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SEASONAL VARIABILITY OF BENTHIC FORAMINIFERAL FAUNAS AT 1000 M DEPTH IN THE BAY OF BISCAY

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ABSTRACT

A 1000-meter-deep station in the Bay of Biscay (station A) was sampled 10 times between October 1997 and April 2001 for the purposes of studying the temporal variability of live foraminiferal faunas in the 63–150 μm and >150 μm size fractions. The results are compared with those obtained earlier for a 550-m-deep station nearby. The study area is marked by prolonged, two-month spring blooms and less clear autumn blooms that result in labile organic matter enrichment of the upper sediment layers. Episodic exportation of phytodetritus had a recognizable impact on early diagenetic processes only in April 2001. During the 2001 spring bloom, bottom-water oxygenation and the depth of the zero-oxygen boundary were minimum.

Foraminiferal faunas respond to bloom events by increases in the abundance of opportunistic taxa. In the >150 μm size fraction, *Uvigerina mediterranea* and *Uvigerina peregrina* preferentially reproduced and thrived in shallow infaunal microhabitats that are seasonally enriched in phytodetritus. Although the seasonal changes in the 63–150 μm size fraction are less straightforward, *Nuttallides pusillus* and *Uvigerina peregrina* did show marked seasonal changes in abundance. The temporal changes in the foraminiferal faunas at the 1000-m-deep station appear to be synchronous with those recorded at the 550-m-deep station.

INTRODUCTION

Deep-sea heterotrophic benthic foraminifera are known to respond to seasonal phytodetrital deposits at the sea floor (e.g., Gooday, 1988; Kitazato and Ohga, 1995; Kitazato and others, 2000; Duijnstee and others, 2001). Various opportunistic foraminiferal taxa are able to quickly colonize and feed on freshly deposited phytoplankton aggregates in deep-sea environments; their occurrence in surface sediment is limited in time and is sometimes characterized by spectacularly high standing stocks (Gooday, 1988; Gooday and Lambshead, 1989; Gooday and Turley, 1990; Barmawidjaja and others, 1992; Gooday, 1993; Kitazato and Ohga, 1995; Jannink and others, 1998; Silva and others, 1996; Gooday and Rathburn, 1999; Kitazato and others, 2000; Duijnstee and others, 2001; Moodley and others, 2002; Gooday and Hughes, 2002). Recently, experimental laboratory studies on deep-sea foraminiferal taxa have confirmed the response of foraminiferal taxa to simulated phytoplankton pulses (Heinz and others, 2001, 2002; Ernst, 2002; Kitazato and others, 2003). Deep-sea foraminiferal faunas appear to play a major role in the cycling of organic carbon and other biolimiting elements (e.g., nitrogen, phosphorous) and in the packaging of freshly deposited organic matter (Moodley and others, 2002).

In a paper discussing the seasonal and small-scale spatial variability of deep-sea foraminiferal faunas at a 550-m-deep station in the Bay of Biscay, Fontanier and others (2003) suggested a strong linkage between the phytoplankton bloom regime and the seasonal dynamics of the foraminiferal faunas. Some weeks after chlorophyll-a concentration peaked in the surface waters, opportunistic taxa (e.g., *Epistominella exigua*, *Uvigerina peregrina*) exhibited standing stock increases in the top centimeter of organic-matter-enriched surficial sediment, into which phytodetritus aggregates are bioturbated. In the deeper parts of the sediment, less opportunistic taxa (e.g., *Melonis barleeanus*, *Globobulimina affinis*), which live preferentially in dysoxic and anoxic microbiotopes, show only a minor seasonal variability. Those taxa appear not to compete for ephemeral labile food particles in the surficial and shallow infaunal niches and might prefer the more trophically and chemically stable conditions deeper in the sediment. There, they could feed on less labile organic compounds that are slowly bioturbated into the sediment, and are remineralized in their preferred infaunal microhabitat, which offers the advantage of limited competition and low predational pressure.

In this paper, we investigate the temporal variability of live foraminiferal faunas (63–150 μm, >150 μm) collected from a considerably deeper open-slope station (Station A, 1000 m deep) from the Bay of Biscay (44°10′N, 2°20′W; Fig. 1). We sampled our station 10 times between October 1997 and April 2001 and collected 12 cores, including two couples of duplicates. As described by Fontanier and others (2003), the Bay of Biscay is under the influence of a typical temperate, mid-latitude seasonal primary production regime marked by a very strong spring bloom and a less clear autumn bloom. Our main intention is to determine whether the interannual and seasonal primary production oscillations in the surface waters provoke important short-term variability of the standing stock and composition of the benthic foraminiferal faunas. To this end, we compare our faunal analyses with geochemical data of the upper sediment layer and with chlorophyll-a concentration values in the surface waters throughout the study period. We used on-line data archives (SeaWIFS data) of the Joint Research Center (European Commission) to estimate chlorophyll-a concentration changes during the study period (Fig. 2).

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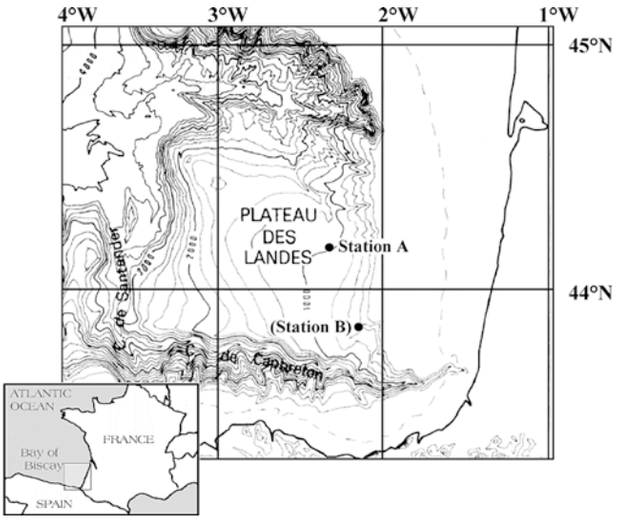


FIGURE 1. Study area, bathymetry and geographic position of station A. Station B, discussed in the text, is also presented (Fontanier and others, 2003).

STUDY AREA

Hydrographical Setting

The vertical hydrologic structure and major physiographic patterns of the study area are described in detail in Fontanier and others (2002, 2003). Our station A (1000 m depth) is bathed in Mediterranean Waters (MW), which are found between 800 and 1200 m deep in our study area. The Mediterranean Waters are characterized by a high salinity (35.80–35.85, Le Floch, 1968), and moderate oxygen concentration values (3.8 ml/l, Ogawa et Tauzin, 1973). At our open-slope station A (just as at station B; Fontanier and others, 2003; Fig. 1), vertical advection of fresh organic matter (phytoplankton productivity) from surface waters is considered to be the main source of exported labile organic compounds. Nevertheless, as suggested by Heussner and others (1999) in a dynamic sedimentary model, the upper part of the Plateau des Landes (<1000 m deep) may also act as a potential source of reworked sediment transported into the Northern Cap-Ferret Canyon head by strong along-slope currents. Thus, sea floor resuspension could be a significant phenomenon affecting the sedimentary deposits in our study area (Heussner and others, 1999).

Primary Production Patterns in the Northeastern Atlantic

The temporal variability of primary production in the Bay of Biscay is described by Fontanier and others (2003). Spring blooms present the highest phytoplankton production of the year. They last for about two months in March, April and May (Boucher, 1985; Laborde and others, 1999, Fontanier and others, 2003). They usually consist of a succession of individual bloom events, represented by different phytoplankton groups (Tréguer and others, 1979, Lampert, 2001). The occurrence of an autumn bloom is unclear, and only a few papers deal with it. In the Bay of Biscay, the autumn bloom may correspond to subsurface primary production triggered by in-situ nutrient regeneration (Le Corre and Tréguer, 1972; Tréguer and others, 1979). However, according to Schiebel and others (2001), who studied a BIOTRANS site (47°N/20°W), a fall bloom does not seem to exist. Phytoplankton biomass increases which are sometimes observed in the fall in surface

