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Seasonal and interannual variability of benthic foraminiferal faunas at 550 m depth in the Bay of Biscay

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Abstract

Live benthic foraminiferal faunas were sampled 10 times between October 1997 and April 2000 at a 550 m depth open-slope station in the Bay of Biscay. Duplicate cores for 5 samplings allow distinguishing between spatial and temporal variability of the foraminiferal faunas. Although spatial patchiness of the foraminiferal faunas is substantial, especially in the 63–150 μm fraction, the temporal variability appears to be larger. The foraminiferal patterns are compared with surface water primary production as assessed by the study of available SeaWIFS satellite images. In the study area, the primary production regime is marked by a pulselike and prolonged spring bloom and possibly a short fall bloom. Such periods of elevated chlorophyll-*a* concentration are followed, after a delay of about 4–6 weeks, by a strong frequency increase of the most opportunistic taxa of benthic foraminifera. Surprisingly, no change of bottom and interstitial water oxygenation and of redox conditions within the sediment is recorded. The small taxa *Epistominella exigua*, *Reophax guttiferus*, *Bolivina spathulata*, *Cassidulina carinata* and *Nuttallides pusillus* appear to respond first to a labile organic matter input, by a reproductive event marked by a strong patchy spatial distribution hypothetically resulting of the spatial heterogeneity of organic matter deposits. *Uvigerina peregrina* and *Uvigerina mediterranea*, the most opportunistic larger taxa, strongly dominate the > 150 μm fraction during eutrophic periods (spring and fall blooms). Intermediate and deep infaunal taxa seem to depend less on fresh organic matter input, even if a small frequency increases are recorded in the > 150 μm fraction during the most productive periods; *Globobulimina affinis* and *Melonis barleeanus* show reproductive events in rather shallow sediment layers in the more oligotrophic periods of the year. A conceptual model explains the increasing delay in the response to important phytoplankton bloom periods for the successive benthic ecosystem compartments.

Keywords: Benthic foraminifera; Microhabitat; Seasonality; Patchiness; Opportunism; Organic flux

1. Introduction

Mid-latitude primary production regimes are marked by a seasonal and interannual alternation

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of algal blooms and low productivity periods (Pfannkuche and Thiel, 1987; Parsons and Lalli, 1988; Berger and Wefer, 1990). This intermittence and seasonality of the surface water primary production is responsible for important fluctuations of the exported organic matter flux (Billet et al., 1983; Pfannkuche and Thiel, 1987; Berger and Wefer, 1990; Lohrenz et al., 1992). Since the biomass of deep-sea foraminifera is closely related to the flux of organic carbon to the seafloor (Altenbach, 1985, 1988; Altenbach and Sarnthein, 1989; Herguera and Berger, 1991; Jorissen et al., 1998; Loubere and Fariduddin, 1999; De Rijk et al., 2000; Fontanier et al., 2002; Morigi et al., 2001), the interannual and seasonal primary production oscillations could thus result in important short-term variability of the standing stocks and composition of the foraminiferal faunas. Several observations of highly opportunistic behaviour of foraminiferal taxa illustrate the capability of this group of organisms to rapidly adapt to changing trophic conditions (Gooday, 1988, 1993; Gooday and Lambshead, 1989; Barmawidjaja et al., 1992; Silva et al., 1996; Ohga and Kitazato, 1997; Jannink et al., 1998; Kitazato et al., 2000). Even in some abyssal environments (e.g. Porcupine Seabight) intermittence of food input appears to be a determinant factor, causing instantaneous and patchy bursts of benthic foraminiferal faunas that colonise freshly deposited phytodetritus (Gooday, 1988, 1993; Lambshead and Gooday, 1990; Turley et al., 1993). A similar reproductive response to artificial food input has recently been shown in laboratory experiments (Heinz et al. 2001, 2002).

Although the impact of phytodetritus deposits on foraminiferal faunas has been clearly shown many important questions about deep-sea foraminiferal ecology remain partially unanswered:

(1) What are the delays between primary production in the euphotic zone the resulting exported organic matter input at the sediment–water interface and the response of the foraminiferal faunas in terms of density composition and microhabitat?
(2) What are the requirements of the various foraminiferal species in terms of quality and quantity of exported organic compounds?
(3) How important is foraminiferal patchiness in the upper sediment layers; is this patchiness related to the micro-distribution of organic matter?
(4) Is the vertical distribution of foraminiferal species in the sediment modified by organic matter input?
(5) Is the foraminiferal response to food input restricted to the sediment surface, or is there a faunal response at depth in the sediment as well?

Whereas most opportunistic taxa rely on fresh phytodetritus, other, less critical taxa may feed on more altered organic substances, such as zooplankton faecal pellets or organic matter in a more or less advanced state of decay. It has been speculated that some taxa may also feed either on bacteria involved in the aerobic or anaerobic degradation of more refractory organic compounds, or on their breakdown products (Lee, 1979; Thomsen and Altenbach, 1993; Kitazato, 1994; Jorissen et al., 1995).

A previous foraminiferal study along a five station bathymetric transect in the Bay of Biscay substantiated the determining role of exported organic matter flux on foraminiferal density, composition, and microhabitat (Fontanier et al., 2002). The foraminiferal density reflects the exported organic matter flux, and shows a clear decrease from 150 to 2000 m depth. Foraminiferal microhabitats, which appear to be linked to principal redox fronts, deepen from the outer continental shelf to the lower slope stations. In the deepest, most oligotrophic stations, infaunal taxa tend to disappear. Finally, Fontanier et al. (2002) propose a species specific adaptation of the TROX microhabitat model of Jorissen et al. (1995). In the present paper, we study the temporal variability of live benthic foraminiferal faunas (63–150 μm, >150 μm) at a single upper bathyal station (550 m depth) from an open-slope environment in the Bay of Biscay (Fig. 1), which is supposed to be under the influence of a typical temperate, mid latitude seasonal primary production regime. For this purpose, 13 sampling cruises took place from October 1997 to April 2000. On-line data archives of the Joint Research Centre (SeaWIFS data) allow estimates of surface water chlorophyll-*a* for

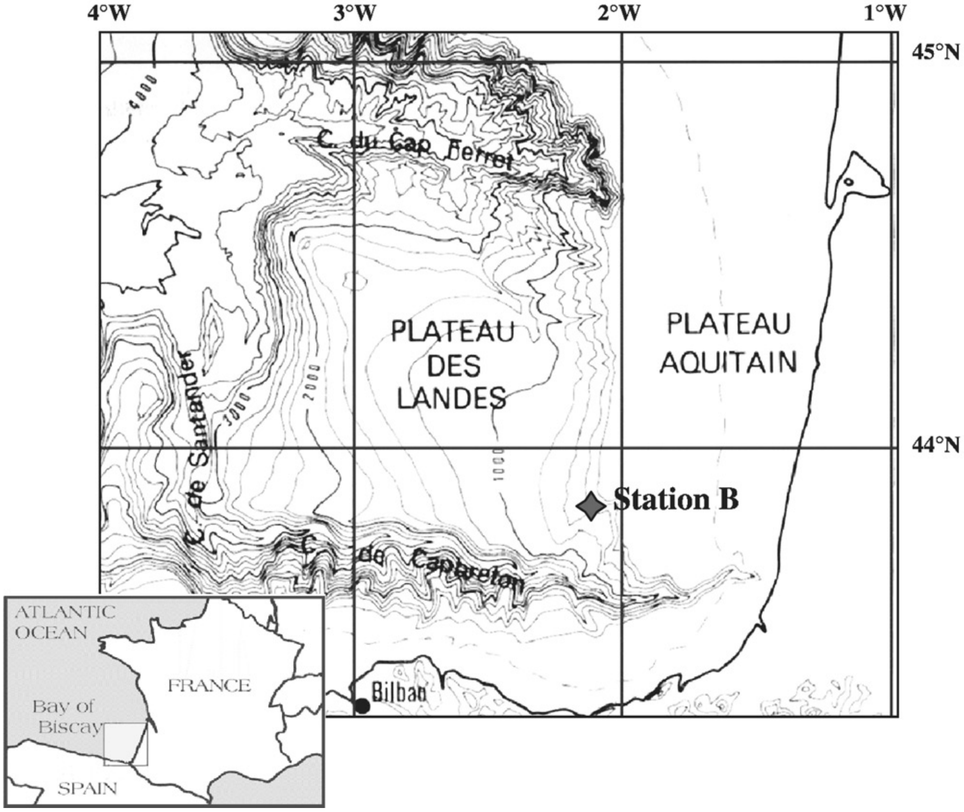

Fig. 1. Study area, bathymetry and geographical position of station B.

the duration of the study period. For all studied cores, geochemical analyses have been performed in order to determine redox conditions in the upper sediment layer. The main objectives of this study are to determine whether the foraminiferal faunas respond to the seasonal and interannual fluctuations of the exported organic matter flux. More precisely, we will concentrate on the seasonal changes of density, composition and vertical distribution of foraminiferal faunas, and their possible relationship with the qualitative and quantitative seasonal variations of the exported organic matter flux.

2. Study area

2.1. Hydrographical setting

The Bay of Biscay is a semi-enclosed basin where water mass circulation is disconnected from the general North Atlantic Drift. The current velocity of the various water masses is generally weak (less than $10\,\mathrm{cm\,s^{-1}}$, Tréguer et al., 1979), and the waters which enter from the north, along the Irish shelf-break, leave the area near Cape Finisterre only after 2 years. The surface waters patterns are strongly dependent on the seasonal variations of the thermocline and mixed layer (Tréguer et al., 1979), and the surface currents (velocity and directions) are widely influenced by local wind regimes (Boucher, 1985). Hydrological patterns of water masses in the southeast part of the Bay of Biscay (our study area) are presented in a previous paper (Fontanier et al., 2002).

The continental slope bordering the French shelf deepens gradually, and is interrupted by two large canyons (Cap-Ferret Canyon, Capbreton Canyon). Vertical fluxes represent the main sedimentary component in open-slope environments, whereas lateral advection may dominate sedimentary processes in the canyons (Heussner et al., 1999). The present paper concentrates on a 550 m deep open-slope station, where the impact of laterally advected particles is supposed to be minimal, and where the linkage between surface water primary production, the vertical particle flux, and benthic life should be rather straightforward. Our station B is positioned within the Northern Atlantic Central Waters (NACW), which has a salinity of 35.60 and a temperature of about 11°C (Ogawa and Tauzin, 1973). The sediment consists predominantly of fine-grained silty mud.

2.2. *Primary production patterns in the north-eastern Atlantic*

In temperate latitudes, the alternation between mixing and stratification of the water column, and the daily input of sunlight appear to be the main factors controlling the seasonal dynamics of phytoplankton (e.g. Harris, 1986; Berger and Wefer, 1990). The moderately strong seasonality found in the Bay of Biscay is characterised by an annual sinusoidal primary production curve, dominated by opportunistic species, with a succession of phytoplankton to zooplankton. The consequences of this temporal variability are seasonal occurrences of zooplankton grazers and predators, a fluctuating explortation of organic debris, and, possibly, seasonal changes in the growth rate of benthic organisms (Bruland et al., 1989; Jumars et al., 1989).

The Bay of Biscay is characterised by phytoplankton blooms occurring in spring, summer and autumn (Tréguer et al., 1979; Froidefond et al., 1996; Laborde et al., 1999). Spring blooms are considered as the highest chlorophyll-*a* concentration events throughout the year. The phytoplankton assemblages are mainly composed of diatoms and coccolithophorids (Tréguer et al., 1979; Fernandez et al., 1995). Wroblewski (1989) suggests a general duration of about 2 weeks for the spring bloom. Fernandez (1990), who studies the Central Cantabrian Sea (southern part of the Bay of Biscay), observes high chlorophyll-*a* and primary production rates in March, predominantly due to microflagellates. In a more recent study Laborde et al. (1999) describe a high productivity period, which lasts for about 2 months. In view of the earlier literature, it seems obvious that this relatively long period is the result of a close succession of several individual bloom events, involving different phytoplankton groups.

Minor upwelling events occur during early summer, in relation to NNW coast-parallel winds and to riverine discharge (Froidefond et al., 1996). Large coccolithophorids blooms are the result; they have been observed on the shelf-break of the Bay of Biscay by satellite imagery as well as by in situ measurements (Holligan et al., 1983; Fernandez et al., 1993; Beaufort and Heussner, 1999). Because this system has probably a very strong interannual variability, it is difficult to determine an average primary production value. Nevertheless, total primary production estimates based on satellite imagery (Antoine et al., 1996) suggest a slight increase in early summer.

In autumn, cooling of the surface waters is generally effective without causing the total disappearance of water column stratification and of the nutricline. Nevertheless, Tréguer et al. (1979) have recorded a chlorophyll-*a* increase in October, which they describe as an autumn bloom. In this period, primary production is rather patchy on a basin scale, and strongly influenced by the hydrological structures. Lohrenz et al. (1992) speculate that primary production increases are generally caused by wind-induced mixing, resulting in nutrient injection from subsurface waters into the nutrient-depleted surface waters. Recently, Sellmer et al. (1998) showed an autumn bloom at the BIOTRANS site (47°N/20°W), occurring around the nutricline, at about 30–50 m depth, mainly composed of autotrophic dinoflagellates, with smaller amount of diatoms.

Very few quantitative data are available on primary production in general, and more specifically, on the individual bloom events occurring in the study area. Tréguer et al. (1979) estimate a primary production between 0.4 and 1.9 $\mathrm{g\,C/m^2/day}$ for the spring bloom of 1973. Primary production measurements during autumn 1972 indicate a bloom with values of 0.3–0.4 $\mathrm{g\,C/m^2/day}$ (Le Corre and Tréguer, 1976). This range of values agrees with recent data obtained in the Cap-Ferret region during five ECOFER cruises: 0.7–1.2 g C/m^2/day in spring (May 1990 and 1991) and 0.3 g C/m^2/day in autumn (October 1990; Laborde et al., 1999). Total annual primary production has been estimated between 145 and 170 g C/m^2/yr (Laborde et al., 1999).

3. Material and methods

In order to complete the rather scarce information about seasonal and interannual changes of phytoplankton biomass in the surface waters from the Bay of Biscay, we used on-line data archives of the Joint Research Center (European Commission) to estimate chlorophyll-*a* concentrations (SeaWIFS data) in the study area for the duration of our sampling period (October 1997–April 2000; Fig. 2). Unfortunately, weather conditions strongly affect the availability of images. Especially during autumn and winter, satellite monitoring is only rarely possible, because of the dense cloud cover.

In order to obtain a good overview of the temporal variability of the benthic foraminiferal assemblages, 13 sampling cruises were organised between October 1997 and April 2000. For meteorological reasons, sampling was impossible during 3 cruises, and consequently, station B (43°49′98N, 2°23′04W, water depth 550 m, Fig. 1) was sampled 10 times (Table 1). Cores were sampled with a Barnett multi-tube corer (Barnett et al., 1984), which allows sampling of first decimeters of the sediment, the overlying bottom waters, and an undisturbed sediment–water interface. Free waters were collected immediately after core recovery for dissolved O_2 measurements by the Winkler titration method (Strickland and Parsons, 1972). Profiles of pore water O_2 were obtained on board with a cathode-type mini-electrode (Revsbech and Jørgensen, 1986; Helder and Bakker, 1985; Revsbech, 1983). The temperature was maintained stable with an insulating device. This operation was completed in duplicate within 30 min after core recovery. Subsequently, the core used for O_2 profiling was sliced into thin horizontal sections (every 0.5 cm for the top 2 cm, 1 or 2 cm below) within 1 h and 30 min. For every level a sub-sample was centrifuged under N_2 at 5000 rpm for 20 min in order to collect pore waters. Two aliquots of water were filtered (0.2 μm) and frozen at −25°C for nutrient analyses. Interstitial water compounds were analysed by techniques adapted for small volumes of samples (Anschutz et al., 1999; Hyacinthe et al., 2001). Nitrate and nitrite were measured by flow

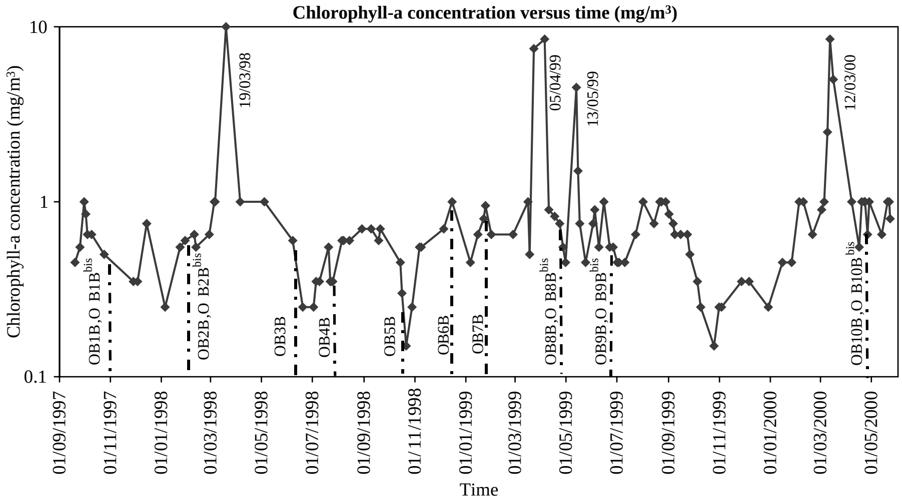

Fig. 2. Chlorophyll-*a* concentrations in the surface waters in our study area between October 1997 and April 2000 (estimates based on SEAWIFS images). Vertical dot–dash lines indicate when the sampling cruises took place.

