G., Koide, M., Sundby, B., Yokoyama, Y., Chesselet, R., 1986. Radio-nuclide profiles, sedimentation rates, and bioturbation in modern sediments of Laurentian Trough, Gulf of St. Lawrence. *Oceanologica Acta* 9, 285–290.
- Stookey, L.L., 1970. A new spectrometric reagent for Iron. *Analytical Chemistry* 42, 779–781.
- Strickland, J.D.H., Parsons, T.R., 1972. A practical handbook of seawater analysis. *Bulletin of Fisheries Resource B Canada* 167, 311.
- Thomson, J., Brown, L., Nixon, S., Cook, G.T., McKenzie, A.B., 2000. Bioturbation and Holocene sediment accumulation fluxes in the north-east Atlantic Ocean (Benthic Boundary Layer experiment sites). *Marine Geology* 169, 21–39.
- Timm, S., 1992. Rezente Tiefsee-Benthosforaminiferen aus Oberflächensedimenten des Golfes von Guinea (Westafrika)—Taxonomie, Verbreitung, Ökologie und Korngrößenfraktionen—Reports, Geologisch-Paläontologisches Institut und Museum Christian-Albrechts-Universität Kiel, Deutschland, vol. 59, 155pp.
- Tréguer, P., Le Corre, P., Grall, J.R., 1979. The seasonal variations of nutrients in the upper waters of the Bay of Biscay region and their relation to phytoplanktonic growth. *Deep-Sea Research* 26 (A10), 1121–1152.
- Turley, C.M., Gooday, A.J., Green, J.C., 1993. Maintenance of abyssal benthic foraminifera under high pressure and low

- temperature: some preliminary results. *Deep-Sea Research* 40, 643–652.
- Vacelet, J., Fiala-Mzdioni, A., Fisher, C.R., Boury-Esnault, N., 1996. Symbiosis between methane oxidizing bacteria and a deep-sea carnivorous cladorhizid sponge. *Marine Ecology-Progress Series* 145, 77–85.
- Van der Zwaan, G.J., Jorissen, F.J., Verhallen, P.J.J., Von Daniels, C.H., 1986. Atlantic-European Oligocene to recent *Uvigerina*: taxonomy, paleoecology and paleobiogeography. *Utrecht Micropaleontological Bulletins* 35 (240pp.).
- Van der Zwaan, G.J., Duijnste, I.A.P., Den Dulk, M., Ernst, S.R., Kouwenhoven, N.T., 1999. Benthic foraminifers: proxies or problems? A review of paleoecological concepts. *Earth Sciences Reviews* 46, 213–236.
- Van Leeuwen, R.J.W., 1989. Sea-floor distribution and Late Quaternary faunal patterns of planktonic and benthic foraminifers in the Angola Basin. *Utrecht Micropaleontological Bulletins* 38 (288pp.).
- Van Weering, T.C.E., de Stigter, H.C., Boer, W., de Haas, H., 2002. Recent sediment transport and accumulation on the NW Iberian margin. *Progress in Oceanography* 52, 349–371.
- Walton, W.R., 1952. Techniques for recognition of living Foraminifera. *Contributions from the Cushman Foundation for Foraminiferal Research* 3, 56–60.
- Young, D.K., Jahn, W.H., Richardson, M.D., Lohanick, A.W., 1985. Photographs of deep-sea lebensspuren: a comparison of sedimentary provinces in the Venezuela basin. *Caribbean Sea. Marine Geology* 68, 269–301.