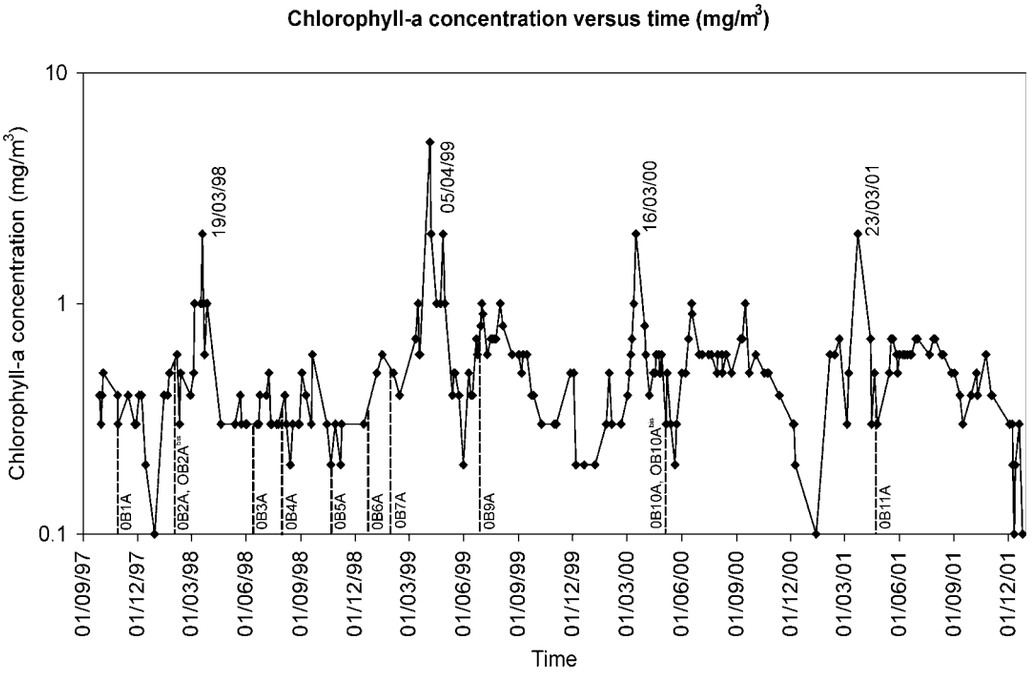


FIGURE 2. Chlorophyll-a concentrations in the surface waters above our station A, between October 1997 and April 2001 (estimates based on SEAWIFS images). Vertical dotted/dashed lines indicate when the sampling cruises took place.

TABLE 1. Sampling dates, bottom water oxygen concentration, depth in the sediment of the zero-oxygen level, foraminiferal density and species richness in 63–150 and >150 μm fractions, and semi-quantitative analysis of the sedimentary residual parts of the first quarter of sediment for 12 cores at station A for the 10 sampling cruises; Phytoplankton and zooplankton components were observed and described according to the following classes: ++ abundant, + common, − rare, −− absent. ND means "No Data". Bottom-water oxygen concentration is measured 5 mm above the sediment-water interface. Foraminiferal density is expressed as number of individuals per 50 cm^2.

Cores Station A	Date	O_2 concentration (μmol/l)	Oxygen penetration Depth (mm)	Whitish filamenteous and/or amorphous phytodetrital aggregates	Radiolarians
OB1A	25/10/1997	196	18	ND	ND
OB2A/OB2A^{bis}	31/01/1998	201	31	-/-	--/--
OB3A	07/06/1998	192	32	-	--
OB4A	23/07/1998	189	30	--	--
OB5A	17/10/1998	200	32	+	--
OB6A	06/12/1998	193	36	-	--
OB7A	23/01/1999	196	34	-	--
OB9A	22/06/1999	200	33	-	++
OB10A/OB10A^{bis}	30/04/2000	199	29	++/++	++/++
OB11A	16/04/2001	138	8	+	+

Cores Station A	Foraminiferal density (/50cm²) (63-150 μm)	(>150 μm)	Specific richness (63-150 μm)	Specific richness (>150 μm)
OB1A	774	359	48	38
OB2A/OB2A^{bis}	579, 1072	308, 238	37, 38	51, 44
OB3A	483	156	58	33
OB4A	335	123	34	28
OB5A	378	158	37	36
OB6A	66	212	19	35
OB7A	98	285	19	39
OB9A	419	353	48	38
OB10A/OB10A^{bis}	150, 374	363, 669	26, 31	54, 61
OB11A	612	444	43	53

and subsurface waters in the boreal realm could be due to the mechanical mixing of residual summer deep chlorophyll production in surface waters with very limited new phytoplankton production (Joanna Waniek, communication 2004).

MATERIAL AND METHODS

As explained in Fontanier and others (2003), we used online 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 2001; Fig. 2). The use of this method has the problem that weather conditions strongly affect the availability of images. As a consequence, we have no precise idea about the temporal variability of chlorophyll-a during late autumn and early winter.

Our sampling surveys were performed with the oceanographic vessel "Le Côte de la Manche", that does not have a dynamic positioning system. Therefore, during successive multicorer deployments, marine drift may have induced a distance of 100–200 m between the initial deployment position and the landing position on the sea floor. Therefore, duplicate cores collected at the same station after two successive multicorer deployments may represent a mesoscale spatial variability (several hundreds meters). Station A (44°10′00 N, 2°20′00 W; Fig. 1) was sampled 10 times with a Barnett multitube corer (Barnett and others, 1984), allowing sampling of the top decimeters of the sediment, the overlying bottom waters, and an undisturbed sediment-water interface (Table 1). Free waters were collected immediately after core recovery for dissolved oxygen measurements by the Winkler titration method (Strickland and Parsons, 1972). Profiles of pore-water oxygen were obtained on board with a cathode-type mini-electrode (Revsbech and Jørgensen, 1986; Helder and Bakker, 1985; Revsbech, 1983). This operation was completed in duplicate within 30 minutes after core recovery. At station A, the temperature is about 10°C. Temperature stability was maintained with an insulating device made of box insulated with 10-cm-thick polystyrene. For spring and summer cruises, the inner part of this device was initially cooled with ice packs before working on cores. Subsequently, the core used for oxygen profiling was sliced into thin horizontal sections (every 0.5 cm for the top 2 cm, and every 1–2 cm below that) within 1.5 hours. For every level, a subsample 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 analyzed by techniques adapted for small volumes of samples (Anschutz and others, 1999; Hyacinthe and others, 2001).

For faunal analysis, one entire 72 cm^2 core was sliced horizontally for each sampling, usually every 0.25 cm for the top centimeter of sediment, every half centimeter between 1 and 4 cm depth, and every centimeter between 4 and 10 cm. Only core OB1A was sampled slightly differently. The two available duplicate cores were analyzed as well. This concerns samples OB2A^{bis} (normally sampled) and OB10A^{bis} (top 1 cm sampled in 0.5 cm intervals; 1–5 cm interval sampled in 1-cm slices; 5–10 cm interval sliced in two 2.5-cm samples). Each duplicate pair was recovered from two different multicorer deployments. Sediment

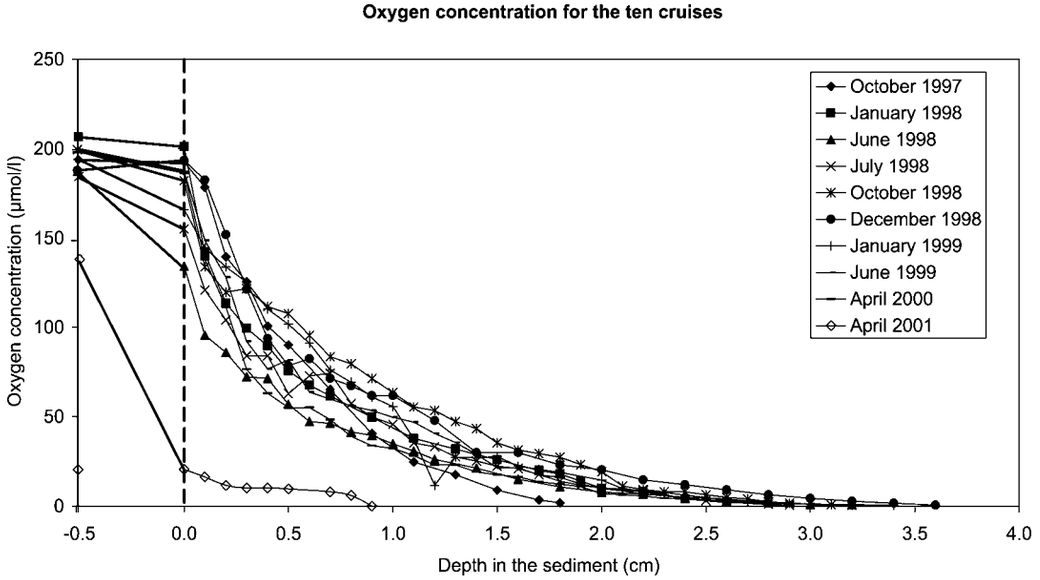


FIGURE 3. Dissolved oxygen concentrations in bottom waters and within the sediment for the ten cruises. The vertical dotted line represents the sediment-water interface.

storage and preparation were done as described by Fontanier and others (2002). Foraminifera belonging to the >150 μm fraction were studied along the 10-cm-long cores, whereas foraminifera from the 63–150 μm fraction were only studied in the top half centimeter of sediment. During picking, semi-quantitative observations were made on the residual parts of >150 μm fractions to evaluate phytodetritus and zooplankton remains (Table 1).