Table 1
Sampling dates, bottom water oxygen concentration, depth in the sediment of the zero oxygen level and semi-quantitative analysis performed on the sedimentary residual parts of the first quarter of sediment for 15 cores at station B for the 10 sampling cruises; Phytoplankton and zooplankton components were observed and described according to the following classes: + + abundant, + common, − rare, — absent

Cores station B	Date	O_2 concentration (μmol/l)	Oxygen penetration depth (mm)	Whitish filamenteous and/or amorphous phytodetrital aggregates	Radiolarians
OB1B/OB1B^{bis}	26/10/1997	217	17	+ +/−	−/−
OB2B/OB2B^{bis}	30/01/1998	216	24	+	—
OB3B	07/06/1998	212	19	−/+	−/−
OB4B	23/07/1998	208	18	+	—
OB5B	17/10/1998	205	21	−	—
OB6B	08/12/1998	212	20	−	—
OB7B	23/01/1999	220	26	+	—
OB8B/OB8B^{bis}	19/04/1999	207	20	−/−	−/+
OB9B/OB9B^{bis}	24/06/1999	215	21	+/+ +	+/+
OB10B/OB10B^{bis}	25/04/2000	221	23	+ +/+ +	−/−

injection analysis (FIA) according to Anderson (1979).

For faunal analysis, one entire 72 cm^2 core was sliced horizontally for each station, usually every 0.25 cm for the first cm of sediment, every half cm between 1 and 4 cm depth, and every cm between 4 and 10 cm. For evaluating the amplitude of spatial heterogeneity, all available duplicate samples were analysed as well. This concerns samples OB1B^{bis} (the top 2 cm of a second core, partially sampled in 0.5 cm intervals), OB2B^{bis} (top 5 cm sampled in 2.5 cm intervals), OB8B^{bis} (sampled down to 5 cm according to the standard sampling protocol), OB9B^{bis} and OB10B^{bis} (both completely sampled). Except for OB10 (two consecutive multi-corer deployments), each duplicates pair was recovered from the same multi-corer deployment. Since in all cores more than 95% of the fauna is found in the top 5 cm, OB2B^{bis}, OB8B^{bis} and OB9B^{bis} can be considered as fully reliable duplicates. Census data of core OB1B (> 150 μm fraction) have already been presented in Fontanier et al. (2002). Nevertheless because of some taxonomic improvements, we present slightly modified census data here (Appendix B).

We follow the same sediments storage and preparation as presented in Fontanier et al. (2002). Foraminifera belonging to the > 150 μm fraction were studied along the 10 cm long cores. Because of its extremely time-consuming character, we limited our study of the 63–150 μm fraction to the first half cm of the sediment. In cases where the sediment surface is oblique, the volume of the top half cm layer may be slightly variable, and therefore, absolute density values for the superficial samples are less reliable. During picking, semi-quantitative analyses were performed on the residual parts of both fractions to evaluate some remarkable sedimentary components (phytodetritus and zooplankton compounds; Table 1).

The Rose Bengal staining technique (Walton, 1952; Bernhard, 1988) is routinely used to recognise foraminifera that were alive at the time of sampling. A problem of this method is that Rose Bengal may also stain the dead foraminiferal protoplasm, which may be partially preserved below the zero oxygen level within the sediment for a considerable period of time after the death of the organism (Bernhard, 1988; Corliss and Emerson, 1990). As a consequence, we use the same strict staining criteria as those detailed in Fontanier et al. (2002). Non-transparent agglutinated and miliolid taxa were broken in order to inspect the test interior. Fragments of the very fragile arborescent agglutinating foraminiferal fragments (such as *Hyperammina* spp., and *Glomospira* spp.)

were not included in the quantitative analyses, because the orange-reddish colour of their test makes it particularly difficult to appreciate whether the organism was alive or dead at the time of sampling.

Our taxonomical framework is given in Appendix A. All foraminiferal census data are listed in Appendices B and C. The total density of the live foraminiferal fauna total density has been determined by summing up the number of individuals for all levels between 0 and 10 cm depth for the >150 μm fraction, but only for the 0–0.5 cm interval for the 63–150 μm fraction. The total density per core is expressed as number of individuals found at and below a 72 cm^2 sediment surface. In all graphs depicting the vertical distribution of the foraminifera in the >150 μm fraction (Figs. 5a–m), the faunal densities have been standardised for a 50 cm^3 sediment volume.

The average living depth (ALD$_x$, Jorissen et al., 1995) seems the best way to describe the overall vertical distribution of the total foraminifera fauna or of individual taxa, and to get a general idea about the microhabitat patterns. After a first classification with four main microhabitats proposed by Corliss and Chen (1988), it has been argued that only species living on elevated substrates can be considered as "epifaunal" (Buzas et al., 1993). Therefore, in the soft bottom communities described in this study, we recognise only three different microhabitat categories: shallow infaunal, intermediate infaunal and deep infaunal taxa. The ALD$_x$ is calculated with the following formula:

$$\mathrm{ALD}_x = \sum_{i=0,x} (n_i \times D_i)/N,$$

where x is the lower boundary of deepest sample, n_i is the number of specimen in interval i, D_i the midpoint of sample interval i, and N is the total number of individuals for all levels.

For all stations, ALD$_{10}$ was calculated for the whole fauna, as well as for individual taxa, on the basis of the numbers of stained individuals found in the successive sediment slices. Isolated individuals separated from the main population by more than 1 cm of "sterile" sediment (without live individuals of the studied taxon) were not integrated in the calculations of the ALD$_{10}$. We suppose that such isolated individuals have been transported downward (outside their normal microhabitat) by bioturbation, or correspond to dead organisms that have been counted erroneously. Overall, weighed ALD$_{10}$ values were calculated for each taxon by integrating the results obtained in the 13 cores:

$$\overline{\mathrm{ALD}_{10}} = \sum_{i=1,n}^{n} (\mathrm{ALD}_{10}^{i} \times n_i) / \sum_{i=1,n}^{n} n_i,$$

where n is the number total of cores, ALD$_{10}^{i}$ the average living depth for the 10 first cms of the core I, and n_i is the number of specimen in the core i.

In order to evaluate the differences between duplicate and temporally distinct samples, a non-standardised principal component analysis (Davis, 1986) was applied for both size fractions, using the percentages of all taxa with an occurrence of more than 5% in at least one sample.

4. Results

4.1. Chlorophyll-a concentrations from October 1997 to April 2000

In the Bay of Biscay, the spring bloom chlorophyll-*a* increase is the most prominent seasonal event of the year (Fig. 2). This gradual or pulse-like increase of chlorophyll-*a* concentration generally starts with a first pulse at the end of winter, in the second part of March (Fig. 2), which affects the whole Bay of Biscay. A second pulse appears in the second half of April, and lasts through the first weeks of May. This second pulse has a more restricted geographical distribution, and at our sampling station, we observed it only in spring 1999.

In summer, the offshore waters of the Bay of Biscay exhibit rather low chlorophyll-*a* concentrations (0.1–0.5 mg/m^3); higher values are present over the shelf and shelf break. However, we can imagine that phytoplankton biomass associated with a putative Deep chlorophyll maximum is not represented in satellite images.

In autumn, the scarcity of satellite images allows far reliable estimates of chlorophyll-*a* concentrations. This period is characterised by low surface water phytoplankton biomass for the whole Bay of Biscay. Chlorophyll-*a* concentrations are minimal in late autumn and early winter.

At our station B, the variability of the chlorophyll-*a* concentrations in the overlying surface waters is in close agreement with the basin-wide patterns inferred before. In late autumn and in the winter, chlorophyll-*a* concentrations are low ($<0.7\,mg/m^3$). They precede high and abrupt chlorophyll-*a* increases (up to $10\,mg/m^3$), which can be noticed every year in late winter (March 1998, 1999 and 2000). Only in 1999 is a second chlorophyll-*a* increase observed, on the 13th of May. The summer is characterised by intermediate chlorophyll-*a* concentrations (about $1\,mg/m^3$). In early autumn (October), the chlorophyll-*a* concentrations are comparable to those in summer. Minimal surface water chlorophyll-*a* values, of about $0.2\,mg/m^3$, are reached in October; surface waters remain oligotrophic (0.2–$0.5\,mg/m^3$) until January.

4.2. Sedimentary organic deposits

Semi-quantitative observations of the sieve residues of the first half centimetre reveal that cores sampled in October 1997, in June 1999 and in April 2000 (OB1B, OB9B^{bis}, OB10B and OB10B^{bis}, respectively) contain high amounts of whitish amorphous aggregates composed of diatoms and of radiolarians (Table 1). These organic aggregates were observed after sieving of the samples, and therefore, benthic eventual foraminiferal faunas living within the organic aggregates could not be substantiated.

4.3. Oxygen concentration and redox conditions of interstitial waters

Bottom water oxygen concentrations (Table 1, Fig. 3a) vary from 205 to 221 μmol/l. The zero oxygen boundary varies from 17 mm depth (0B1B, October 1997) to 26 mm depth (OB7B, January 1999). In all cases, there is a steep decrease of oxygen concentration in the first half cm of the sediment. The nitrate and nitrite concentrations (Fig. 3b) have maximum values (of about 20 μmol/l) in the first half cm, and show a rapid decrease to background values at about 2.5 cm depth.

4.4. Faunal density and number of taxa

In the $>150\,\mu m$ fraction, foraminiferal densities vary from 245 to 1346 individuals per core (Fig. 4). Maxima of 1346 and 845 individuals are found in October 1997 (OB1B) and April 2000 (OB10B), respectively. Minimum values are recorded in July 1998 (OB4B, 281 individuals), October 1998 (OB5B, 322 individuals) and April 1999 (245 and 465 individuals in two replicate cores). For the 63–150 μm fraction, foraminiferal densities (only for the topmost 0.5 cm) vary from about 40–2195 individuals (Fig. 4). Maxima of 1505 and 2195 individuals are found in October 1997 (OB1B) and in April 2000 (OB10B^{bis}); minimum values are found in December 1998 (OB6B, 37 individuals) and in October 1998 (OB5B, 73 specimens). Part of this variability, however, may be due to the variable sample size of the first 0.5 cm in the case of oblique sediment surfaces.

In the $>150\,\mu m$ fraction, perforate foraminifera form the main faunal component (60% to 90% of the fauna). Non-fossilising agglutinated taxa account for 10–30%, whereas fossilising agglutinated taxa (maximum 10%) and miliolids (maximum 3.5%) are rare in all cores. Also in the 63–150 μm fraction, the perforate group is largely dominant (50–95%), but non-fossilising agglutinated individuals can represent up to 48% of the total fauna (in April 1999, OB8B). Miliolids and fossilising agglutinated foraminifera account for less than 5% of the foraminiferal faunas.

The number of taxa in the $>150\,\mu m$ fraction varies from 31 (December 1998, OB6B) to 57 (June 1999, OB9B^{bis}), without a clear relation to faunal density. In the 63–150 μm fraction, where only the topmost 0.5 cm was studied, the number of taxa varies from 16 (December 1998, OB6B) to 65 (October 1997, OB1B); there is a clear positive correlation with the faunal density here.

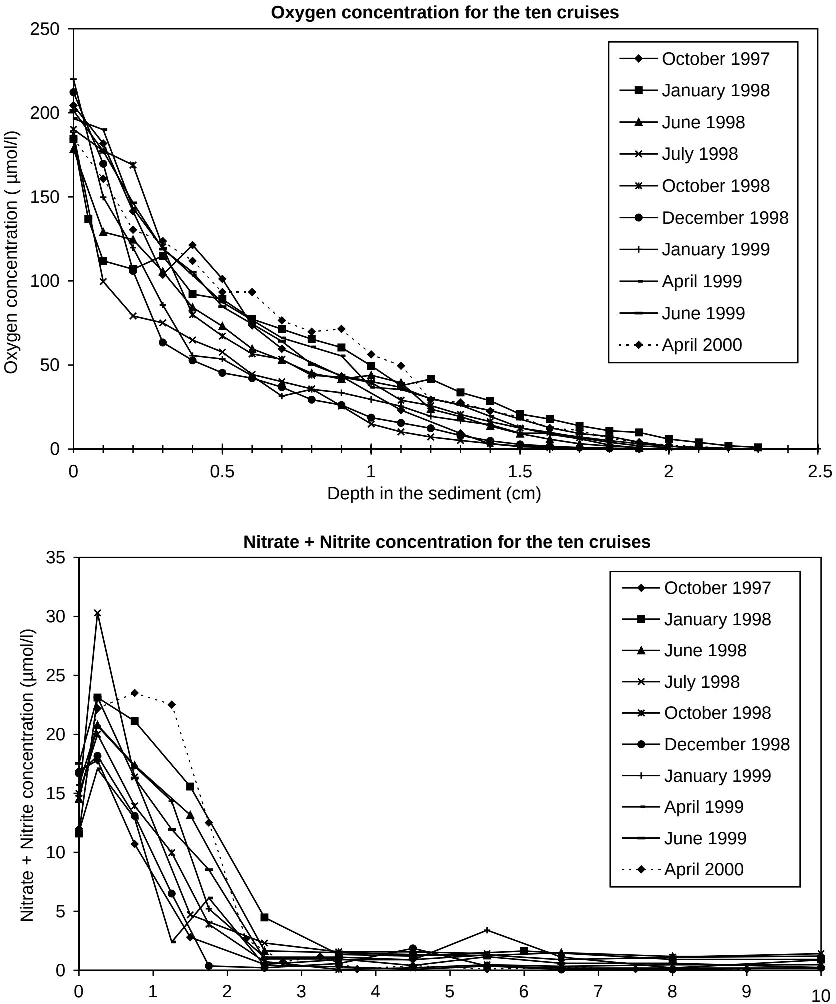

Fig. 3. (a) Dissolved oxygen concentrations in the sediment for the ten cruises; (b) Nitrate + nitrite concentrations in the sediment for the ten cruises.

4.5. Faunal composition and microhabitat

(1) *>150 µm fraction*: For most of the cores, the foraminiferal fauna is strongly concentrated in the oxygenated sediment top layers (Figs. 5a–m). The highest density is normally found in the first half cm. Maximum values were observed in October 1997 (OB1B; ~800 specimens/50 cm^3) and April 2000 (OB10B; ~500 specimens/50 cm^3). In most cores, the faunal density drops rapidly in the second cm, where dysoxic conditions prevail. Only low-density foraminiferal faunas are found in the generally anoxic sediments below 2 cm depth. The cores taken in December 1998 (OB6B) and April 1999 (OB8B^{bis}), which contain fair amounts of live individuals below the zero oxygen level, form notable exceptions. Consequently, for most of the cores, the ALD$_{10}$ of the total fauna is about 1 cm. Maximum ALD$_{10}$ values are found in December 1998 (OB6B; 2.0 cm) and April 1999 (OB8B^{bis}; 1.6 cm). The shallowest microhabitat depth was observed in July 1998 (ALD$_{10}$ = 0.6 cm).