Live foraminiferal individuals were colored with the rose Bengal staining technique (Walton, 1952). Several authors (e.g., Bernhard, 1988; Corliss and Emerson, 1990; Bernhard, 2000) have dealt with the potential problems of the rose Bengal staining method. Protoplasm of dead foraminiferal individuals that has been temporarily preserved from degradation in anoxic parts of the sediment may still be colored. Furthermore, coloration in translucent tests of dead foraminifera may be due to the presence of organisms inhabiting one or several chambers of the shell (nematodes, bacteria). As a consequence, we used the same strict staining criteria as those described in Fontanier and others (2002). Nontransparent 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., *Bathysiphon* spp. and most species of *Rhabdammina* spp.) were not included in the quantitative analyses. Our taxonomical framework is given in Appendix A. All foraminiferal census data are listed in Appendices B and C which are placed in the JFR online data repository (www.CushmanFoundation.org; JFR DR200601). Typical species are figured at http://sciences.univ-angers.fr/geologie/atlas/Taxo_tophe.htm. Census data of core OB1A (>150 μm fraction) were presented in Fontanier and others (2002). The total density of the live foraminiferal fauna (standing stock) has been determined by summing up the number of individuals for all levels between 0–10 cm depth for the >150 μm fraction, but only for the 0–0.5 cm interval for the 63–150 μm fraction. Thus, the total density per core is generally expressed as the number of individuals found at and below a 50 cm^2 sediment surface (Table 1). In all graphs depicting the vertical distribution of the foraminifera in the >150 μm fraction, the faunal densities have been standardized for a 50 cm^3 sediment volume.

The average living depth (ALD_x, Jorissen and others, 1995) is a convenient way to describe the overall vertical distribution of the total foraminiferal fauna or individual taxa, and to get a general idea about the microhabitat patterns. To this end, we used the methods and formula presented in Fontanier and others (2003). 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}. In Appendix B (JFR DR200601), those counts are presented in brackets. We presume that such isolated individuals either have been transported downward (outside their normal microhabitat) by bioturbation, or correspond to decaying organisms that have been counted erroneously.

RESULTS

CHLOROPHYLL-A CONCENTRATIONS, OCTOBER 1997 TO APRIL 2001

At our station A (Fig. 2), the temporal variability of chlorophyll-a concentrations in the overlying surface waters exhibited the same trends as those observed for the entire Bay of Biscay. The spring blooms were recurrent throughout the 3.5 years of our investigation. They were systematically recorded at the end of winter and the beginning of the boreal spring (second half of March and April) and lasted about 2 months, until June. They are associated with

eutrophic conditions prevailing in the surface waters of our study area ($\geq$1 mg/m^3). Chlorophyll-a maxima were recorded on March 19, 1998, April 5, 1999, March 16, 2000 and March 23, 2001. In summer, station A is under the moderate influence of the mesotrophic, plume-like structures that spread from the highly productive French shelf-break area. In our study area, chlorophyll-a concentration ranges from 0.6 to 0.8 mg/m^3. Such plume-like structures are rather stable for several weeks and generally disappear at the end of the boreal summer (in September). These summer structures do not exhibit the same magnitude and geographic distribution throughout the investigated years; they were spatially limited in the summer of 1998. They may be associated with well-known coastal upwelling cells that are mainly related to Northern winds blowing along the coast (Holligan and others, 1983; Froidefond and others, 1996). As suggested by Beaufort and Heussner (1999) and shown by our observations, the spreading of the upwelling systems and the intensity of the accompanying phytoplankton production may present a strong interannual variability. From late summer to early winter, chlorophyll-a concentrations tended to gradually decrease to oligotrophic values (0.2 mg/m^3). No autumn bloom was detectable in the surface waters.

Organic Sedimentary Components

Semi-quantitative observations of the sieve residues of the first 0.5 cm of the >150 μm fraction are presented in Table 1. No observation could be performed for October 1997 (OB1A core) because the samples were stored dry after picking, and therefore, possible organic compounds have not been preserved.

Cores sampled in June 1999, April 2000 and April 2001 (OB9A, OB10A, OB10A^{bis} and OB11A, respectively) contained high amounts of whitish amorphous aggregates and abundant radiolarians. Because the spring bloom started several weeks before these three cruises (Table 1, Fig. 2), we presume that this organic detritus resulted from the vertical transport of spring bloom zooplankton and phytoplankton remains to the sea floor. OB9A was indeed collected seven weeks after the 1999 spring bloom maximum. OB10A and OB10A^{bis} were collected six weeks after the 2000 spring bloom maximum. OB11A was collected three weeks after the 2001 spring bloom maximum. Phytodetritus deposits have been observed for the same period at the 550-m-depth station B close to our study area (June 1999 and April 2000; Fontanier and others, 2003; Fig. 1). Cores collected during summer and early autumn (OB3A, OB4A and OB5A) did not exhibit any zooplankton and phytoplankton remains that may be related to enhanced surface water primary production.

Oxygen Concentration and Redox Conditions of Interstitial Waters

Bottom water oxygen concentrations measured 5 mm above the sediment-water interface (Table 1) varied from 138–201 μmol/l (3.07–4.47 ml/l). At the sediment-water interface, oxygen concentration values were 20–201 μmol/l (in April 2001 and January 1998, respectively). The depth of the zero-oxygen boundary was only 8 mm in April 2001 (OB11A). For the other cores, oxygen concentration profiles from the sediment-water interface to deeper layers are rather similar, although the depth of the zero-oxygen boundary varied from 18 mm (0B1A, October 1997) to 36 mm (OB6A, December 1998, Fig. 3).

Faunal Density and Number of Taxa

In the >150 μm fraction, foraminiferal densities varied from 123–669 individuals per 50 cm^2 core (Table 1). Maxima of 669 and 444 individuals were recorded in April 2000 (OB10A^{bis}) and in April 2001 (OB11A), respectively. The minimum value occurred in July 1998 (OB4A, 123 individuals per core). For the 63–150 μm fraction, foraminiferal densities (for the topmost 0.5 cm) varied from 66–1072 individuals (Table 1). Maxima of 612, 774 and 1072 individuals were recorded in April 2001 (OB11A), October 1997 (OB1A) and in January 1998 (OB2A^{bis}) respectively. Minimum values occurred in December 1998 (OB6A, 66 individuals) and in January 1999 (OB7A, 98 specimens).

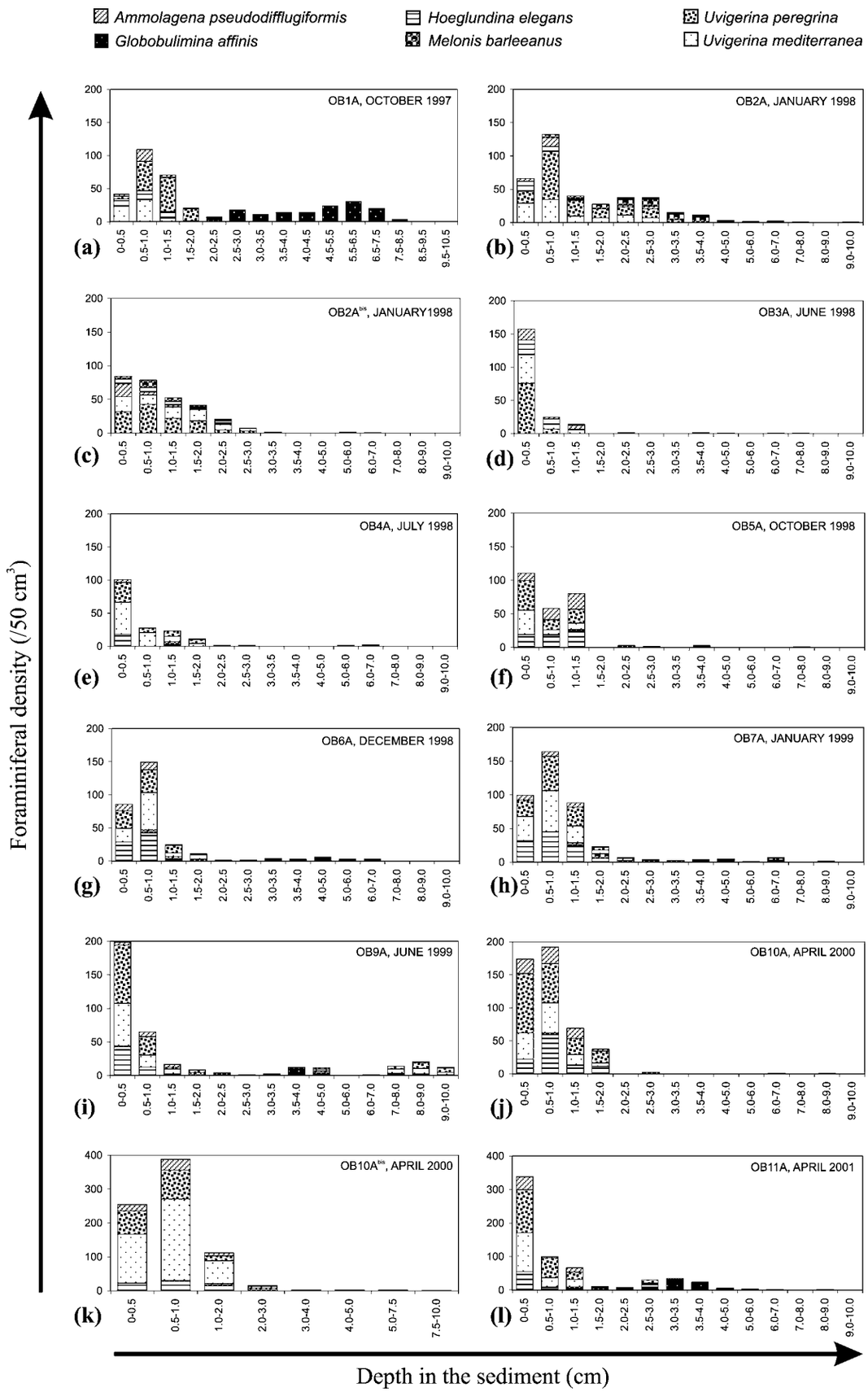
In the >150 μm fraction, perforate foraminifera formed the main faunal component (64%–78%). Nonfossilizing agglutinated taxa accounted for 20–33%. Miliolids (maximum 6.5%) were rare in all cores. Fossilizing agglutinated taxa were almost absent. In the 63–150 μm fraction, perforate taxa also formed the largest group (62–87%). Nonfossilizing agglutinated foraminifera represented 12–36% of the total fauna. Miliolids and fossilizing agglutinated foraminifera accounted for less than 2.5% of the foraminiferal faunas.