Uvigerina mediterranea dominates the faunas in every core (Appendix B); its relative abundance

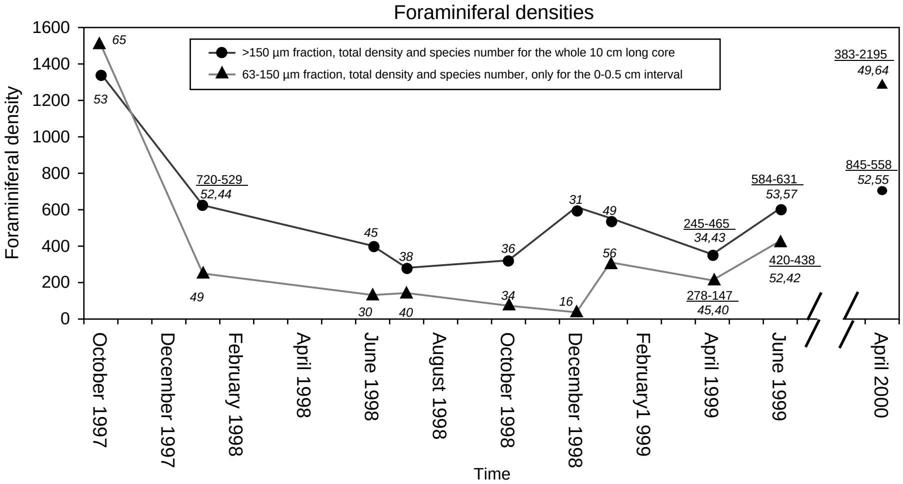

Fig. 4. Foraminiferal density for both size fractions during the ten cruises. The foraminiferal density for the $>150\,\mu m$ fraction is calculated as the total number of live individuals per core of $72\,cm^2$. The foraminiferal density for the 63–150 µm fraction is calculated as the total number of live foraminifera in the first half cm of the core. When duplicate cores are available, an average value is plotted, and the values of the individual cores are given (underlined numbers). For all cores, the number of species is given in italics. When duplicate cores are available, the values of the individual cores are also presented (couple of numbers in italics).

fluctuates from 17.8% to 39.9%, with maximum percentages observed in January 1998 (OB2B) and June 1999 (OB9B^{bis}). Minimum values are found in July 1998 (OB4B) and April 1999 (OB8B^{bis}). *Melonis barleeanus* is the second most abundant species; in most samples it counts for about 10% of the total fauna (4.1–16.7%). *U. peregrina* has a much more variable percentage. It is very frequent in October 1997 (OB1B and OB1B^{bis}), when its percentage reaches 21%. In many other samples, the species is rather infrequent (2–5%). *Globobulimina affinis* is well represented in most cores, with relative abundances of about 5%. The highest percentage (12–15%) is found in April 1999 (OB8B and OB8B^{bis}). *U. elongatastriata* and *Reophax scorpiurus* account each for about 5% of the faunas. Some other taxa show relatively low background values (1–3%), but can occasionally occur with high percentages. *Cibicidoides pachydermus* shows a 7.2% maximum in January 1998 (OB2B), whereas *Clavulina cylindrica* is well represented (7.7%) in June 1998 (OB3B). *Cribrostomoides subglobosus* shows peak values (9–12%) in June 1998 (OB3B), October 1998 (OB5B), and April and June 1999 (OB8B^{bis} and OB9B^{bis}). *Pseudoclavulina crustata* shows one single peak occurrence (9%), in April 1999 (OB8B).

The microhabitat of the majority of the taxa is very shallow (Table 2). The overall, weighed, values are lowest for *C. pachydermus* ($ALD_{10}=0.54$ cm), *P. crustata* ($ALD_{10}=0.71$ cm), *R. scorpiurus* ($ALD_{10}=0.75$ cm), *U. mediterranea* ($ALD_{10}=0.77$ cm), *U. peregrina* ($ALD_{10}=0.78$ cm) and *C. subglobosus* ($ALD_{10}=0.82$ cm); these species are largely restricted to the shallow infaunal microhabitats in the first cm of the sediment (Figs. 5a–m). Their ALD_{10} shows very little variability between the 13 cores (Table 2), with the exception of core OB6B, where the microhabitat of all taxa is significantly deeper than normal. The anomalously low numbers in the first 0.5 cm level at this station (in the 63–150 µm as well as in the $>150\,\mu m$ fraction) suggest that, because of a strongly oblique sediment surface, only a minor part of the $72\,cm^2$ surface was sampled. This sampling artefact effects the calculation of the microhabitat, and the density value in the 63–150 µm fraction, but not the total density values (down to 10 cm) in the $>150\,\mu m$ fraction.

M. barleeanus (overall weighed $ALD_{10}=1.30$ cm), *U. elongatastriata* (overall weighed

$ALD_{10} = 1.47$ cm) and *C. cylindrica* (overall weighed $ALD_{10} = 1.46$ cm) show a rather constant intermediate infaunal microhabitat, with the exception of core OB6B, where all occurrences are deeper. *G. affinis* (overall weighed $ALD_{10} =$ 2.84 cm) occupies a deep infaunal microhabitat, in dysoxic or sometimes totally anoxic sediment layers.

(2) *63–150 μm fraction*: The densities of the main taxa in the topmost 0.5 cm of the fifteen cores are shown in Fig. 6 and Appendix C. Because of the extreme variability of foraminiferal density, which may be partially due to a varying sampling volume (see Methods section), the faunal variability may be better represented by percentage data, which are presented in Appendix C. The faunas in this small size fraction are much more variable than those in the >150 μm fraction. *R. guttiferus* is a frequent taxon in many cores; it accounts for about 27% in June 2000 (OB9B^{bis}), and for 10–15% in October 1997 (OB1B), January 1998 (OB2B), December 1998 (OB6B), January 1999

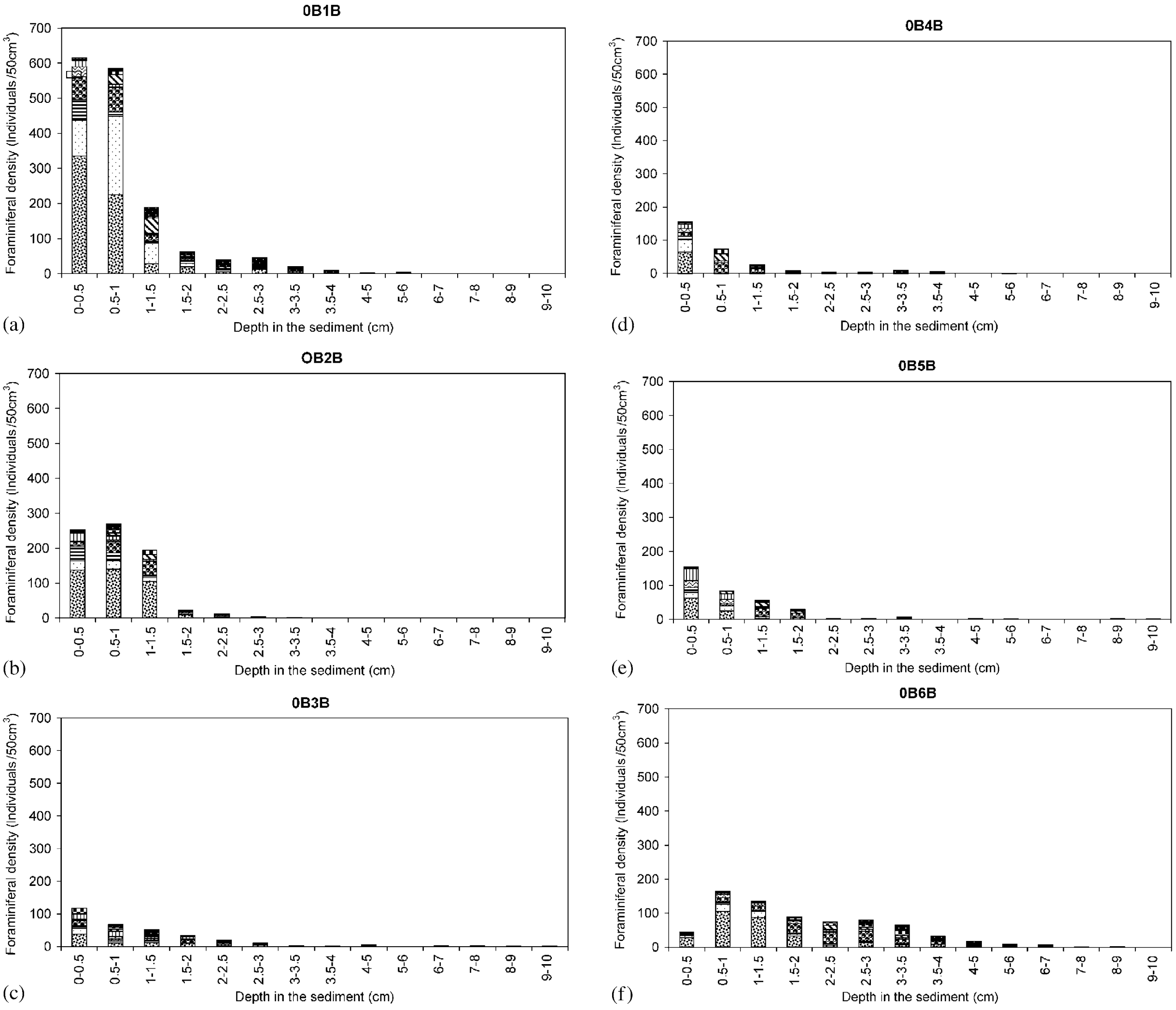

Fig. 5. (a—m) Foraminiferal distribution (number of individuals >150 μm fraction found in each level, standardised for a 50 cm^3 sediment volume) for 14 available cores. Data for core OB1B in (a) comes from corrected data presented in Fontanier et al. (2002).

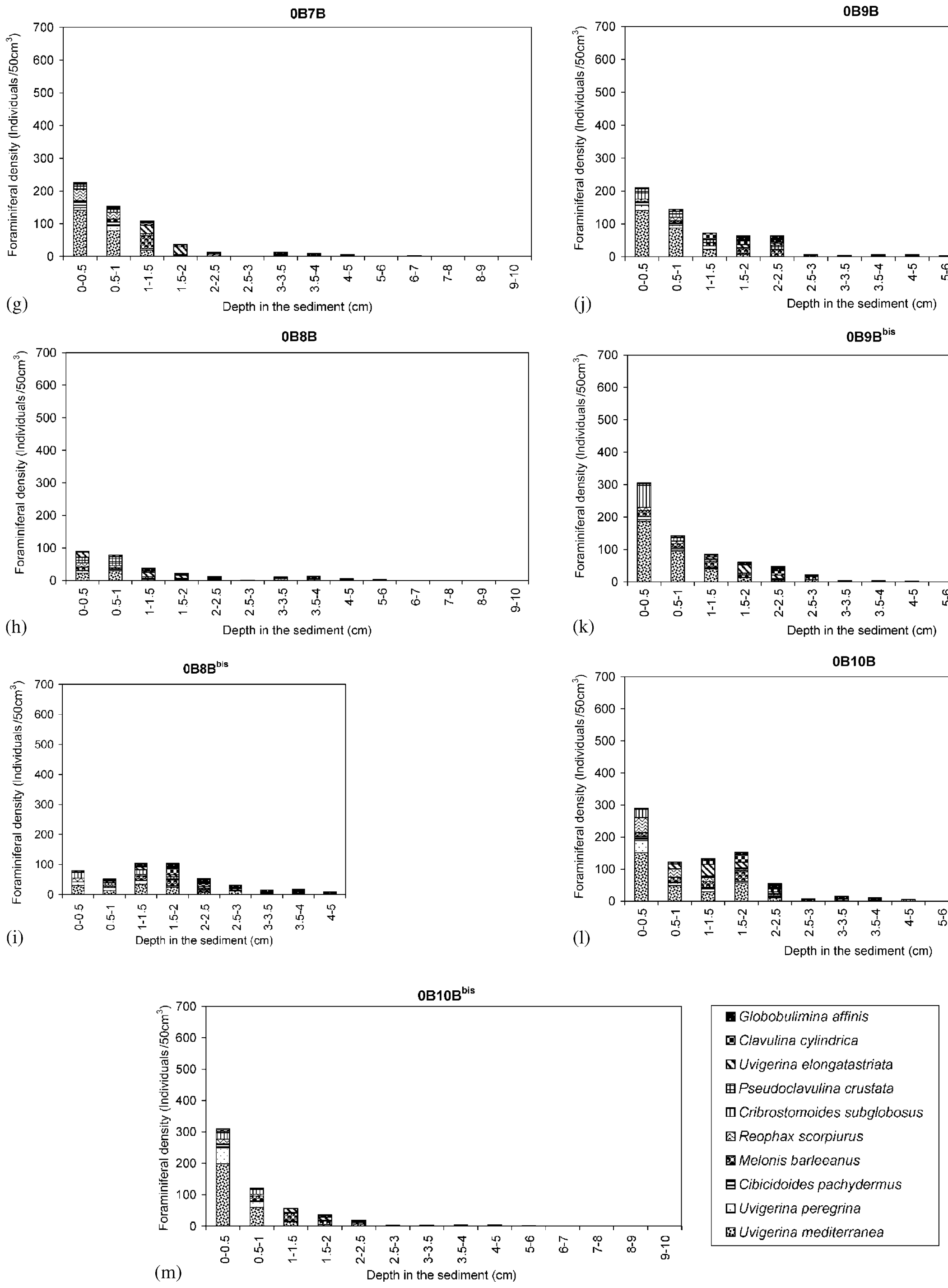

Fig. 5 (*continued*).