The number of taxa in the >150 μm fraction varied from 28 (July 1998, OB4A) to 61 (April 2000, OB10A^{bis}), with a clear positive correlation with faunal density. In the 63–150 μm fraction, for which only the topmost 0.5 cm was studied, the number of taxa varied from 19 (December 1998, OB6A) to 58 (June 1998, OB3A), with no clear correlation with faunal density.

Faunal Composition and Microhabitat

Fraction >150 μm

Live foraminiferal faunas were normally concentrated in the upper 0.5–1.0 cm of the sediment (Fig. 4a–l). The highest surface foraminiferal density was recorded in April 2001 (OB11A; ~400 specimen/50 cm^3). In one of the duplicate cores collected in April 2000, we recorded a very high subsurface density maximum in the 0.5–1 cm interval (OB10A^{bis}; ~450 specimen/50 cm^3). In most cores, foraminiferal density quickly decreased down to 2 cm. Consequently, for most of the cores, the ALD_{10} of the total fauna was between 0.5 and 1.5 cm. The shallowest microhabitat depth was observed in June 1998 (ALD_{10} = 0.5 cm). In the deeper sediment layers, foraminiferal densities increased moderately in October 1997 (OB1A) and in April 2001 (OB11A). In these two cores, monospecific assemblages consisting of *Globobulimina affinis* individuals appeared in anoxic sediments (with maximum values close to 30 individuals/50 cm^3). In June 1999 (OB9A), a deep multispecies foraminiferal assemblage was found in the 7–10 cm depth interval. As a consequence, maximum ALD_{10} values


Ammolagena pseudodiffugiformis
Globobulimina affinis
Hoeglundina elegans
Melonis barleeanus
Uvigerina peregrina
Uvigerina mediterranea
OB1A, OCTOBER 1997
OB2A, JANUARY 1998
OB2A bis, JANUARY1998
OB3A, JUNE 1998
OB4A, JULY 1998
OB5A, OCTOBER 1998
OB6A, DECEMBER 1998
OB7A, JANUARY 1999
OB9A, JUNE 1999
OB10A, APRIL 2000
OB10A bis, APRIL 2000
OB11A, APRIL 2001
(a)
(b)
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(d)
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Foraminiferal density (/50 cm3)
Depth in the sediment (cm)

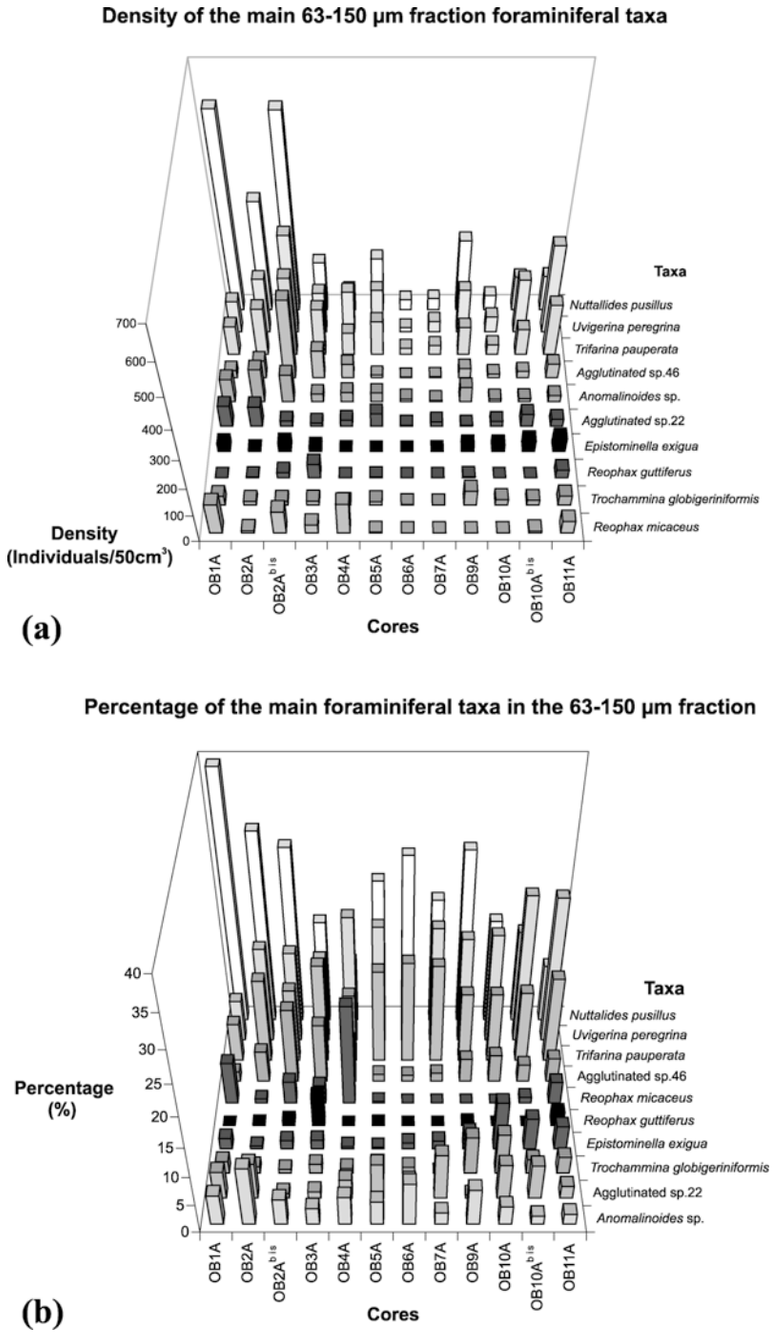

FIGURE 5. Fig. 5a Foraminiferal density of the main foraminiferal taxa in the 63–150 µm fraction for the 12 cores. Densities are standardized to a 50 cm³ sediment volume. Fig. 5b Percentages of the main foraminiferal taxa in the 63–150 µm fraction for the 12 cores.

were found in October 1997 (OB1A; 1.9 cm) and June 1999 (OB9A; 2.0).

Uvigerina peregrina dominated the fauna in most cores with maximum percentages recorded in January 1998 (both replicate cores), June 1998 (OB3A), April 2000 (OB10A) and April 2001 (OB11A; Appendix B, JFR DR200601). Minimum values were recorded in the second replicate core collected in April 2000 (OB10A^{bis}), in October 1997 (OB1A) and in December 1998 (OB6A). *Uvigerina mediterranea* was the second most dominant taxon. It exhibited its highest

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FIGURE 4a–l. Foraminiferal distribution (number of individuals >150 µm fraction found in each level, standardized for a 50 cm³ sediment volume) for 12 available cores.