Table 2
Average living depth (ALD_{10}) of foraminiferal species and (in parentheses) the number of individuals on which the calculation is based. Only occurrences of ⩾5 individuals are shown. The grey boxes represent dominant taxa with a relative proportion ⩾5% at least one of the stations. Microhabitat patterns are summarised as shallow infaunal (SI), intermediate infaunal (II) or deep infaunal taxa (DI)

Taxa	ALD_{10}													Average weighted ALD_{10}	Microhabitat
	OB1B	OB2B	OB3B	OB4B	OB5B	OB6B	OB7B	OB8B	OB8B^{bis}	OB9B	OB9B^{bis}	OB10B	OB10B^{bis}		
Amphicoryna scalaris											0.7 (6)	0.3 (9)		0.49	SI
Bolivina alata	1.1 (6)	0.9 (7)			1.5 (8)	2.7 (7)	1.7 (20)		2.0 (8)			1.6 (18)	2.0 (8)	1.68	II
Bolivinita quadrilatera	0.2 (7)											0.4 (6)		0.31	SI
Bulimina marginata	1.2 (19)	2.7 (18)	2.8 (9)			1.8 (5)			0.9 (9)	0.4 (9)		1.0 (8)	0.2 (5)	1.54	II
Chilostomella oolina									3.2 (19)	4.2 (12)		2.4 (31)	3.5 (18)	3.09	DI
Cibicides wuellerstorfi		0.6 (6)												0.63	SI
Cibicidoides pachydermus	0.6 (63)	0.5 (52)	0.5 (11)	0.1 (8)	0.2 (10)	1.5 (14)	0.4 (23)			0.5 (11)	0.4 (11)	0.6 (16)	0.3 (10)	0.54	SI
Cibicidoides ungerianus				0.1 (5)			0.3 (8)				0.8 (5)	1.2 (7)	0.8 (8)	0.63	SI
Globobulimina affinis	2.4 (80)	0.9 (19)	2.5 (33)	2.3 (17)	3.1 (13)	4.1 (55)	3.8 (38)	2.9 (31)	2.7 (71)	3.1 (51)	2.5 (24)	2.5 (41)	3.2 (20)	2.84	DI
Gyroidina altiformis	0.2 (9)													0.24	SI
Hyalinea balthica	0.8 (12)	0.8 (7)					0.3 (14)			0.4 (10)	0.3 (6)	0.6 (7)		0.54	SI
Lenticulina peregrina	0.2 (7)													0.23	SI
Melonis berleeanus	0.8 (121)	1.1 (69)	1.1 (40)	0.9 (43)	1.4 (34)	2.3 (103)	1.2 (40)	0.5 (10)	1.7 (35)	1.7 (41)	1.2 (52)	1.3 (61)	1.2 (41)	1.30	II
Nuttallides umboniferus	0.3 (5)									0.8 (5)				0.58	SI
Pullenia quinqueloba		1.1 (9)			1.3 (6)									1.16	II
Siphogenerina columellaris	0.6 (30)	0.5 (17)		0.2 (11)	0.6 (6)	1.3 (9)	0.4 (12)			0.6 (8)	0.5 (14)	0.8 (22)	0.4 (14)	0.60	SI
Uvigerina elongatastriata	1.3 (61)	1.4 (20)	1.8 (11)	0.7 (20)	1.2 (20)	2.5 (21)	1.5 (42)	1.1 (32)	1.7 (22)	1.7 (15)	1.7 (37)	1.4 (58)	1.8 (25)	1.47	II
Uvigerina mediterranea	0.6 (453)	0.7 (287)	1.4 (88)	0.4 (50)	0.5 (50)	1.6 (225)	0.5 (177)	1.2 (50)	1.3 (90)	0.6 (189)	0.6 (251)	0.8 (216)	0.4 (206)	0.77	SI
Uvigerina peregrina	0.8 (289)	0.6 (44)	1.2 (36)	0.5 (31)	0.6 (26)	1.4 (45)	0.7 (19)	1.1 (13)	1.3 (33)	0.7 (27)	0.8 (11)	0.6 (45)	0.4 (50)	0.78	SI
Cornuspira involvens		0.8 (5)		0.4 (8)										0.59	SI
Agglut. sp.A											0.3 (8)			0.28	SI
Adercotryma glomerata							0.1 (7)			1.0 (9)				0.63	SI
Ammolagena sp.	0.4 (5)													0.38	SI
Ammoscalaria sp.									1.0 (17)				0.3 (10)	0.71	SI
Clavulina cylindrica	1.0 (10)	1.0 (17)	0.9 (31)	0.9 (14)	1.2 (6)	2.6 (32)	1.3 (13)	0.9 (8)	1.7 (30)	1.4 (27)	2 (16)	1.6 (35)	0.2 (5)	1.46	II
Cribrostomoides subglobosus	0.5 (20)	0.5 (30)	1.1 (43)	0.5 (13)	0.9 (41)	2.0 (25)	0.2 (7)	1.2 (14)	1.2 (41)	0.9 (25)	0.4 (61)	0.5 (23)	0.4 (27)	0.82	SI
Cyclammina sp.1													0.3 (5)	0.28	SI
Cyclammina sp.2	0.2 (5)	1.0 (6)			2.5 (8)		0.3 (5)			0.4 (6)				1.01	II
Cyclammina sp.3	0.3 (7)	0.4 (14)										0.3 (7)		0.37	SI
Eggerella scabra	0.6 (6)	0.8 (15)	1.1 (6)	0.5 (12)	1.0 (11)	0.6 (6)				0.5 (6)	0.5 (10)	0.9 (11)	0.3 (7)	0.71	SI
Haplophragmoides bradyi								0.9 (5)		0.9 (6)		0.6 (6)		0.82	SI
Reophax sp.1												0.2 (7)		0.16	SI
Reophax fusiformis	0.7 (7)									0.7 (6)				0.71	SI
Reophax guttiferus	0.3 (19)	0.9 (14)										0.3 (14)		0.50	SI
Reophax scorpiurus	0.3 (25)		1.1 (14)	0.2 (9)	0.4 (25)	1.2 (20)	0.5 (41)	1.0 (22)	0.8 (18)	0.6 (14)	0.9 (21)	1 (74)	0.5 (15)	0.75	SI
Rhabdammina cornuta												0.4 (9)		0.39	SI
Saccammina spp.							0.6 (8)		1.9 (5)	0.8 (21)		0.9 (19)		0.91	SI
Technitella melo												0.6 (8)		0.59	SI
Bigenerina nodosaria	0.4 (9)					0.9 (5)	0.5 (8)				0.5 (8)	0.3 (27)	0.4 (8)	0.43	SI
Pseudoclavulina crustata	0.9 (10)						0.5 (14)	0.7 (22)		0.9 (24)	0.5 (5)		0.3 (5)	0.71	SI
Siphotextularia affinis	0.5 (9)													0.51	SI

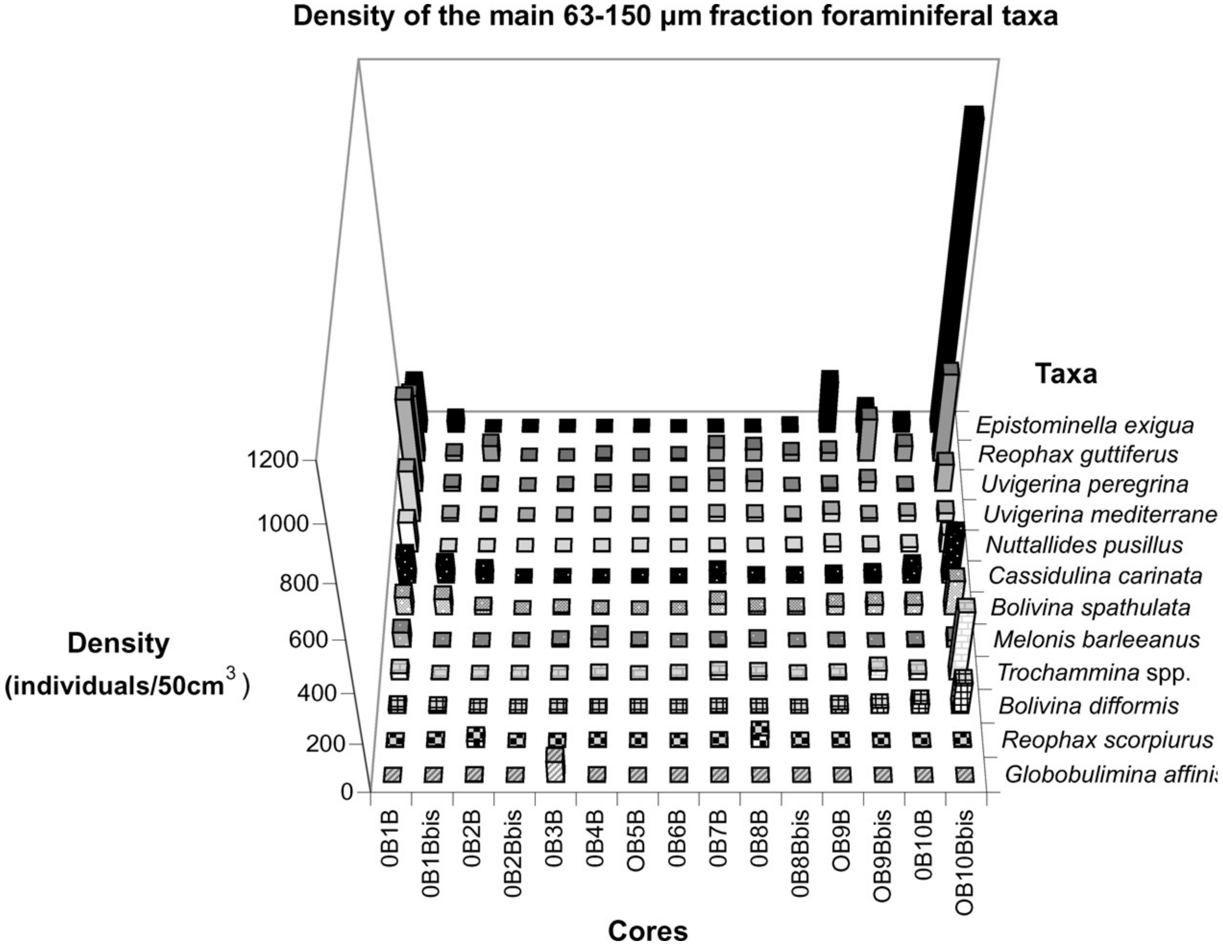

Fig. 6. Foraminiferal density of the main foraminiferal taxa in the 63–150 μm fraction for the 15 cores. Densities are standardised to a 50 cm^3 sediment volume.

(OB7B), April 1999 (OB8B and OB8B^{bis}) (OB9B) and April 2000 (OB10B and OB10B^{bis}). *Epistominella exigua* occurs with spectacular peak abundances in April 2000 (OB10Bbis—35.6%), June 1999 (OB9B—32.5%; OB9B^{bis}—14%) and October 1997 (9% in both OB1B and OB1B^{bis}). *U. peregrina* occurs with about 15% abundance in October 1997 and October 1998 (OB1B and OB5B), whereas *C. carinata* exhibits values from 10–15% in October 1997 (OB1B^{bis}), April 2000 (OB10B), January 1998 (OB2B) and December 1998 (OB6B). *G. affinis* shows a spectacular peak occurrence in June 1998 (OB3B—45%), whereas *M. barleeanus* is frequent in July 1998 (OB4B—15%). Many other species, such as *Bolivina spathulata*, *Gyroidina umbonata*, *Nonionella* spp., *Siphogenerina columellaris*, *U. mediterranea*, *R. scorpiurus*, and *Trochammina* spp. show shifts from near-absence to values of about 10%, highlighting the extreme variability of the 63–150 μm fraction.

5. Discussion and conclusions

5.1. Organic matter deposits

The presence of organic aggregates at the sediment–water interface appears to follow phytoplankton bloom events taking place several weeks before the cruises (Table 1, Fig. 2). This is especially the case for OB10 (6 weeks after the first 2000 spring bloom) OB9 (6 weeks after the second 1999 spring bloom) and 0B1 (4 weeks after a 1997 autumn chlorophyll-*a* maximum). We suppose that the organic aggregates represent the remains of phytoplankton deposits following these surface water bloom periods.

5.2. Spatial heterogeneity of the benthic ecosystem at station B

Most of studies dealing with temporal variability of benthic foraminiferal faunas taxa (e.g. Gooday, 1988; Gooday and Lambshead, 1989; Thiel et al., 1990; Gooday and Turley, 1990; Thurston et al., 1994; Kitazato and Ohga, 1995; Silva et al., 1996; Kitazato et al., 2000) avoid the fundamental question what part of the observed differences is due to spatial variability (patchiness) and what part is really due to temporal variability, resulting from the intermittence of export production. Barmawidjaja et al. (1992) moderate their conclusions about seasonal changes of foraminiferal faunas from the Northern Adriatic Sea by underlining the possible importance of a patchiness effect and insist on the necessity to study replicate cores. Thiel et al. (1990) suggest that current activity and microtopography may induce a patchy distribution of phytodetritus at the sea floor. Organic deposits create a mosaic of ephemeral organic rich patches on the ocean floor, which maintain sea floor heterogeneity, and contribute to the high diversity of deep sea benthic communities (Grassle and Morse-Porteous, 1987; Grassle, 1989; Snelgrove et al., 1994, 1996). Hohenegger et al. (1993) demonstrate that foraminiferal faunas have patchy distributions which are interpreted as being food controlled. In a study using duplicate cores, in recently enriched sediments, Silva et al. (1996) show that spatial faunal variability (patchiness) exists but does not obscure studies on the temporal and seasonal changes of the foraminiferal faunas, which are much more prominent.

In order to distinguish between spatial and temporal variability in our cores we performed a non-standardised principal component analysis (Davis, 1986) on the basis of the percentage data of all taxa which appear with at least 5% in one of the cores. For the $>150\,\mu m$ fraction, this multivariate analysis is based on 15 samples (10 samples and 5 duplicates) and 10 taxa, and yields two significant axes, explaining 68% of the total variability. The eigenvalues for these two axes and the species loadings on the axes are given in Table 3a. The positive side of axis 1 is highly dominated by *U. mediterranea* (0.90), whereas *G. affinis*, *R. scorpiurus*, *U. elongatastriata*, *Cribrostomoides subglobosus*, and *Clavulina cylindrica* all load negatively on the first axis. The positive side of the second axis is strongly dominated by *U. peregrina* (0.92), while *U. mediterranea*, *G. affinis* and *C. subglobosus* load negatively. Fig. 7 shows the position of the 15 cores in the axial plot. The first axis allows separation of all rather poor samples (total density less than 500 individuals, PCA1 $\leqslant 16.0$) from all relatively rich samples (total density $>$ 500 specimens, PCA1 >18.0), suggesting that the first axis is related to ecosystem enrichment due to phytodetritus deposits, a phenomenon which is always accompanied by an increase of the percentage of *U. mediterranea*. The second axis tends to separate cores OB1B and OB1B$^{\mathrm{bis}}$, which are both strongly enriched in *U. peregrina*, from all other cores with high scores on axis 1. This suggests that there are two possible responses to ecosystem enrichment; in most cases *U. mediterranea* shows the clearest response, but in October 1997 the large increase of *U. peregrina* is the most obvious phenomenon accompanying the faunal density increase. These two possible responses, translated by a different position on axis 2, could be explained by a different quality of the organic matter between the spring and autumn blooms. All five pairs of duplicate cores are fairly close to each other. Although individual cores of these duplicate couples may have a higher similarity to other cores (e.g. core OB9B is much closer to OB7B than to OB9B$^{\mathrm{bis}}$), showing the presence of significant spatial variability, the distances between extreme samples are much bigger than the maximum distance between duplicate couples. This suggests that for the $>150\,\mu m$ fraction, temporal variability is more important than spatial variability.