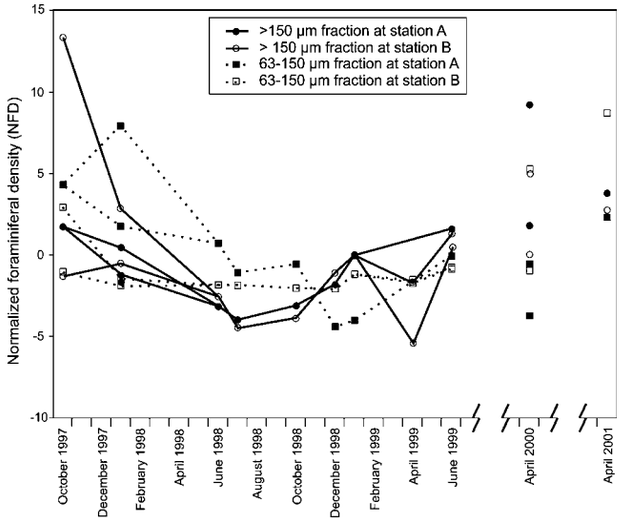

FIGURE 6. Normalized foraminiferal density (*NFD*) for both size fractions at station A and B between September 1997 and April 2001 (see discussion for calculation details of *NFD*).

relative abundance in April 2000 (OB10A^{bis}, 39.6%) and its lowest percentage in October 1997 (OB1A; 8.7%). As the third most dominant taxon, *Hoeglundina elegans* percentages ranged from 4.1–19.0%. Low values were recorded in October 1997 (OB1A), and January 1998 (both replicate cores), whereas high percentages occurred in December 1998 and January 1999. *Lagenammina pseudodifflugiformis* ranged from 2.3–10.5% with the highest value recorded in October 1998 (OB5A). *Globobulimina affinis* had very high percentages in October 1997 (OB1A, 26.5%) and April 2001 (OB11A, 7.0%). *Melonis barleeanus* was a minor species with percentages generally below 10.0%.

ALD values for most taxa are presented in Table 2. *Hoeglundina elegans* (overall weighted ALD_{10} = 0.86 cm) was consistently present in a shallow infaunal microhabitat. *Uvigerina mediterranea*, *U. peregrina* and *Lagenammina pseudodifflugiformis* exhibited overall weighted values of ALD_{10} close to 1 cm deep (0.96, 0.99 and 1.04 cm, respectively). For all these taxa, microhabitats were rather constant throughout the study period (Table 2). The exception is the core collected in June 1999 (OB9A), where normally surface-dwelling species occurred in the deeper part of the sediment, which may be related to the presence of an irrigated burrow 5–9 cm deep. This phenomenon caused a significant deepening of all ALD_{10} values (Table 2, Fig. 4i). *Melonis barleeanus* with a weighted ALD_{10} of 2.05 cm lives in an intermediate to deep infaunal microhabitat. In our study, the microhabitat of *M. barleeanus* varied over a rather wide depth range (1.0–3.1 cm), but always coincided with weakly oxygenated conditions. *Globobulimina affinis* occupied deep infaunal niches in anoxic sediments (overall weighed ALD_{10} = 4.05 cm). Its average microhabitat depth ranged from 3.6–5.6 cm.

Fraction 63–150 µm

The densities and percentages of the main taxa in the topmost 0.5 cm of the twelve cores are shown in Fig. 5a–b and Appendix C (JFR DR200601). Because of the large variability in foraminiferal density, which may be partially due to a varying sampling volume, the faunal variability is probably better represented by percentage data. *Nuttallides pusillus* was the most abundant taxon, ranging from 9.6 to 39.7% (in April 2001 and October 1997, respectively). When *N. pusillus* was less dominant, juvenile specimens of *Uvigerina peregrina* dominated the foraminiferal assemblage. *Uvigerina peregrina* accounts for 6.9–24.3% of the total faunas. Highest percentages were recorded in July 1998 (OB4A), April 2000 (both duplicate cores) and April 2001 (OB11A). Its lowest abundance was recorded in October 1997 (OB1A). This variability largely coincides with that found in the >150 µm fraction. *Trifarina pauperata* is the third most dominant taxon, which exhibited much less temporal variability than the two more abundant taxa. It showed high percentages (about 16%) in June 1998 (OB3A), December 1998 (OB6A) and January 1999 (OB7A). Its lowest percentage was recorded in October 1997 (OB1A, 6.5%). Other taxa such as *Anomalinoides* sp. and Agglutinated sp. 22 and 46 (Appendix A) showed some isolated, minor relative abundance peaks. *Epistominella exigua* and *Trochammina globigeriniformis* each occurred at less than 10% in all cores. They both had their highest relative abundances in June 1999 (OB9A), April 2000 (both duplicate cores) and April 2001 (OB11A). Finally, *Reophax guttiferus* showed a small percentage maximum in June 1999 (OB3A; 5.3%).

Taxonomic Remarks

Agglutinated sp. 22 only occurred in the 63–150 µm size fraction. This slightly elongated agglutinated taxon consists of a chaotic aggregate of small tests or fragments of planktonic foraminifera with rare terrigenous material. No inner chamber structure is visible and no aperture is detectible. This taxon may belong to the family Psammosphaeridae as defined by Loeblich and Tappan (1988).

Agglutinated sp. 46 occurred in both size fractions. This monothalamous, soft-shelled taxon has an oval, more or less elongated, flask-shaped test consisting of very fine white grains. A single aperture is visible at the tapered end. This taxon may belong to the family Saccamminidae as defined by Loeblich and Tappan (1988).

DISCUSSION

TEMPORAL VARIABILITY OF BOTTOM AND PORE WATER CHEMISTRY

Our data show a surprising constancy in the chemistry of the bottom waters at the 1000-m-deep station A. Bottom-water oxygen concentration values range from 138–201 µmol/l (3.07–4.47 ml/l), close to the value of 202 µmol/l (4.49 ml/l) measured by Vangrieshem (1985) at a 900-m depth off Brittany (47°35′N, 9°39′W; EDYLOC 82 survey).

At the sediment-water interface, oxygen concentrations are much more variable than in the bottom waters (Fig. 3). A marked decrease in oxygen concentration in the 0.5 cm of bottom waters overlying the sediment-water interface was

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 one or more of the stations. Microhabitat patterns are summarized as shallow infaunal (SI), intermediate infaunal (II) or deep infaunal (DI).

Taxa	Cores, ALD_{10}											Average weighted ALD_{10}	Microhabitat
	OB1A	OB2A	OB2A^{bis}	OB3A	OB4A	OB5A	OB6A	OB7A	OB9A	OB10A	OB10A^{bis}	OB11A		
Anomalinoides sp.	0.3 (7)												0,34	SI
Bulimina inflata	0.4 (5)								4.2 (13)	0.7 (12)	0.8 (22)	0.7 (11)	1,42	II
Cibicidoides pachydermus	0.4 (11)												0,40	SI
Globobulimina affinis	4.7 (137)	3.6 (14)					5.0 (20)	4.7 (11)	4.0 (13)		5.6 (10)	3.9 (45)	4,50	DI
Gyroidina orbicularis		2.3 (14)	1.8 (15)	1.8 (8)	1.9 (5)	2.3 (7)	1.8 (8)	3.0 (12)	3.2 (9)		1.9 (11)	1.4 (5)	2,18	II/DI
Hoeglundina elegans	0.8 (26)	0.5 (18)	1.0 (19)	0.5 (23)	0.3 (15)	0.5 (28)	0.6 (54)	0.8 (78)	1.9 (53)	0.8 (76)	0.9 (57)	0.9 (61)	0,86	SI
Melonis barleeanus	1.7(6)	2.4 (37)	1.0 (18)			1.6 (5)	1.6 (11)	2.2 (15)	3.1 (16)	1.7 (5)	2.1 (27)	1.8 (13)	2,05	II/DI
Nuttallides umboniferus	0.4 (27)		1.2 (11)			0.2 (7)	0.5 (5)		0.3 (15)	0.8 (13)	0.6 (6)	0.4 (6)	0,56	SI
Trifarina bradyi											0.5 (5)	0.7 (5)	0,59	SI
Uvigerina mediterranea	0.6 (45)	1.3 (75)	1.2 (59)	0.4 (40)	0.5 (60)	0.4 (34)	0.8 (67)	1.0 (97)	2.7 (94)	0.7 (77)	0.8 (381)	0.6 (128)	0,96	SI
Uvigerina peregrina	1.1 (85)	1.3 (114)	1.0 (88)	0.2 (60)	0.6 (37)	0.4 (46)	0.7 (53)	1.1 (83)	2.4 (120)	0.7 (139)	0.7 (135)	0.8 (168)	0,99	SI
Pyrgo depressa	0.1 (10)												0,06	SI
Pyrgo murrhina										0.7 (8)	0.6 (5)		0,62	SI
Pyrgo subsphaerica	1.3 (5)										0.9 (16)		0,98	SI
Pyrgoella sphaera												0.9 (8)	0,92	SI
Quinqueloculina sp.2			0.8 (12)										0,84	SI
Triloculina tricarinata		1.5 (21)											1,49	II
Agglutinated sp.11	0.6 (5)		0.8 (5)									0.5 (12)	0,59	SI
Agglutinated sp.29								0.9 (7)		1.2 (9)			1,03	SI
Agglutinated sp.46		1.7 (8)							1.2 (6)		4.0 (5)		2,13	DI
Ammobaculites agglutinans	0.6 (10)	1.3 (9)	0.8 (12)			0.3 (16)	1.1 (11)	0.8 (12)	0.9 (24)	0.6 (18)	0.8 (36)	0.4 (28)	0,72	SI
Ammolagena clavata											1.1 (26)		1,06	II
Cribrostomoides sp.						0.1 (7)							0,13	SI
Cribrostomoides subglobosus									0.7 (41)	0.7 (13)	0.8 (16)	0.7 (12)	0,74	SI
Crithionina abyssorum					1.2 (5)								1,20	II
Eggerella bradyi		0.9 (5)									1.3 (10)		1,14	SI/II
Karreriella bradyi	0.5 (5)	0.7 (9)									1.3 (9)		0,86	SI
Lagenammina pseudodifflugiformis	1.4 (17)	1.2 (18)	0.7 (22)	0.6 (18)		0.6 (23)	0.6 (16)	1.5 (19)	2.6 (14)	0.8 (47)	1.4 (56)	0.8 (44)	1,04	SI/II
Paratrochammina challengeri										0.6 (7)			0,55	SI
Psammosphaera spp.		0.8 (6)	0.5 (6)				0.6 (5)			1.0 (8)	2.2 (7)	0.5 (5)	0,98	SI
Recurvoides sp.	1.7 (6)												1,67	II
Reophax guttiferus		0.7 (5)									0.8 (6)		0,70	SI
Reophax scorpiurus	0.3 (31)	0.6 (20)	0.5 (6)	0.2 (18)	0.2 (6)		0.6 (9)	1.0 (11)	0.3 (13)	0.8 (5)	1.1 (21)		0,57	SI
Saccammina spp.										0.9 (9)	0.6 (6)		0,75	SI
Thurammina albicans	0.9 (16)	1.1 (13)					1.2 (5)	1.6 (14)		1.4 (6)	1.4 (11)	1.1 (7)	1,22	II
Thurammina papillata			1.3 (6)	1.2 (5)		1.4 (6)				2.0 (6)	2.3 (8)		1,67	II
Oxygen penetration depth (cm)	1,8	3,1	3,1	3,2	3,0	3,2	3,6	3,4	3,3	2,9	2,9	0,8		