Table 3

(a–c) Results of non-standardised principal component analyses based on the percentages of the main foraminiferal taxa in the >150 and 63–150 μm fraction (percentage ⩾5%). (a) Eigenvalues and species loadings of the two significant axes for the >150 μm fraction. (b) Same, for the 63–150 μm fraction. (c) The normative distance between cores in the five-dimensional space (normative distance between the five pairs of replicate cores are given in bold letters)

(a)

>150 μm fraction	PCA1	PCA2
Eigenvalues column	67.8	37.3
Percent of trace	44.3	24.4
Cumulative percent of trace	44.3	68.7
Taxa		
Cibicidoides pachydermus	0.11	0.12
Globobulimina affinis	−0.28	−0.16
Melonis barleeanus	0.03	0.09
Uvigerina elongatastriata	−0.16	−0.11
Uvigerina mediterranea	0.90	−0.19
Uvigerina peregrina	0.04	0.92
Clavulina cylindrica	−0.14	−0.12
Cribrostomoides subglobosus	−0.16	−0.15
Reophax scorpiurus	−0.17	−0.07
Pseudoclavulina crustata	−0.09	−0.06

(b)

63–150 μm fraction	PCA1	PCA2	PCA3	PCA4	PCA5
Eigenvalues column	172.4	123.9	51.3	36.4	23.6
Percent of trace	36.7	26.4	10.9	7.8	5.0
Cumulative percent of trace	36.7	63.1	74.1	81.8	86.8
Taxa					
Bolivina sp.1	0.00	−0.04	0.09	0.06	0.05
Bolivina spathulata	−0.04	0.04	0.16	0.40	0.10
Bolivina difformis	−0.06	0.06	0.04	0.05	−0.06
Bulimina marginata	−0.03	−0.05	0.08	−0.06	−0.02
Cassidulina carinata	−0.06	−0.12	0.21	0.38	0.17
Ceratobulimina sp.	0.03	0.00	−0.03	0.02	0.04
Epistominella exigua	−0.57	0.76	−0.10	−0.08	−0.04
Globobulimina affinis	0.75	0.53	0.29	−0.18	0.03
Gyroidina umbonifera	−0.02	−0.04	−0.12	−0.20	0.27
Melonis barleeanus	0.14	−0.05	−0.38	0.04	−0.50
Nonionella spp.	0.09	0.00	−0.13	0.10	−0.22
Nuttalides pusillus	−0.04	0.03	−0.06	−0.07	0.05
Pullenia spp.	−0.02	0.02	−0.13	−0.05	0.04
Siphogenerina columellaris	−0.08	−0.09	−0.09	0.05	−0.52
Uvigerina mediterranea	−0.01	−0.12	−0.10	−0.18	0.11
Uvigerina peregrina	0.02	−0.17	−0.32	−0.55	0.25
Haplophragmoides sp.	0.00	−0.03	0.09	0.09	0.17
Psammosphaera fusca	−0.01	−0.07	0.01	0.18	−0.06
Reophax guttiferus	−0.24	−0.19	0.68	−0.42	−0.28
Reophax scorpiurus	0.01	−0.11	0.04	0.02	0.17
Reophax sp.1	−0.02	−0.09	0.09	0.07	0.10
Trochammina spp.	−0.09	−0.01	0.13	−0.17	−0.31

Table 3 (*continued*)

(c)

	OB1B$^{\text{bis}}$	OB2B	OB2B$^{\text{bis}}$	OB3B	OB4B	OB5B	OB6B	OB7B	O8BB	OB8B$^{\text{bis}}$	OB9B	OB9B$^{\text{bis}}$	OB10B	OB10B$^{\text{bis}}$
OB1B	22.4	20.2	19.2	50.1	21.2	13.6	14.2	14.1	10.9	15.2	28.0	19.8	17.4	31.1
OB1B$^{\text{bis}}$		16.1	15.1	49.4	27.2	24.6	24.5	16.0	18.6	11.1	26.3	26.7	11.9	31.1
OB2B			17.6	49.2	25.9	26.4	12.4	7.9	11.8	8.0	36.0	21.1	10.7	38.3
OB2B$^{\text{bis}}$				47.1	12.7	20.6	20.9	12.1	14.7	13.7	31.6	27.8	11.0	34.9
OB3B					46.6	48.8	52.1	48.2	48.1	48.4	56.2	55.1	48.5	59.3
OB4B						21.1	23.7	18.8	19.1	23.1	38.1	32.5	20.8	40.5
OB5B							23.3	20.1	15.7	22.2	33.7	32.9	24.4	39.3
OB6B								9.8	9.3	13.8	37.5	18.2	16.1	39.0
OB7B									5.7	6.8	33.3	20.7	8.5	35.9
OB8B										**11.4**	32.7	22.3	23.5	37.8
OB8B$^{\text{bis}}$											28.4	18.2	5.5	31.2
OB9B												**27.6**	27.9	8.9
OB9B$^{\text{bis}}$													18.6	25.7
OB10B														**29.9**

The 63–150 μm data (for the topmost 0.5 cm of the sediment) were subjected to a similar analysis, this time with 22 taxa. Because of extreme variability of the data set, with many different taxa having occasional peak occurrences, this second principal component analyses yields no less than five significant axes, explaining 86.8% of the total variability (Table 3b). In order to evaluate differences between samples, we calculated distances between all samples in the five-dimensional space defined by the significant axes (Table 3c). This table confirms that differences between duplicate samples (11–30 units) are larger in the 63–150 than in the > 150 μm fraction (2–12 units), but that maximum temporal differences (59 units) are still about two times higher than maximum spatial differences.

These multidimensional analyses suggest that small-scale patchiness exists, and cannot be completely ruled out, as a parameter explaining differences between the cores taken at different times. In the > 150 μm fraction, spatial variability seems to be smaller than in the 63–150 μm fraction, and, consequently, temporal variation should be more prominent in this larger size fraction. An important question is why duplicate samples are more different in the 63–150 μm than in the > 150 μm fraction. It is very probable that the high degree of patchiness is related to micro-relief and current activity, which cause a patchy distribution of organic matter on the ocean floor. In case of abundant input of organic detritus, phytodetritus aggregates will concentrate in depressions on the sea floor. This may explain important small-scale spatial variability in terms of concentration of phytodetrital compounds between duplicate samples (see for example the difference between OB1B and OB1B$^{\text{bis}}$). Small opportunistic taxa, such as *E. exigua*, may have a faster response than larger (> 150 μm) taxa, and will be first in colonising freshly deposited phytoplankton floccules (Gooday and Turley, 1990). This can be seen in October 1997 (OB1B and OB1B$^{\text{bis}}$), in June 1999 (OB9B and OB9B$^{\text{bis}}$) and in April 2000 (OB10B$^{\text{bis}}$), when organic aggregates are observed in the sieve residues, and when *E. exigua* reaches high densities (Table 1, Fig. 6). This taxon could feed on fresh microalgae and reproduce rapidly after phytodetritus deposits following the important surface water bloom periods preceding our sampling (Fig. 2). Furthermore, different small opportunistic taxa may colonise different organic-rich patches, increasing local patchiness. Still another possible explanation for the much higher variability of the 63–150 μm fraction could be that reproductive response to phytodetritus inputs of larger taxa would first be noticed by the presence of juveniles in the small

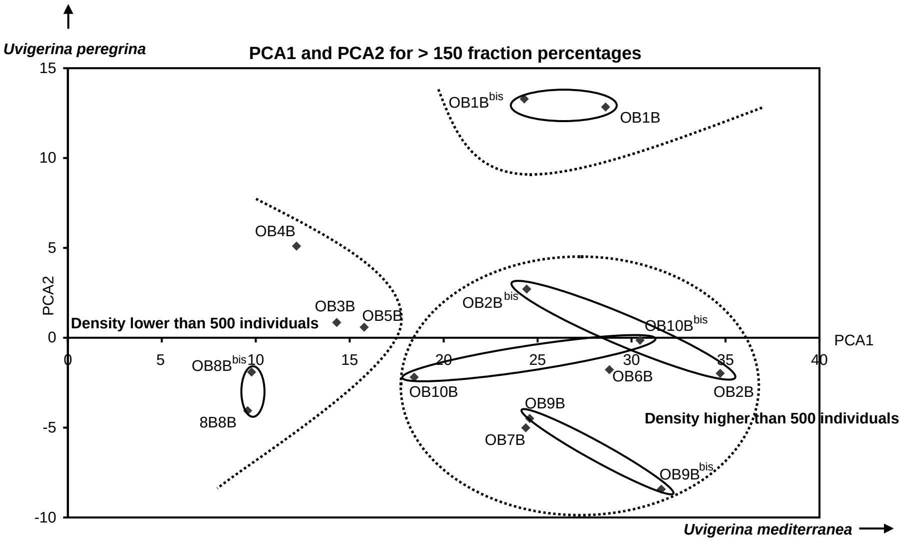

Fig. 7. Plot of the 15 cores in the 2-D space defined by the two main axes of the non-standardised principal component analysis (PCA1, PCA2), and three distinct faunal assemblages (indicated by the dotted lines).

size fraction. This is clearly the case in October 1997, when juvenile *U. peregrina* peak in the 63–150 µm fraction, and in June 1998, when *G. affinis* exhibits a similar reproductive event. Apparently, the response of the > 150 µm fraction is delayed, and increased numbers of the larger opportunistic taxa are found only after the impact of organic input has already been homogenised for a large surface area. Except for cores OB10B and OB10B^{bis}, which were collected in two different multi-tube corer deployments, spatial patchiness recorded for each other couple of duplicate samples suggests strong spatial variability of foraminiferal faunas on a scale of less than a meter. Faunal differences between cores OB10B and OB10B^{bis} reflect a larger scale (several hundred metres) foraminiferal variability.

Our results suggest that at least part of the foraminiferal patchiness is due to a spatially heterogeneous distribution of organic matter aggregates at the sediment–water interface. Just as heterotrophic bacterial consortia, which can respond quickly to patchy organic matter deposits (Turley et al., 1988; Thiel et al., 1990), some foraminiferal taxa can also take rapid advantage of freshly deposited organic patches. According to Gooday and Turley (1990), the patchy distribution of the organic material deposited after bloom events play a major role in structuring deep-sea benthic ecosystems.

5.3. *Temporal variability of bottom and pore water chemical characteristics*

Our data show a relative constancy in the chemistry of the bottom and interstitial waters. Bottom water oxygen concentrations are almost invariable throughout the investigated years; values range from 205 to 221 µmol/l. The vertical profiles of dissolved oxygen and nitrate in the uppermost sediment are rather similar for the 1997–2000 period (Figs. 3a and b). Deeper in the sediment bacterial consortia are able to reduce nitrate in anoxic environments in order to decompose the available organic compounds (Froelich et al., 1979; Fenchel and Finlay, 1995). The ammonia that is created during the mineralisation of organic nitrogen migrates upward to oxygenated layers, where it is transformed back into nitrate and nitrite by nitrifying bacterial consortia (Anschutz et al., 1999). Nitrate and nitrite diffuse downward to the anoxic layer, thus creating a gradient that overlies the oxygen zero boundary. In our cores, the downward nitrate–nitrite gradients always occur in the 0.25–2.5 cm depth range (Fig. 3b). The depth and amplitude variability is rather limited. No clear sulphate reduction zone was detected at station B; i.e. we detected no decrease with depth of sulphate and no significant increase of sulphide (Anschutz, 2002, pers. com.). Apparently, in this deep open-slope environment, the exported organic matter fluxes are not high enough to sustain a sharp sulphate gradient in the sampled cores. However, sulphate reduction may be a discrete phenomenon in the anoxic part of the core.

It seems that the seasonal variability of the exported organic matter flux is not high enough to induce significant fluctuations of the early diagenetic processes in the upper sediment. Apparently, we are far away from the variable conditions prevailing in the lower part of oxygen minimum zone areas (Jannink et al., 1998) or in some oligotrophic basins where sudden organic matter deposits may severely modify redox patterns at and below the sediment–water interface (Kitazato and Ohga, 1995; Kitazato et al., 2000; Duijnstee et al., 2001). At our station B, the phytodetritus deposits following main bloom periods (October 1997, June 1999 and April 2000; Table 1) have at most a minor impact on the redox conditions within the sediment and at the sediment–water interface. This is probably because of the overall eutrophic conditions reigning at our site. Fresh organic matter deposits, which are strongly concentrated at the sediment surface, are preferentially used as food by bacteria (Turley et al., 1988; Thiel et al., 1990; Danovaro et al., 2000a,b), but also by meiofaunal foraminifera, which as a whole appear to be an opportunistic group of organisms. This explains why most foraminiferal taxa are concentrated in the first cm and why the highest foraminiferal densities are most times recorded in the first half cm. The restriction of ^{234}Th (half-life time 24.1 days) activity to the uppermost 1.5 cm, and the vertical aspect of the ^{210}Pb profile in the upper cm, strongly suggest that macrofaunal bioturbation is largely limited to the topmost part of the sediment (Jouanneau, 2001, pers. comm.). This rather shallow bioturbation zone will cause an absence of labile components deeper in the sediment. There, a constant, much slower flux of more refractory organic matter sustains a rather invariable succession of redox zones, where stable dysaerobic and anaerobic bacterial pools develop, which may form a food source for some highly specialised deeper dwelling taxa. Thus, the microhabitat of many foraminiferal taxa appears to be controlled largely by their trophic requirements (Jorissen et al., 1995).

5.4. *Temporal variability of foraminiferal faunas at station B*

E. exigua shows the most important frequency variations in our successive samples. Whereas this taxon is almost absent for most of the winter and summer months, it exhibits strong density increases after the spring and autumn phytoplankton bloom periods; density peaks are recorded in October 1997, in June 1999 and April 2000 (Fig. 6). These strong absolute and relative density variations show a highly opportunistic behaviour, and suggest that this species feeds on fresh organic phytodetritus. These results confirm similar observations in other deep-sea environments (Gooday, 1988, 1993; Gooday and Lambshead, 1989; Gooday and Turley, 1990; Thurston et al., 1994; Loubere, 1998; Jannink et al., 1998). Boltovskoy and Lena (1969) show that in eutrophic shallow water environments, *Epistominella* has a very short reproductive cycle (about one month), and reproduces throughout the year. We think that the intermittent occurrences of *E. exigua* at our station B are a direct response to phytodetritus deposits of a rather ephemeral nature. The species responds to the freshly deposited organic matter by a reproductive event, which is especially clear during the spring bloom of the year 2000 (see OB10B$^{\mathrm{bis}}$ data). Such a reproductive response has also been shown after food addition in culture experiments (Heinz et al., 2001, 2002).

Other small taxa, which are largely restricted to the 63–150 μm fraction, such as *R. guttiferus*, *N. pusillus*, *C. carinata*, and *B. spathulata*, show a similar density variability, albeit to a lesser degree. The peak periods are essentially the same as those for *E. exigua*, but the weaker response of these taxa suggests a slightly less opportunistic behaviour (Fig. 6).

Trochammina spp. and *Bolivina difformis*, which are also limited to the 63–150 μm fraction, show only a strong density increase after the spring bloom of 2000 (Fig. 6). This differential response suggests that not only the quantity, but also the quality, of the organic matter input could be a controlling factor. The quality of the organic matter may vary in function of the different phytoplankton groups responsible for the surface water bloom conditions.

In the >150 μm fraction, the shallow infaunal species *U. mediterranea* and *U. peregrina* show by far the largest frequency variations and can thus be considered as most opportunistic (Figs. 5a–m). *U. peregrina* shows a major peak (in both size fractions) after the putative 1997 autumn bloom. Apparently it is the most opportunistic species occurring in the >150 μm fraction. *U. mediterranea* is responsible for most of the density variations of the total foraminiferal fauna in this larger size fraction, and shows a relative, as well as absolute, frequency increase in all eutrophic periods. The different behaviour of the two *Uvigerina* species suggests slightly different trophic requirements, where *U. peregrina* and other taxa (e.g. *N. pusillus*), which exclusively show a density increase in the October 1997 sample, may prefer a diet based on microflagellates remains, which are especially abundant in the autumn bloom (Sellmer et al., 1998). Species that peak only after the spring bloom, such as *Trochammina* spp. and *B. difformis*, could prefer to feed on diatoms, coccolithophores, or other microalgae typical of spring blooms (Tréguer et al., 1979; Bender et al., 1992; Fernandez et al., 1995). Finally, *U. mediterranea*, and other species occurring both in autumn and spring, may be less critical with respect to food quality.

U. mediterranea and *U. peregrina* have been described in a wide range of mesotrophic to eutrophic settings (e.g. Lutze, 1980; Lutze and Coulbourne, 1984; Corliss, 1985, 1991; Corliss and Emerson, 1990; Jannink et al., 1998; Schmiedl et al., 2000; Morigi et al., 2001). According to De Rijk et al. (2000), they would need an exported labile organic flux of at least 2.5 g C/m^2/year. The observations made by Fontanier et al. (2002) at OB1B, where *U. peregrina* is found slightly deeper than *U. mediterranea*, suggesting a higher tolerance to slightly more degraded organic matter, are not confirmed during the other sampling periods, where the microhabitat of both species is very similar. However, in all other samples, *U. peregrina* is much poorer than in OB1B, and the present data may not be representative for its optimum conditions.

The infaunal niches deeper in the sediment are permanently occupied by *M. barleeanus, U. elongatastriata* and, still deeper, *G. affinis*. A deeper infauna dominated by *M. barleeanus* and *G. affinis* has been described in numerous mesotrophic-eutrophic oceanic ecosystems (e.g. Corliss, 1985; Harloff and Mackensen, 1997; Jorissen et al., 1995, 1998; Schmiedl et al., 2000). Jorissen (1999) and Fontanier et al. (2002) observe that *M. barleeanus* occurs systematically in the lower part of the oxic zone whereas *G. affinis* is consequently found in the upper part of the totally anoxic zone. Our present results fully confirm this pattern, suggesting that deeper infaunal species may be dependent on anaerobic bacterial stocks degrading more or less refractory organic matter. They could either directly prey on the bacterial stocks (Lee, 1979; Kitazato, 1994), or feed on the organic matter breakdown products (Caralp, 1989; Alve, 1990; Bernhard, 1992; Jorissen, 1999). Although we do not think that *G. affinis* and *M. barleeanus* feed directly on fresh organic matter (concentrated in the upper first cm of the sediment), they do show a significant frequency increase (in the >150 μm fraction) in some of the most productive months (October 1997, December 1998; Figs. 5a–m). A very similar increase of the population density was observed by Heinz et al. (2001) in a culture experiment. This suggests that increased surficial biological activity is rapidly transmitted towards deeper sediment layers, perhaps by an increase of bioturbation and accompanying bacterial activity.