recorded in June 1998, July 1998, January 1999 and April 2001. The steepest oxygen concentration gradient between bottom water and sediment-surface interstitial waters occurred in April 2001, with a marked decrease from 138 to about 20 μmol/l. This may have been due to enhanced oxygen consumption at the sediment-water interface related to biogenic degradation of freshly deposited organic matter deposits (Table 1).

At our 1000-m-deep station A, the vertical profiles of dissolved oxygen in the uppermost sediment (Fig. 3) show that for most cores, oxygen concentration decreased sharply in the top centimeter and the zero-oxygen boundary was reached at about 3 cm depth, suggesting intense oxygen consumption due to degradation of reactive organic matter available in the topmost sediment. In April 2001, the zero-oxygen boundary was encountered at 8 mm depth, which suggests an important remineralization of labile organic matter deposits (phytodetritus) related to the 2001 spring bloom. This observation differs significantly from the early diagenetic processes recorded at the previously studied 550-m-deep station B (Fontanier and others, 2003). There, the deposits of phytoplankton and zooplankton remains in the eutrophic periods (June 1999, April 2000, April 2001) did not induce marked changes in the oxygen concentration at the sediment-water interface, and did not significantly modify oxygen penetration within the sediment.

COMPARISON OF TEMPORAL VARIABILITY OF FORAMINIFERAL DENSITY BETWEEN STATIONS A AND B

In Figure 6, normalized foraminiferal densities (*NFD*) for both size fractions collected between September 1997 and April 2001 are shown for stations A and B, according to the following formula:

$$NFD_{core(i)} = \left(FD_{core(i)} - \overline{FD}\right)/SE,$$

where $NFD_{core(i)}$ is the normalized density for *core i* in the 63–150 μm or >150 μm size fraction, $FD_{core(i)}$ is the observed density in core i, $\overline{FD}$ is the mean density for all cores in the same size fraction, and *SE* is the standard error related to mean density. The foraminiferal density for the >150 μm fraction is initially calculated as the total number of live individuals per core (72 cm^2 surface area). The foraminiferal density for the 63–150 μm fraction is calculated as the total number of live foraminifera in the top 0.5 cm of the core. Normalized densities allow a better comparison between the density changes in both fractions at stations A and B. At station B (550 m depth, Fig. 1), foraminiferal faunas in the 63–150 μm and >150 μm

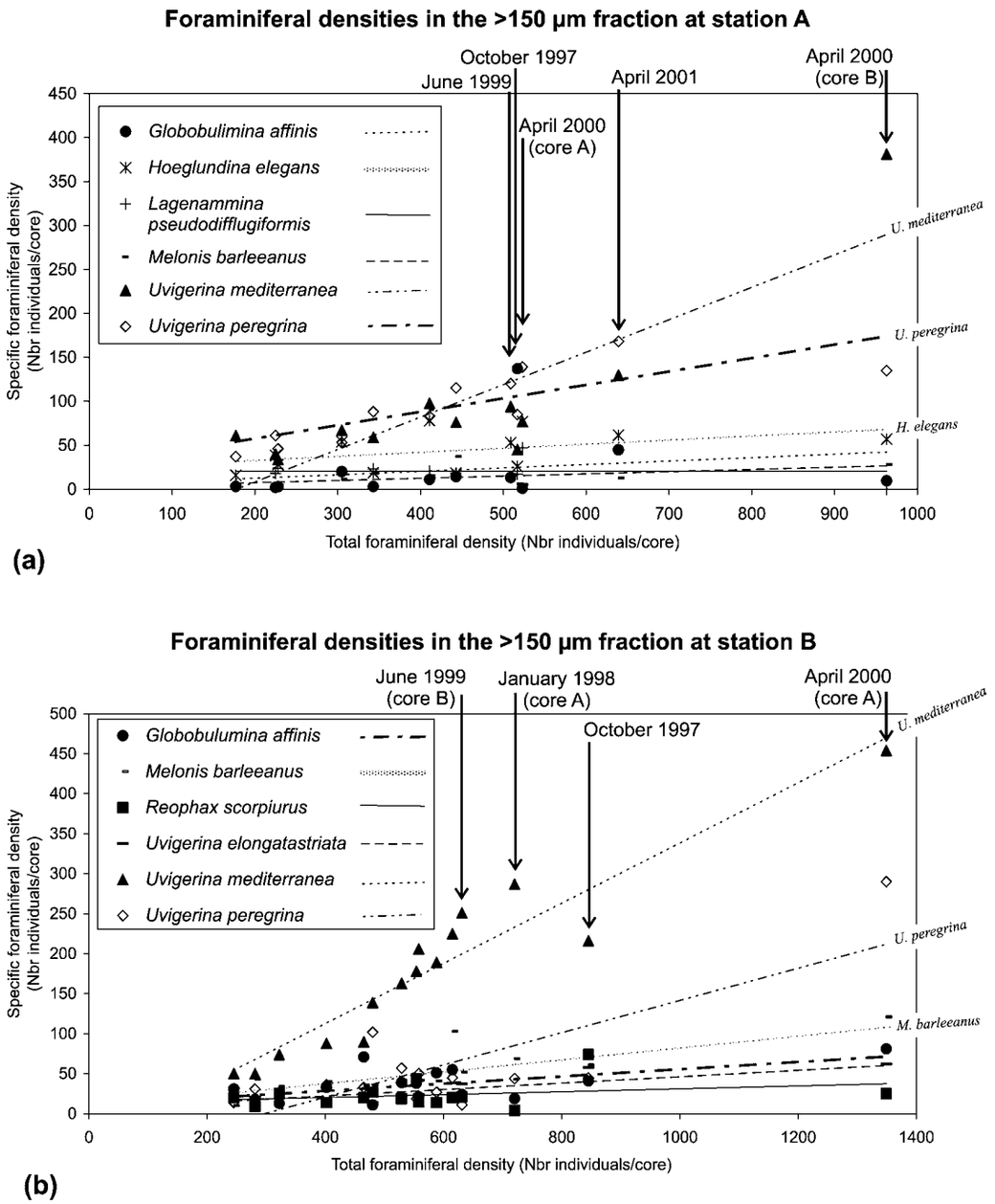

FIGURE 7a–b. Densities of the six main taxa compared to the total foraminiferal densities in the >150 µm. Figure 7a, station A. Figure 7b, station B (Fontanier and others, 2003).

fractions exhibited significant seasonal variability, with a clear foraminiferal response to increased organic matter input recorded in eutrophic periods (Fontanier and others, 2003).