In a previous study, Barmawidjaja et al. (1992) suggested that some infaunal taxa (e.g. *Eggerella scabra*, *Morulaeplecta bullosa*, *Textularia agglutinans*) could reproduce close to the sediment–water interface with a time lag with respect to more

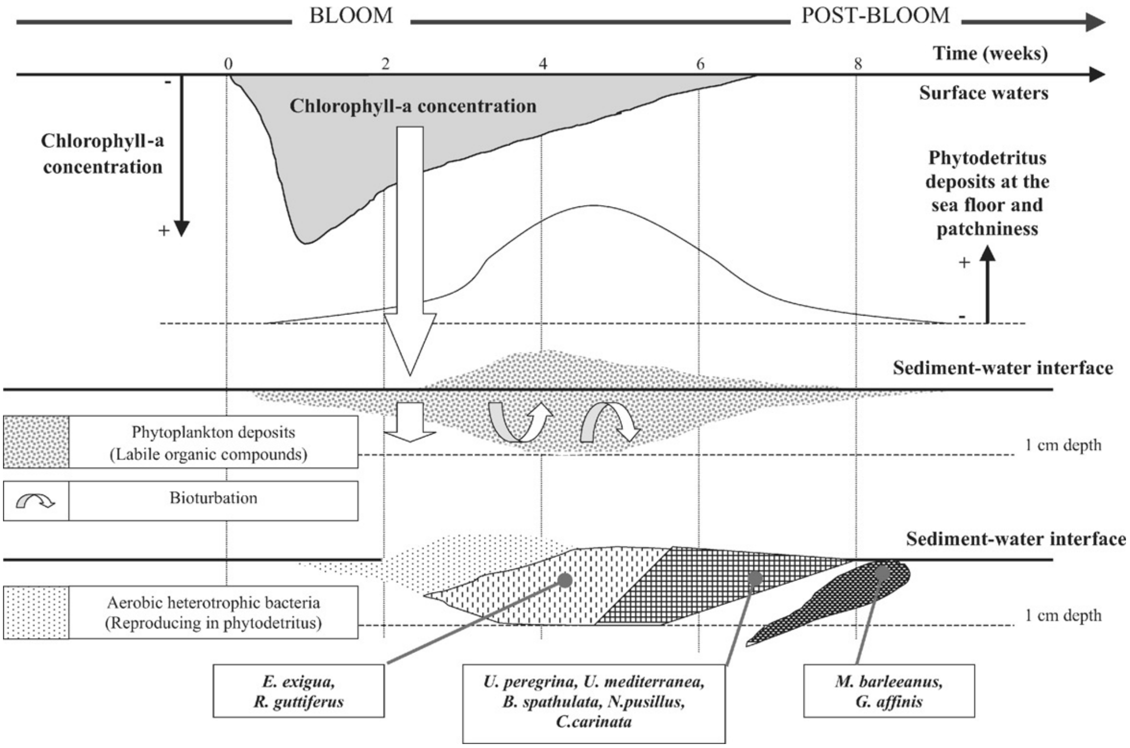

Fig. 8. Pelagic–benthic coupling and stepwise benthic ecosystem response to phytodetritus input. See text for further explanation.

opportunistic epifaunal taxa. More recently, Kitazato et al. (2000) speculated that deep infaunal taxa (*Chilostomella ovoidea* and *G. affinis*) are able to profit from fresh organic matter supplies after spring blooms, by moving to the sediment–water interface in order to feed on fresh organic matter and to reproduce at the end of the spring bloom. At our site, *G. affinis* shows a clear reproductive event in June 1998, when an abundant fauna consisting exclusively of juvenile specimens is found in the first half cm (Fig. 6). We think that this reproductive event is a delayed response to the 1998 spring bloom, which took place only when all other species have fallen back to background level (Figs. 5a–m and 6). This taxon does obviously not reproduce at the same time as the more opportunistic shallow infaunal taxa (e.g. *E. exigua*), which are more adapted to profiting quickly from labile phytodetritus input. The *G. affinis* reproductive event could be triggered by increased bacterial activity due to the delayed input (by bioturbation) of large amounts of less labile material in dysoxic microenvironments, once the more labile components have been consumed by more opportunistic taxa. Such a reproductive behaviour would also characterise intermediate infaunal taxa. An increase in the density of *M. barleeanus* in July 1998 (in both size fractions), accompanied by a shoaling of its microhabitat, could represent a similar reproductive event at one of the least productive moment of our 3-year study. In the eutrophic context of the Bay of Biscay, this migrational and reproductive behaviour is apparently independent of changes of redox gradients but is triggered by changes in the trophic level (presence of bacterial pools; quantity and quality of organic remains).

5.5. Stepwise benthic ecosystem response to phytodetritus input

The results of our study show that it is not easy to detect a straightforward relationship between phytoplankton bloom and benthic foraminiferal faunal characteristics. In case of the important

Table 4

Species	References
Adercotryma glomerata (Brady), 1878	Jones (1994), pl. 34, Figs. 15–18
Ammoscalaria pseudospiralis (Williamson), 1958	Jones (1994), pl. 33, Figs. 1–4
Amphicoryna scalaris (Batsch), 1791	Jones (1994), pl. 63, Figs. 28–31
Astacolus crepidulus (Fichtel & Moll), 1798	Jones (1994), pl. 67, Fig. 20; pl. 68, Fig. 1 and 2
Bigenerina nodosaria d'Orbigny, 1826	Jones (1994), pl. 44, Figs. 19–24
Biloculinella irregularis (d'Orbigny) 1839	d'Orbigny (1839), pl. 8, Fig. 20 and 21
Bolivina alata (Seguenza), 1862	Schiebel (1992), pl. 1, Fig. 2
Bolivina difformis (Williamson), 1958	Cushman (1937), pl. 15, Fig. 5 and 6
Bolivina spathulata (Williamson), 1858	Jorissen (1987), pl. 1, Fig. 5
Bolivina striatula (Cushman), 1922	Cushman (1937), pl. 18, Fig. 30 and 31
Bolivina subaenariensis Cushman, 1922	Phleger et al. (1953), pl. 7, Fig. 24 and 25
Bolivina variabilis (Williamson), 1958	Cushman (1937), pl. 16, Figs. 6, 12–14
Bolivinita quadrilatera (Schwager), 1866	Jones (1994), pl. 42, Figs. 8–12
Bulimina aculeata d'Orbigny, 1826	Jones (1994), pl. 51, Figs. 7–9
Bulimina costata d'Orbigny, 1826	Van Leeuwen (1989), pl. 8, Fig. 2 and 3
Bulimina inflata Seguenza, 1862	Van Leeuwen (1989), pl. 8, Fig. 4
Cancris auriculus (Fichtel & Moll), 1942	Jones (1994), pl. 106, Fig. 4
Cassidulina carinata Silvestri, 1896	Phleger et al. (1953), pl. 9, Figs. 32–37
Cassidulina crassa d'Orbigny, 1839	Jones (1994), pl. 54, Fig. 4 and 5
Chilostomella oolina Schwager, 1878	Jones (1994), pl. 55, Figs. 12–14
Cibicides lobatulus Walker & Jacob, 1798	Jones (1994), pl. 92, Fig. 10
Cibicides wuellerstorfi (Schwager), 1866	Van Leeuwen (1989), pl. 10, Figs. 1–9
Cibicidoides pachydermus (Rzehac), 1886	Jones (1994), pl. 94, Fig. 9
Cibicidoides robertsonianus (Brady), 1881	Van Leeuwen (1989), pl. 9, Figs. 1–3
Cibicidoides ungerianus d'Orbigny, 1846	Jones (1994), pl. 94, Fig. 9
Clavulina cylindrica d'Orbigny, 1952	Hofker (1932), Fig. 18 and 19
Cornuspira involvens (Reuss), 1950	Jones (1994), pl. 11, Figs. 1–3
Cribrostomoides subglobosus (Cushman), 1910	Jones (1994), pl. 34, Figs. 8–10
Cyclammina cancellata Brady, 1879	Jones (1994), pl. 37, Figs. 8–16
Cystammina pauciloculata (Brady), 1879	Jones (1994), pl. 41, Fig. 1
Dentalina advena (Cushman), 1923	Jones (1994), pl. 63, Fig. 1
Dentalina ariena Patterson & Pettis, 1986	Jones (1994), pl. 62, Figs. 27–31
Dentalina bradyensis (Dervieux), 1894	Jones (1994), pl. 62, Fig. 19 and 20
Dentalina subemaciata Parr, 1950	Jones (1994), pl. 62, Fig. 25 and 26
Eggerella scabra (Williamson), 1858	Jones (1994), pl. 47, Figs. 15–17
Elphidium advenum Cushman, 1922	Phleger et al. (1953), pl. 6, Fig. 15
Epistominella exigua (Bradyi), 1884	Schiebel (1992), pl.5, Fig. 9
Gavelinopsis translucens (Phleger & Parker), 1951	Schiebel (1992), pl. 4, Fig. 5
Glandulina ovula d'Orbigny, 1846	Jones (1994), pl. 61, Figs. 17–22
Globobulimina affinis d'Orbigny, 1826	Phleger et al. (1953), pl. 6, Fig. 32
Globocassidulina subglobosa (Bradyi), 1881	Jones (1994), pl. 54, Fig. 17
Gyroidina altiformis Stewart & Stewart, 1930	Jorissen (1987), pl. 1, Fig. 11
Gyroidina umbonata (Silvestri), 1898	Parker (1958), pl. 3, Fig. 19 and 20
Hanzawaia boueana (d'Orbigny), 1846	Jorissen (1987), pl. 3, Fig. 10
Hoeglundina elegans (d'Orbigny), 1826	Phleger et al. (1953), pl. 9, Fig. 24 and 25
Hyalinea balthica (Schroeter), 1783	Jones (1994), pl. 112, Fig. 1 and 2
Karreriella bradyi (Cushman), 1911	Jones (1994), pl. 41, Figs. 1–4
Lagena multilatera McMulloch, 1977	Jones (1994), pl. 58, Figs 2–3, 7–8, 22–24
Lenticulina peregrina (Schwager), 1866	Cushman and McCulloch (1950), pl. 39, Fig. 5
Lenticulina vortex (Fichtel and Moll), 1798	Jones (1994), pl. 69, Figs. 14–16
Marginula obesa (Cushman), 1923	Jones (1994), pl. 65, Fig. 5 and 6
Melonis barleeanus (Williamson), 1858	Van Leeuwen (1989), pl. 13, Fig. 1 and 2
Nonion scaphum (Fichtel & Moll), 1798	Jones (1994), pl. 109, Fig. 12
Nonionella turgida (Williamson), 1858	Jones (1994), pl. 109, Figs. 17–19

Table 4 (*continued*)

Species	References
Nouria polymorphinoides Heron-Allen & Earland, 1914	Loeblich and Tappan (1988), pl. 123, Fig. 11 and 12
Nuttallides pusillus (Parr), 1950	Phleger et al. (1953), pl. 9, Fig. 5 and 6
Nuttallides umboniferus (Cushman), 1933	Van Leeuwen (1989), pl. 15, Figs. 11–13; pl. 16, Figs. 1–7
Oridorsalis umbonatus Reuss, 1851	Van Leeuwen (1989), pl. 17, Figs. 1–13
Psammosphaera fusca Schulze, 1875	Jones (1994), Pl. 18, Fig. 1–8
Pseuclavulina crustata Cushman, 1936	Jorissen (1987), pl. 1, Fig. 1
Pseudoeponides falsobeccarii Rouvillois, 1974	Jorissen (1987), pl. 4, Fig. 3a
Pullenia bulloides (d'Orbigny), 1826	Phleger et al. (1953), pl. 10, Fig. 19
Pullenia quinqueloba (Reuss), 1851	Jones (1994), Pl. 84, Fig. 14 and 15
Pyrgo depressa (d'Orbigny), 1826	Jones (1994), Pl. 2, Figs. 12, 16 and 17
Pyrgo subsphaerica d'Orbigny, 1839	Cushman (1929), pl. 18, Fig. 1 and 2
Pyrgoella sphaera (d'Orbigny), 1839	Jones (1994), pl. 2, Fig. 4
Quinqueloculina seminula (Linné), 1758	Jones (1994), pl. 5, Fig. 6
Rectuvigerina phlegeri Le Calvez, 1959	Schiebel (1992), pl. 3, Fig. 10a–d
Reophax ampullacea Brady, 1881	Jones (1994), pl. 30, Fig. 6
Reophax dentiliniformis Brady, 1881	Jones (1994), pl. 30, Fig. 21 and 22
Reophax fusiformis (Williamson), 1858	Jones (1994), pl. 30, Figs. 7–10, ?11
Reophax guttiferus Brady, 1881	Jones (1994), pl. 31, Fig. 10–15
Reophax scorpiurus Montfort, 1808	Loeblich and Tappan (1988), pl. 44, Figs. 1–3
Reophax spiculifer Brady, 1879	Jones (1994), pl. 31, Fig. 16 and 17
Rhabdamina cornuta (Brady), 1879	Jones (1994), pl. 22, Fig. 11 and 13
Robertinoides bradyi (Cushman and Parker), 1936	Jones (1994), pl. 50, Fig. 18
Sigmoilopsis schlumbergeri Silvestri, 1904	Jones (1994), pl. 8, Figs. 1–4
Siphogenerina columellaris (Brady), 1881	Jones (1994), pl. 75, Figs. 15–17
Siphotextularia affinis Fornasini, 1883	Kohl (1985), pl. 2, Fig. 5
Siphotextularia concava (Karrer), 1868	Jones (1994), pl. 42, Figs. 13–14
Spiroloculina tenuiseptata Brady, 1884	Jones (1994), pl. 10, Fig. 5 and 6
Stainforthia concava (Höglund), 1947	Timm (1992), pl. 5, Fig. 11
Technitella melo Norman, 1978	Jones (1994), pl. 25, Fig. 7
Textularia agglutinans d'Orbigny, 1839	Jones (1994), pl. 43, Figs. 1–3
Textularia conica d'Orbigny, 1839	Le Calvez (1977), p. 18, Fig. 1 and 2
Textularia sagittula Defrance, 1824	Jorissen (1987), pl. 3, Fig. 12
Textularia truncata Höglund, 1947	Le Calvez (1958), pl. 1, Fig. 5
Trifarina angulosa (Williamson), 1858	Jones (1994), pl. 74, Fig. 17 and 18
Trifarina bradyi Cushman, 1923	Jones (1994), pl. 67, Figs. 1–3
Trochammina inflata (Montagu), 1808	Jones (1994), pl. 41, Fig. 4
Uvigerina elongatastriata (Colom), 1952	Van der Zwaan et al. (1986), pl. 6, Figs. 1–8
Uvigerina mediterranea Hofker, 1932	Van der Zwaan et al. (1986), pl. 5, Figs. 1–7
Uvigerina peregrina Cushman, 1923	Van der Zwaan et al. (1986), pl. 1, Figs. 1–6
Uvigerina proboscidea Schawger, 1866	Van der Zwaan et al. (1986), pl. 12, Figs. 1–4
Valvulineria bradyana (Fornasini), 1900	Jorissen (1987), pl. 4, Fig. 1 and 2

spring phytoplankton blooms of 1999 and 2000 and the putative autumn bloom of 1997, a significant response of the foraminiferal fauna was only noticed about 6 weeks after surface water chlorophyll maxima. Fig. 8 graphically represents our ideas about the time delays between the surface water phytoplankton bloom and the responses in the benthic ecosystem. A first important delay will exist between the time of maximum chlorophyll-*a* concentrations and phytodetritus deposits at the ocean floor. This delay is caused by the longevity of the phytoplankton assemblages, the time involved in the formation of organic aggregates, and the time for physical transport to the ocean floor. We do not have a precise idea about the first two parameters