For the >150 µm fraction, a simple bivariate analysis comparing the normalized density values for both stations shows a significant ($\alpha = 0.01$) correlation ($r^2 = 0.61$). In the case of duplicate samplings, the mean value has been used. The seasonal trends are roughly the same; the lowest normalized densities were recorded in oligotrophic periods (winter 1998/1999, summer 1998), whereas the highest normalized density values were recorded during more eutrophic periods (April 2000, April 2001 and October 1997; Fig. 6). The similar response at both stations suggests that foraminiferal faunas may have reacted to organic matter deposits related to basin-wide bloom events. Moreover, higher foraminiferal densities recorded in October 1997 at both stations suggest the presence of a fall bloom in our study area. In this case, foraminifera may have responded to phytodetritus deposited after a very short and not easily detectable Chlorophyll-a increase in surface waters (e.g., possible autumn bloom). However, they could have also reacted to partially degraded organic matter laterally advected by slope currents acting from

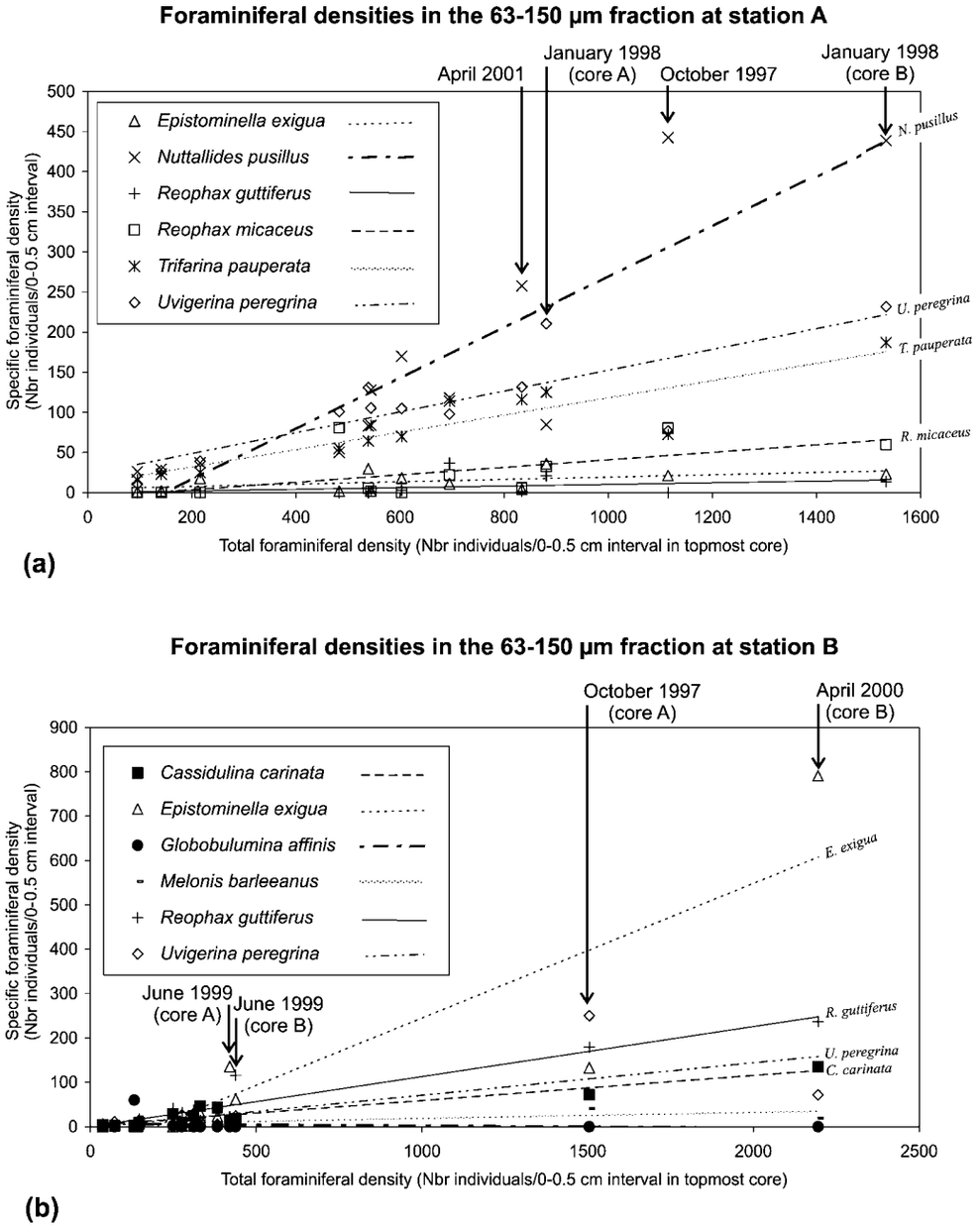

FIGURE 8a–b. Densities of the six main taxa compared to the total foraminiferal densities in the 63–150 µm. Figure 8a, station A. Figure 8b, station B (Fontanier and others, 2003).

a homogeneous source on the shelf and upper slope (<380 m; Plateau des Landes), according to the conceptual model of Heussner and others (1999).

A bivariate analysis comparing the normalized foraminiferal densities in the 63–150 µm fraction does not show a significant correlation between both stations (r^2 = 0.08). The absence of such a correlation may reflect the difficulties of working with density values of the 63–150 µm fraction for only the top 0.5 cm. As discussed above, we think that the variable sample size volume of the 0–0.5 cm interval is the main reason for the differences in foraminiferal density.

TEMPORAL VARIABILITY OF FORAMINIFERAL FAUNAS AT STATION A

In the >150 µm fraction, most of foraminifera were concentrated in the oxygenated layers of the sediment and more specifically, in the oxic zone where dissolved oxygen concentrations exceeded 50 µmol/l (Fig. 4a–l). Fontanier and others (2002) presented an adaptation for the Bay of Biscay of the TROX-model of Jorissen and others (1995). They suggested that foraminiferal microhabitats at station A are mainly food controlled. According to their model, most foraminiferal taxa thrive preferentially in the well-

oxygenated surficial sediment, enriched by fresh organic matter that originates from the labile organic matter flux to the ocean floor. Abundant intermediate and deep infaunal taxa, which are minor species, are closely related to redox gradients and buried organic matter.

When looking at our present results, the occurrence of a high density of foraminifera in the upper sediment layer of the cores collected in October 1997, June 1999, April 2000 and April 2001 (OB1A, OB9A, OB10A^{bis} and OB11A, respectively) suggests a significant foraminiferal response to organic matter enrichment of the topmost sediment. Figures 7 and 8, in which the specific density of dominant taxa is plotted as a function of the total faunal density in each of the two size fractions, show that the shallow infaunal taxa *Uvigerina mediterranea* and *U. peregrina* have by far the largest contribution to the density increase of the total fauna in the >150 μm fraction, at station A as well as station B. These increased absolute densities in the weeks following the spring bloom maxima (June 1999, April 2000 and April 2001) suggest an ability of these taxa to reproduce and/or to grow rapidly in eutrophic periods. The faunas found in October 1997, following a possible autumn bloom or increased lateral advection of organic matter, differ by much lower densities of these two species, suggesting the input of organic matter of lower quality. The results of the 63–150 μm fraction show a different response at both stations. Although juveniles of *U. peregrina* respond to eutrophic conditions at both stations, *Nuttallides pusillus* appears to be the most opportunistic small species at the 1000-m-deep station A, whereas *Epistominella exigua* occupies this niche at the 550-m-deep station B. These observations are in agreement with a recent experimental study by Ernst and Van der Zwaan (2002), who show that *U. peregrina* is able to reproduce in simulated phytoplankton deposits in the shallow infaunal microhabitat. At station A, *Hoeglundina elegans*, the third most dominant taxon in the >150 μm fraction, had its highest relative densities in the most oligotrophic periods. This agrees with numerous observations describing *H. elegans* as typical of areas with low organic carbon areas (Lutze and Coulbourne, 1984; Corliss, 1985; Corliss and Emerson, 1990; Corliss, 1991; Fontanier and others, 2002; Morigi and others, 2002). At station A, *H. elegans* was a dominant faunal element only during oligotrophic periods (December 1998 and January 1999), but was replaced by the more reactive *Uvigerina* species during the more eutrophic periods.

At station A, where stable redox conditions prevail throughout the year, the exported labile organic matter flux from the surface waters represents an essential food source for most benthic foraminifera. In oligotrophic periods, foraminiferal faunas react to a lower exported organic matter flux by being strongly concentrated in the surficial sediment. In eutrophic periods, opportunistic taxa thrive abundantly in shallow infaunal and deeper microhabitats in well-oxygenated sediments, where fresh phytodetritus is temporarily available. Thus, as suggested by the TROX-model adapted for the Bay of Biscay by Fontanier and others (2003), shallow infaunal microhabitats at station A are strongly controlled by the exported organic matter flux.