Table 5

	OB1B		OB1B$^{\text{bis}}$		OB2B		OB2B$^{\text{bis}}$		OB3B		OB4B		OB5B	
Taxa	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna
Perforate														
Indet.	1	0.07					1	0.19			1	0.36		
Amphicoryna scalaris	4	0.30	5	1.04	1	0.14	2	0.38	3	0.75	2	0.71	1	0.31
Astacolus sp.														
Astacolus crepidulus														
Bolivina alata	6	0.44			7	0.97	3	0.57	2	0.50	2	0.71	8	2.48
Bolivina spathulata														
Bolivina subaenariensis														
Bolivinita quadrilatera	8	0.59							1	0.25			1	0.31
Bulimina aculeata														
Bulimina costata									2	0.50	1	0.36	3	0.93
Bulimina inflata			2	0.42										
Bulimina marginata	19	1.41	11	2.29	18	2.50	9	1.70	9	2.24	4	1.42	1	0.31
Cassidulina carinata			2	0.42	2	0.28								
Cassidulina crassa							1	0.19						
Chilostomella oolina	3	0.22			3	0.42	13	2.46	2	0.50	1	0.36		
Cibicides lobatulus	1	0.07			1	0.14	3	0.57	2	0.50	2	0.71		
Cibicides wuellerstorfi	1	0.07			6	0.83	2	0.38			1	0.36		
Cibicidoides pachydermus	63	4.67	20	4.17	52	7.22	33	6.24	13	3.23	8	2.85	10	3.11
Cibicidoides ungerianus			11	2.29					3	0.75	6	2.14	3	0.93
Dentalina sp.1	1	0.07												
Dentalina advena													1	0.31
Dentalina ariena														
Dentalina bradyensis					1	0.14	2	0.38	3	0.75				
Dentalina subemaciata	1	0.07					2	0.38					1	0.31
Elphidium sp.	1	0.07							1	0.25				
Epistominella sp.														
Gavelinopsis translucens	1	0.07												
Glandulina ovula	3	0.22	1	0.21			1	0.19	3	0.75			1	0.31
Globobulimina affinis	81	6.00	11	2.29	19	2.64	39	7.37	33	8.21	18	6.41	13	4.04
Gyroidina altiformis	10	0.74	4	0.83	3	0.42					2	0.71		
Gyroidina orbicularis	3	0.22	5	1.04			2	0.38	1	0.25	1	0.36	2	0.62
Hanzawaia boueana			2	0.42					2	0.50	1	0.36	1	0.31
Hoeglundina elegans							1	0.19						
Hyalinea balthica	12	0.89	3	0.63	7	0.97	2	0.38	2	0.50			1	0.31
Lagena sp.					2	0.28	1	0.19						
Lenticulina sp.1	1	0.07												
Lenticulina sp.2														
Lenticulina peregrina	7	0.52			3	0.42	3	0.57	4	1.00	2	0.71		
Lenticulina vortex	3	0.22			3	0.42	1	0.19	4	1.00	1	0.36	2	0.62
Maginula obesa					3	0.42	1	0.19						
Melonis berleeanus	121	8.97	36	7.50	69	9.58	42	7.94	40	9.95	43	15.30	34	10.56
Nodosaria sp.													1	0.31
Nonion scaphum														
Nonionella turgida									1	0.25	1	0.36		
Nuttallides pusillus														
Nuttallides umboniferus	6	0.44	4	0.83	4	0.56			3	0.75	2	0.71	1	0.31
Polymorphinidae			2	0.42	3	0.42					1	0.36		
Pseudoeponides falsobeccarii	1	0.07												
Pullenia quinqueloba					9	1.25	4	0.76	2	0.50	1	0.36	6	1.86

OB6B		OB7B		OB8B		OB8B$^{\text{bis}}$		OB9B		OB9B$^{\text{bis}}$		OB10B		OB10B$^{\text{bis}}$	
Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna
						1	0.22	4	0.68	1	0.16	2	0.24		
1	0.16	5	0.90			1	0.22			7	1.11	9	1.07	2	0.36
1	0.16	1	0.18					1	0.17						
														1	0.18
7	1.14	20	3.61	1	0.41	9	1.94	3	0.51	2	0.32	18	2.13	8	1.43
										3	0.48				
						1	0.22					1	0.12		
		3	0.54	1	0.41	2	0.43	3	0.51			6	0.71	1	0.18
						1	0.22								
4	0.65									1	0.16			1	0.18
6	0.98	2	0.36			10	2.15	9	1.53	4	0.63	8	0.95	5	0.90
								1	0.17	1	0.16			2	0.36
								1	0.17						
4	0.65	3	0.54	2	0.82	19	4.09	12	2.04	2	0.32	31	3.67	18	3.23
		2	0.36							3	0.48	2	0.24	1	0.18
15	2.44	23	4.15	3	1.22	1	0.22	11	1.87	11	1.74	16	1.89	10	1.79
		9	1.62			3	0.65	3	0.51	5	0.79	7	0.83	8	1.43
1	0.16	1	0.18	1	0.41	1	0.22								
								1	0.17						
				1	0.41	1	0.22	2	0.34	4	0.63	1	0.12	1	0.18
		2	0.36	1	0.41	1	0.22	2	0.34	1	0.16	3	0.36	1	0.18
										1	0.16				
				1	0.41			3	0.51	1	0.16	3	0.36		
55	8.94	38	6.86	31	12.65	71	15.27	51	8.67	24	3.80	41	4.85	21	3.76
1	0.16	3	0.54	1	0.41	1	0.22	1	0.17	2	0.32	1	0.12	2	0.36
3	0.49	1	0.18	2	0.82	1	0.22	1	0.17	1	0.16	1	0.12	2	0.36
1	0.16					1	0.22	3	0.51	1	0.16	1	0.12	1	0.18
		14	2.53			5	1.08	10	1.70	6	0.95	7	0.83	2	0.36
		2	0.36			1	0.22								
								1	0.17						
				1	0.41										
		2	0.36			2	0.43	3	0.51	4	0.63	3	0.36	1	0.18
1	0.16	3	0.54	1	0.41	1	0.22	1	0.17	4	0.63	1	0.12	3	0.54
						1	0.22							1	0.18
103	16.75	40	7.22	10	4.08	36	7.74	39	6.63	52	8.24	61	7.22	42	7.53
														1	0.18
										1	0.16				
1	0.16	1	0.18					5	0.85	7	1.11				
		1	0.18					7	1.19			1	0.12	4	0.72

Table 5 (*continued*)

	OB1B		OB1B^{bis}		OB2B		OB2B^{bis}		OB3B		OB4B		OB5B	
Taxa	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna
Rectuvigerina phlegeri													1	0.31
Robertinoides bradyi	3	0.22	1	0.21	1	0.14								
Rosalina sp.					3	0.42					2	0.71		
Siphogenerina columellaris	30	2.22	2	0.42	17	2.36	12	2.27	3	0.75	13	4.63	6	1.86
Sphaeroidina bulloides			1	0.21										
Trifarina sp.	1	0.07												
Trifarina angulosa	2	0.15			1	0.14								
Uvigerina elongatastriata	62	4.60	14	2.92	20	2.78	39	7.37	11	2.74	20	7.12	20	6.21
Uvigerina mediterranea	454	33.65	139	28.96	287	39.86	163	30.81	88	21.89	50	17.79	74	22.98
Uvigerina peregrina	290	21.50	102	21.25	44	6.11	57	10.78	36	8.96	31	11.03	27	8.39
Uvigerina proboscidea	1	0.07									1	0.36		
Porcellaneous														
Biloculinella sp.					1	0.14								
Biloculinella irregularis					2	0.28			1	0.25	1	0.36		
Cornuspira involvens	1	0.07			5	0.69	5	0.95	2	0.50	8	2.85	3	0.93
Cruciloculina sp.	1	0.07			1	0.14								
Miliolinella sp.														
Pyrgo sp.														
Pyrgo depressa	1	0.07												
Pyrgo subsphaerica			15	3.13	1	0.14					1	0.36		
Pyrgoella spharea					1	0.14								
Quinqueloculina sp.														
Quinqueloculina seminula														
Scutuloris sp.														
Sigmoilina sp.	1	0.07			1	0.14							1	0.31
Spiroloculina tenuiseptata									1	0.25				
Triloculina spp.														
Non fossilising agglutinated														
Indet.			3	0.63									1	0.31
Agglutinated sp.1														
Adercotryma glomerata							1	0.19						
Ammolagena sp.	5	0.37			1	0.14								
Ammoscalaria sp.	2	0.15	4	0.83	2	0.28			2	0.50			1	0.31
Ammoscalaria pseudospiralis							1	0.19						
Clavulina cylindrica	10	0.74	4	0.83	17	2.36	11	2.08	31	7.71	14	4.98	6	1.86
Cribrostomoides subglobosus	20	1.48	21	4.38	30	4.17	7	1.32	45	11.19	13	4.63	41	12.73
Cyclammina sp.1	1	0.07					1	0.19						
Cyclammina sp.2	6	0.44	5	1.04	6	0.83	4	0.76	4	1.00	1	0.36	8	2.48
Cyclammina sp.3	7	0.52			8	1.11	2	0.38	3	0.75				
Eggerella scabra	6	0.44	1	0.21	15	2.08	2	0.38	6	1.49	12	4.27	11	3.42
Haplophragmoides sp.														
Haplophragmoides sp.1														
Haplophragmoides bradyi	2	0.15			2	0.28			2	0.50	1	0.36		
Karreriella sp.														
Martinotiella sp.														
Psammosphaera fusca							1	0.19						
Reophax sp.					8	1.11			2	0.50				
Reophax sp.1	3	0.22					1	0.19						

OB6B		OB7B		OB8B		OB8B^{bis}		OB9B		OB9B^{bis}		OB10B		OB10B^{bis}	
Total	% of total	Total	% of total	Total	% of total	Total	% of total	Total	% of total	Total	% of total	Total	% of total	Total	% of total
		2	0.36					2	0.34	2	0.32				
9	1.46	12	2.17			4	0.86	8	1.36	14	2.22	18	2.13	14	2.51
												1	0.12	2	0.36
21	3.41	42	7.58	32	13.06	22	4.73	15	2.55	37	5.86	57	6.75	24	4.30
225	36.59	178	32.13	50	20.41	90	19.35	189	32.14	251	39.78	216	25.56	206	36.92
45	7.32	19	3.43	14	5.71	33	7.10	27	4.59	11	1.74	45	5.33	50	8.96
		1	0.18			1	0.22	1	0.17	1	0.16	2	0.24	4	0.72
										1	0.16				
3	0.49	1	0.18	1	0.41			1	0.17	1	0.16	2	0.24	1	0.18
		1	0.18			2	0.43	2	0.34	3	0.48	1	0.12		
												1	0.12		
3	0.49														
										1	0.16	3	0.36	1	0.18
2	0.33											1	0.12	1	0.18
		1	0.18												
				3	1.22			1	0.17						
												5	0.59		
		1	0.18									1	0.12		
						1	0.22								
		1	0.18												
														1	0.18
3	0.49					4	0.86					6	0.71		
										8	1.27				
		7	1.26					9	1.53						
				1	0.41					1	0.16	4	0.47	5	0.90
3	0.49	4	0.72	2	0.82	18	3.87	1	0.17	3	0.48	2	0.24	11	1.97
				1	0.41			2	0.34	2	0.32				
32	5.20	13	2.35	8	3.27	30	6.45	27	4.59	16	2.54	36	4.26	6	1.08
25	4.07	7	1.26	14	5.71	41	8.82	28	4.76	61	9.67	23	2.72	27	4.84
								1	0.17					5	0.90
2	0.33	5	0.90	3	1.22			6	1.02	4	0.63	4	0.47	1	0.18
4	0.65			2	0.82	1	0.22	1	0.17	1	0.16	7	0.83	4	0.72
6	0.98					5	1.08	6	1.02	10	1.58	11	1.30	7	1.25
										1	0.16				
						1	0.22			4	0.63				
		3	0.54	5	2.04			6	1.02	1	0.16	6	0.71		
										1	0.16				
														1	0.18
						4	0.86			1	0.16			6	1.08
								3	0.51	1	0.16	7	0.83	2	0.36
				1	0.41	1	0.22			1	0.16	4	0.47	3	0.54

Table 5 (*continued*)

	OB1B		OB1B^{bis}		OB2B		OB2B^{bis}		OB3B		OB4B		OB5B	
Taxa	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna
Reophax dentaliniformis	1	0.07							3	0.75	1	0.36		
Reophax fusiformis	7	0.52					5	0.95						
Reophax guttiferus	19	1.41	1	0.21	14	1.94	3	0.57						
Reophax scorpiurus	25	1.85	27	5.63	4	0.56	19	3.59	14	3.48	9	3.20	25	7.76
Reophax spiculifer														
Rhabdammina cornuta														
Saccammina sp.							3	0.57						
Technitella melo					1	0.14	2	0.38					1	0.31
Trochammina sp.	2	0.15	1	0.21	1	0.14			1	0.25			1	0.31
Fossilising agglutinated														
Bigenerina nodosaria	9	0.67	4	0.83	4	0.56	1	0.19	1	0.25	1	0.36	3	0.93
Karrerulina sp.							1	0.19						
Pseudoclavulina crustata	10	0.74	14	2.92	3	0.42	9	1.70	4	1.00			2	0.62
Sigmoilopsis schlumbergeri														
Siphotextularia affinis	9	0.67			1	0.14			3	0.75	1	0.36		
Textularia sp.					1	0.14			1	0.25				
Textularia agglutinans														
Textularia conica					1	0.14								
Textularia sagittula			3	0.63					2	0.50				
Total live foraminifera	1349	100.00	480	100.00	720	100.00	529	100.00	402	100.00	281	100.00	322	100.00
Nbr species	53		33		52		44		45		38		36	
Glomospira spp.	56		2		63		49		2		2		1	
Arborescent indet.	203		78		50				95		52		59	
Ostracoda			8		9								4	

Table 6

	0B1B		0B1B^{bis}		0B2B		0B2B^{bis}		0B3B		0B4B		OB5B	
Taxa	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna
Perforate														
Indet.	1	0.07	2	0.60					2	1.52				
Amphicoryna scalaris	3	0.20							1	0.76				
Animalinoides sp.	1	0.07	3	0.91							2	1.40	1	1.37
Astacolus sp.									1	0.76				
Baggina sp.													1	1.37
Bolivina sp.	8	0.53	2	0.60	3	1.20	1	0.83	4	3.03				
Bolivina sp.1					18	7.23								
Bolivine alata							3	2.48	1	0.76				
Bolivina difformis	10	0.66	7	2.11	1	0.40	1	0.83	1	0.76	1	0.70	1	1.37
Bolivina spathulata	49	3.26	44	13.29	12	4.82	8	6.61	6	4.55	2	1.40		
Bolivina striatula	2	0.13												
Bolivina subaenariensis	1	0.07												
Bolivina variabilis	5	0.33			2	0.80			1	0.76			1	1.37
Bolivinita quadrilatera	15	1.00					1	0.83			2	1.40	1	1.37

OB6B		OB7B		OB8B		OB8B^{bis}		OB9B		OB9B^{bis}		OB10B		OB10B^{bis}	
Total	% of total	Total	% of total	Total	% of total	Total	% of total	Total	% of total	Total	% of total	Total	% of total	Total	% of total
				1	0.41	1	0.22	6	1.02			3	0.36		
		2	0.36			4	0.86			3	0.48	14	1.66		
20	3.25	44	7.94	20	8.16	20	4.30	14	2.38	21	3.33	74	8.76	15	2.69
														1	0.18
								3	0.51			9	1.07	2	0.36
		8	1.44	4	1.63	5	1.08	20	3.40	4	0.63	19	2.25	1	0.18
						3	0.65			2	0.32	8	0.95	1	0.18
		2	0.36	1	0.41			1	0.17						
5	0.81	8	1.44	3	1.22			3	0.51	8	1.27	27	3.20	8	1.43
2	0.33	14	2.53	22	8.98	3	0.65	24	4.08	5	0.79	4	0.47	5	0.90
								1	0.17						
		2	0.36					2	0.34					3	0.54
										2	0.32				
		1	0.18												
														1	0.18
615	100.00	554	100.00	245	100.00	465	100.00	588	100.00	631	100	845	100	558	100.00
31		49		34		43		53		57		52		55	
3		52		67		35		84		71				34	
38						2								7	
6															

0B6B		0B7B		0B8B		0B8B^{bis}		OB9B		OB9B^{bis}		0B10B		OB10B^{bis}	
Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna
								2	0.48			2	0.52	3	0.14
		1	0.32							2	0.46	4	1.04	1	0.05
		4	1.29			5	3.40	1	0.24			2	0.52	6	0.27
		1	0.32	3	1.08	1	0.68	3	0.71	4	0.91	9	2.35	4	0.18
												1	0.26	1	0.05
		3	0.96	2	0.72			11	2.62	15	3.42	27	7.05	87	3.96
		30	9.65	9	3.24	9	6.12	23	5.48	27	6.16	27	7.05	96	4.37
														2	0.09
				1	0.36										
		4	1.29					2	0.48			2	0.52		
		1	0.32	1	0.36	1	0.68	3	0.71	18	4.11	17	4.44	10	0.46

Table 6 (*continued*)

	0B1B		0B1B$^{\text{bis}}$		0B2B		0B2B$^{\text{bis}}$		0B3B		0B4B		OB5B	
Taxa	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna
Bulimina aculeata													1	1.37
Bulimina costata	11	0.73	2	0.60	3	1.20					1	0.70	1	1.37
Bulimina inflata														
Bulimina marginata	35	2.33	5	1.51	3	1.20	4	3.31	1	0.76	2	1.40	1	1.37
Cassidulina carinata	72	4.78	47	14.20	29	11.65	11	9.09	3	2.27	2	1.40	3	4.11
Cassidulina crassa	9	0.60	4	1.21	1	0.40								
Cassidulinoides sp.									1	0.76				
Ceratobulimina sp.	10	0.66	3	0.91	1	0.40	2	1.65	3	2.27	2	1.40	1	1.37
Chilostomella oolina									4	3.03				
Cibicides lobatulus			1	0.30	1	0.40								
Cibicidoides pachydermus	1	0.07							1	0.76				
Cibicidoides ungerianus	2	0.13	1	0.30					1	0.76				
Coryphostoma sp.	29	1.93	3	0.91							1	0.70		
Dentalina sp.														
Dentalina sp.1	1	0.07												
Dentalina ariena														
Dentalina bradyensis	1	0.07					1	0.83			3	2.10	3	4.11
Dentalina subemaciata	1	0.07												
Epistominella exigua	133	8.84	30	9.06			5	4.13	1	0.76	1	0.70	2	2.74
Fissurina sp.	5	0.33	2	0.60							4	2.80		
Glandulina sp.	1	0.07												
Globobulimina affinis					2	0.80			60	45.45	2	1.40		
Globocassidulina subglobosa														
Gyroidina sp.			1	0.30										
Gyroidina sp.1	1	0.07			1	0.40								
Gyroidina sp.2					1	0.40								
Gyroidina altiformis	6	0.40	1	0.30	1	0.40	1	0.83						
Gyroidina orbicularis	4	0.27												
Gyroidina umbonata	40	2.66	8	2.42	5	2.01	1	0.83	1	0.76	2	1.40	7	9.59
Hanzawaia boueana														
Hoeglundina elegans							1	0.83						
Hyalinea balthica	4	0.27	5	1.51	1	0.40			1	0.76				
Lagena sp.			1	0.30	1	0.40								
Lagena multilatera					1	0.40								
Lenticulina sp.	15	1.00			1	0.40					2	1.40	1	1.37
Lenticulina sp.1	4	0.27			2	0.80	1	0.83			1	0.70	3	4.11
Lenticulina peregrina	13	0.86	2	0.60	7	2.81	6	4.96					3	4.11
Lenticulina vortex														
Margunula obesa														
Melonis barleeanus	41	2.72	2	0.60	1	0.40	11	9.09	7	5.30	22	15.38	4	5.48
Nonion scaphum													1	1.37
Nonionella spp.	41	2.72	8	2.42	11	4.42	8	6.61	7	5.30	11	7.69	1	1.37
Nuttallides pusillus	83	5.51	1	0.30	1	0.40	2	1.65	1	0.76	1	0.70	2	2.74
Nuttallides umboniferus	8	0.53	5	1.51	5	2.01	1	0.83	1	0.76	2	1.40	2	2.74
Oolina sp.	1	0.07	1	0.30									1	1.37
Parafissurina sp.	1	0.07									1	0.70		
Polyporphina sp.	6	0.40			1	0.40			1	0.76	2	1.40		
Pullenia quinqueloba	3	0.20	1	0.30							3	2.10	4	5.48
Robertinoides sp.			1	0.30										
Rosalina sp.														

0B6B		0B7B		0B8B		0B8B^{bis}		OB9B		OB9B^{bis}		0B10B		OB10B^{bis}	
Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna
1	2.70	2	0.64	2	0.72			7	1.67	1	0.23	5	1.31	8	0.36
		1	0.32												
3	8.11	7	2.25			8	5.44	12	2.86	14	3.20	8	2.09	15	0.68
4	10.81	25	8.04	9	3.24	9	6.12	13	3.10	18	4.11	43	11.23	135	6.15
		5	1.61			1	0.68	3	0.71			7	1.83	11	0.50
												1	0.26		
		2	0.64	14	5.04	4	2.72	6	1.43	1	0.23	5	1.31	19	0.87
				1	0.36							1	0.26	1	0.05
		1	0.32											1	0.05
		1	0.32	1	0.36										
		3	0.96	1	0.36	2	1.36	1	0.24			6	1.57	8	0.36
														1	0.05
						1	0.68								
		1	0.32			1	0.68							3	0.14
		1	0.32			1	0.68	2	0.48			1	0.26	1	0.05
		2	0.64	2	0.72	8	5.44	136	32.38	62	14.16	23	6.01	781	35.58
		1	0.32			1	0.68			3	0.68	3	0.78	11	0.50
				1	0.36										
		1	0.32					1	0.24						
				1	0.36			2	0.48			1	0.26		
		1	0.32												
								1	0.24	1	0.23	2	0.52	5	0.23
2	5.41	2	0.64	8	2.88	2	1.36	19	4.52	18	4.11			2	
														2	0.09
		1	0.32					1	0.24					1	0.05
		2	0.64	3	1.08	1	0.68	3	0.71					12	0.55
				2	0.72							1	0.26		
								1	0.24						
		8	2.57	2	0.72			1	0.24	1	0.23	4	1.04		
1	2.70							2	0.48	1	0.23			2	0.09
		1	0.32	1	0.36	1	0.68	3	0.71	5	1.14	4	1.04	4	0.18
														1	0.05
										1	0.23				
		5	1.61	10	3.60	1	0.68	3	0.71	1	0.23	5	1.31	19	0.87
		3	0.96	12	4.32			6	1.43	1	0.23	3	0.78	41	1.87
		3	0.96	2	0.72	5	3.40	14	3.33	8	1.83	12	3.13	48	2.19
		7	2.25	2	0.72			1	0.24	3	0.68			3	0.14
												2	0.52	1	0.05
				3	1.08									1	0.05
		1	0.32	3	1.08	3	2.04	3	0.71	1	0.23	3	0.78	84	3.83
						1	0.68					2	0.52		

Table 6 (*continued*)

	0B1B		0B1B^{bis}		0B2B		0B2B^{bis}		0B3B		0B4B		OB5B	
Taxa	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna
Siphogenerina columellaris	46	3.06	1	0.30	3	1.20	8	6.61	5	3.79	16	11.19		
Stainforthia sp.	1	0.07												
Stainforthia concava	1	0.07			1	0.40	1	0.83						
Trifarina angulosa														
Trifarina bradyi	31	2.06	5	1.51							1	0.70	2	2.74
Uvigerina elongatastriata	7	0.47	4	1.21	1	0.40	2	1.65					1	1.37
Uvigerina mediterranea	138	9.17	8	2.42	5	2.01	10	8.26	3	2.27	3	2.10	5	6.85
Uvigerina peregrina	250	16.61	10	3.02	5	2.01	2	1.65	4	3.03	11	7.69	11	15.07
Uvigerina proboscidea														
Uvigerina spp.			1	0.30									1	1.37
Porcellaneous														
Biloculinella sp.											1	0.70		
Cornuspira involvens	4	0.27			2	0.80	3	2.48	1	0.76	7	4.90	2	2.74
Cruciloculina sp.											1	0.70		
Pyrgo subsphaerica			4	1.21										
Quinqueloculina sp.	5	0.33	3	0.91	6	2.41								
Sigmoilina sp.	1	0.07	1	0.30	2	0.80								
Triloculina sp.			1	0.30										
Non fossilising agglutinated														
Agglut. sp.A	3	0.20	1	0.30	1	0.40								
Indet.	11	0.73	2	0.60	1	0.40								
Adercotryma glomerata	18	1.20	8	2.42	10	4.02	1	0.83			2	1.40	1	1.37
Ammoscalaria sp.			2	0.60										
Clavulina cylindrica														
Cribrostomoides subglobosus	5	0.33	12	3.63	6	2.41	1	0.83	5	3.79	1	0.70		
Eggerella scabra	1	0.07			1	0.40					2	1.40		
Haplophragmoides sp.	3	0.20	9	2.72	11	4.42			2	1.52	1	0.70		
Psammosphaera fusca	8	0.53	18	5.44	6	2.41	5	4.13			5	3.50		
Reophax sp.1	19	1.26	12	3.63	6	2.41	4	3.31						
Reophax dentaliniformis	4	0.27			1	0.40	3	2.48			3	2.10	1	1.37
Reophax fusiformis					1	0.40								
Reophax guttiferus	179	11.89	14	4.23	41	16.47	5	4.13			8	5.59		
Reophax scorpiurus	1	0.07	3	0.91	18	7.23					2	1.40	1	1.37
Reophax spiculifer	2	0.13	2	0.60										
Saccammina spp.	50	3.32	1	0.30							2	1.40	1	1.37
Spiroplectinella sp.			1	0.30	4	1.61								
Technitella melo	15	1.00	1	0.30			3	2.48						
Trochammina spp.	19	1.26	1	0.30	1	0.40	4	3.31	1	0.76	5	3.50		
Fossilising agglutinated														
Bigenerina nodosaria	5	0.33	11	3.32	1	0.40							1	1.37
Siphotextularia affinis	1	0.07	1	0.30										
Siphotextularia concava			1	0.30										
Total live foraminifera	1505	100.00	331	100.00	249	100.00	121	100.00	132	100.00	143	100.00	73	100.00
Nbr species	65		55		49		33		30		40		34	
Ostracoda	32		5		9				2		11		3	
Glomospira spp.	14				3		9		1		4		6	

0B6B		0B7B		0B8B		0B8B^{bis}		OB9B		OB9B^{bis}		0B10B		OB10B^{bis}	
Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna	Total	% of total fauna
2	5.41	17	5.47	4	1.44	3	2.04			3	0.68	24	6.27	29	1.32
												2	0.52	3	0.14
														22	1.00
		6	1.93	3	1.08	1	0.68	11	2.62	2	0.46	8	2.09	13	0.59
		4	1.29			1	0.68	20	4.76					3	0.14
5	13.51	11	3.54	10	3.60	6	4.08	7	1.67	8	1.83	15	3.92	22	1.00
3	8.11	29	9.32	26	9.35	2	1.36	1	0.24	24	5.48	5	1.31	72	3.28
												1	0.26	2	0.09
		2	0.64					2	0.48	1	0.23			4	0.18
												2	0.52		
1	2.70	2	0.64			2	1.36	1	0.24	1	0.23	1	0.26	2	0.09
		1	0.32												
		3	0.96	3	1.08	1	0.68	1	0.24	5	1.14			9	0.41
						1	0.68	3	0.71						
										1	0.23				
		5	1.61			2	1.36	2	0.48			4	1.04		
														28	1.28
1	2.70	8	2.57	10	3.60	5	3.40	9	2.14	9	2.05	10	2.61	38	1.73
		1	0.32	1	0.36	1	0.68	2	0.48	4	0.91	1	0.26	9	0.41
		1	0.32												
		3	0.96	2	0.72	4	2.72	18	4.29	13	2.97	1	0.26		
		4	1.29	1	0.36					1	0.23			11	0.50
1	2.70	5	1.61	13	4.68	10	6.80	15	3.57					5	0.23
1	2.70	10	3.22	8	2.88	5	3.40	2	0.48	3	0.68	4	1.04	35	1.59
2	5.41	4	1.29	13	4.68	9	6.12	3	0.71	5	1.14	2	0.52	11	0.50
1	2.70	1	0.32	2	0.72	2	1.36	1	0.24					3	0.14
								2	0.48					2	0.09
6	16.22	37	11.90	32	11.51	17	11.56	22	5.24	116	26.48	41	10.70	237	10.80
		3	0.96	35	12.59	2	1.36	2	0.48	1	0.23	1	0.26	2	0.09
				4	1.44					1	0.23	8	2.09		
								1	0.24	1	0.23				
		1	0.32	2	0.72							2	0.52	3	0.14
		3	0.96					1	0.24					2	0.09
4	10.81	13	4.18	10	3.60	3	2.04	6	1.43	26	5.94	17	4.44	194	8.84
		6	1.93	1	0.36	2	1.36	1	0.24	7	1.60	1	0.26		
				2	0.72									1	0.05
								1	0.24					1	0.05
37	100.00	311	100.00	278	100.00	147	100.00	420	100.00	438	100.00	383	100.00	2195	100.00
16		56		45		40		52		42		49		64	
		5		11				8		8				13	
1		21		16				3		3				12	

(Lampitt, 1985); transport to 550 m depth will take about one week (McCave, 1975; Lampitt, 1985; Deuser, 1986). Many publications suggest that the first response in the benthic environment will be by heterotrophic bacteria (Fenchel and Jørgensen, 1977; Lochte and Turley, 1988; Jumars et al., 1989; Rowe, 1991; Della Groce et al., 1996; Danovaro et al., 2000a, b). Meiofaunal organisms, such as ostracods, nematode, and annelids, are thought to be secondary deposit feeders, which will have a delayed response. Larger meiofauna and macrofauna are extremely scarce at our 550 m station (Sorbe, 2001, pers. com.). The first foraminiferal response to phytodetritus supply, about 4–6 weeks after maximum surface water chlorophyll-*a* values, can be seen in the most opportunistic, small surface dwelling taxa like *E. exigua* and *R. guttiferus*. This delay may be shorter, but the temporal resolution of our study does not allow us to precisely determine the exact timing of the response of the foraminiferal opportunistic taxa. However, this estimate corresponds very well with the observations of Heinz et al. (2002), who describe a clear increase of the foraminiferal density about three weeks after food addition in a laboratory experiment. Slightly less opportunistic taxa such as *B. spathulata*, *C. carinata*, *N. pusillus*, *U. peregrina* and *U. mediterranea* could respond somewhat later. In the first phase of benthic foraminiferal response, the degree of patchiness appears to be very high, probably due to the spatial heterogeneity of phytodetritus deposits at the sea floor. Because of the rather superficial depth of bioturbation, the transmission of benthic ecosystem enrichment towards deeper sediment layers is a slow process. This explains why a reproductive event of intermediate and deep infaunal taxa is only noticed 2–3 months after maximum chlorophyll-*a* values (e.g. *G. affinis* in June 1998, and *M. barleeanus* in July 1998).

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Appendix A

Species of benthic foraminifera recognised at station B from the Bay of Biscay, with references to plates and figures in the literature on Atlantic and Mediterranean foraminifera (Table 4).

Appendix B

Census data for benthic foraminifera in the $>150\,\mu m$ size fractions for all 15 cores. Data for core OB1B comes from corrected data presented in Fontanier et al. (2002).

N.B. Numbers are not standardised for sediment volume (Table 5).

Appendix C

Census data for benthic foraminifera in the 63–150 μm size fractions for all 15 cores. N.B.

Numbers are not standardised for sediment volume (Table 6).

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