Melonis barleeanus occupies an intermediate to deep infaunal microhabitat (Table 2; Fig. 4a–l). It lives preferentially in an ecological niche where oxygen concentrations range from 40–1 μmol/l (dysoxic to suboxic conditions according to Tyson and Pearson, 1991). Similar observations were discussed in numerous other in situ studies (e.g., Corliss, 1988; Corliss et Emerson, 1990; Jorissen and others, 1995, 1998; Jorissen, 1999; Fontanier and others, 2002; 2003). The lower densities recorded at station A (1000 m depth, mean of 13 individuals per core) in comparison with *M. barleeanus* populations at station B (500 m depth, mean of 51 individuals per core; Fontanier and others, 2003) are an argument for a potential linkage between exported organic matter fluxes at the sea floor at both stations and *M. barleeanus* standing stocks. Higher fluxes of organic matter may sustain higher populations of adult *M. barleeanus* (>150 μm), which may feed on small quantities of labile organic matter buried in their intermediate infaunal niches by meifaunal and/or macrofaunal organisms. Alternatively, as suggested by Licari and others (2003) and Fontanier and others (2003, 2005), *M. barleeanus* may also feed on heterotrophic bacteria or live in mutualism with chemoautotroph-nitrifying or manganese-oxidizing bacterial consortia that thrive in the dysoxic part of the sediment.

When present in our cores, *Globobulimina affinis* always settled in a deep infaunal microhabitat in anoxic sediments (Table 2; Fig. 4a–l). This is in agreement with numerous studies describing *Globobulimina* spp. as a deep infaunal taxon (e.g., Corliss, 1985; Mackensen and Douglas, 1989; Corliss, 1991; Jorissen and others, 1995, 1998; Schmiedl and others, 2000; Fontanier and others, 2002, 2003, 2005). In Fontanier and others (2003, 2005), *G. affinis* was considered a highly specialized taxon which lives in a stable biogeochemical microhabitat where fresh phytodetritus is scarce or only related to macrofaunal burrowing. According to Fontanier and others (2003), seasonal frequency variations of *G. affinis* at station B may be related to supplies of labile organic matter (by macrofaunal burrowing) some weeks or months after initial phytodetritus deposits (in autumn and spring blooms) and an associated increase of bacterial activity. In the present study, the relatively high densities of *G. affinis* in October 1997 and April 2001 (OB1A and OB11A; Figs. 4a, 4l) suggest that *G. affinis* may have responded to (1) an organic matter enrichment of the deeper sediment parts related to intensified bioturbation in eutrophic periods (possible autumn bloom 1997 and spring bloom 2001), and to (2) the upward migration of the zero-oxygen boundary into organic-matter-enriched surficial sediment. Bioturbation structures (burrows) are indeed very abundant along the 10-cm-long cores collected in October 1997 and April 2001, and oxygen penetration is limited for both samplings. Mature *Globobulimina* populations that tolerate suboxic and anoxic conditions prevailing close to the zero-oxygen boundary appear to be able to track movements of these redox fronts (Kitazato and Ohga, 1995; Ohga and Kitazato, 1997). Heterotrophic bacterial consortia associated with the degradation of bioturbated organic matter compounds may act as an alternative food source for *G. affinis*. A very similar increase in the population density was observed by Heinz and others (2001) in a culture experiment after addition of low-quality organic matter.

The interpretation of our results for the smaller fraction (63–150 μm) is less straightforward. Because of the possibility of strongly varying sediment volumes, the density variations cannot be used as criteria of a temporal variability of foraminiferal faunas. As indicated by Fontanier and others (2003), in cases where the sediment surface is sloped, the volume of the top 0.5 cm layer may show important differences between cores. Thus, we must base our discussion mainly on percentage values. *Nuttallides pusillus* is the dominant taxon and showed the highest temporal variability in the 63–150 μm fraction (Fig. 5a–b, Fig. 8a). This species is known to behave as an opportunistic taxon, able to feed on and to show a reproductive response to ephemeral organic matter deposits. *Nuttallides pusillus* is described by Heinz and others (2001, as *Epistominella pusilla*) as an opportunistic taxon responding to food addition in laboratory studies, based on material collected at a 900-m-depth station in the Gulf of Lions. Gooday and Hughes (2002) described a very large population of *Eponides pusillus* (= *Nuttallides pusillus*) living embedded in lumps of phytodetritus related to spring bloom at a 1920-m-deep bathyal station in the northeastern Atlantic. At our station A, *N. pusillus* dominated foraminiferal faunas collected in autumn 1997 and early winter 1998, as well as April 2001 and June 1999 (OB1A, OB2A, OB2A^{bis}, OB11A and OB9A, respectively). In autumn 1998 and winter 1999, the weaker frequencies of *N. pusillus* in the very low-density faunas collected in our study area are rather striking in comparison with the previous year (Fig. 5a). It may suggest a differential response of *N. pusillus* to strong interannual variability of phytodetrital inputs. Juveniles of *Uvigerina peregrina* and adults of *Trifarina pauperata* (63–150 μm) dominated the faunas in spring (April 2000 and April 2001; Fig. 5b, Fig. 8a), which suggests a reproductive behavior strongly related to the ephemeral spring bloom phytodetritus. As a main result, *U. peregrina* exhibited an absolute frequency increase in the >150 μm fraction shortly after the spring bloom periods. This confirms the reactive behavior of this taxon.

The significant occurrence of *Epistominella exigua, Trochammina globigeriniformis* and *Reophax guttiferus* in the samples from June and April (June 1999, April 2000, April 2001) may be connected to the impact of freshly deposited phytodetritus. *Epistominella exigua* is known to respond to ephemeral organic matter deposits at the sea floor (Gooday, 1988; Gooday and Lambshead, 1989; Gooday and Turley, 1990; Gooday, 1993; Loubere, 1998; Jannink and others, 1998). At station B (550 m depth), *E. exigua* and *R. guttiferus* responded to spring phytodetrital deposits with large increases in frequency and percentage (Fontanier and others, 2003). At station A, the response of these taxa is less strong, perhaps because the organic matter flux at station A during the spring bloom is lower than at station B. Nevertheless, it seems that their presence reflects phytoplankton deposits at the sediment-water interface.

CONCLUSIONS

1. Redox conditions at the 1000-m-deep station A were relatively stable during our ten consecutive sampling surveys. The exception was in April 2001, during the spring bloom, when a significant decrease in bottom-water oxygenation and the penetration depth of free oxygen into the sediment occurred, suggesting an important increase in benthic respiration in response to a massive phytoplankton deposit.
2. The temporal variability of the faunal density and composition of the >150 μm fraction shows a strong similarity to those described by Fontanier and others (2002) for a nearby, 550-m-deep station. This strong similarity indicates that the benthic foraminiferal upper slope faunas are strongly influenced by surface-water primary productivity events and the subsequent flux of organic remains to the sea floor.
3. Significant increases in the faunal density of the >150 μm fraction, observed in samples taken in the spring of 1999, 2000 and 2001, were largely caused by a strong increase in *Uvigerina mediterranea* and *U. peregrina* that are apparently the two taxa most reactive to phytodetritus. In the 63–150 μm fraction, *Nuttallides pusillus* showed the clearest response to seasonal organic flux events.

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APPENDIX. Species of benthic foraminifera recognized at station A, Bay of Biscay, with references to plates and figures in the literature on Atlantic and Mediterranean foraminifera.

Species	References
Adercotryma glomerata (Brady), 1878	Jones (1994), pl. 34, Figs. 15-18
Ammobaculites agglutinans (d'Orbigny), 1846	Hess (1998), pl. 4, Fig. 4
Ammolagena clavata (Jones and Parker), 1860	Jones (1994), pl. 41, Figs. 12-16
Amphicoryna scalaris (Batsch), 1791	Jones (1994), pl. 63, Figs. 28-31
Biloculinella irregularis(d'Orbigny) 1839	d'Orbigny (1839), pl. 8, Fig. 20 and 21
Bolivina albatrossi Cushman, 1922	Schiebel (1992), pl.1, Fig. 1a-b
Bolivina spathulata (Williamson), 1858	Jorissen (1987), pl. 1, Fig. 5
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
Bulimina marginata d'Orbigny, 1826	Hess (1998), pl. 10, Fig. 7
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
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
Cornuspira foliacea (Philippi), 1844	Jones (1994), pl. 11, Fig. 5 and 6
Cornuspira involvens (Reuss), 1950	Jones (1994), pl. 11, Figs. 1-3
Cribrostomoides subglobosus (Cushman), 1910	Jones (1994), pl. 34, Figs. 8-10
Crithionina abyssorum Kiaer, 1899	Kiaer (1899), pl.1, Figs.1-4
Cystammina argentea Earland, 1934	Timm (1992), pl.3, Fig. 8
Cystammina pauciloculata (Brady), 1879	Jones (1994), pl. 41, Fig. 1
Dentalina albatrossi (Cushman), 1923	Jones (1994), pl. 64, Figs. 11-14
Dentalina bradyensis (Dervieux), 1894	Jones (1994), pl. 62, Fig. 19 and 20
Dentalina subsoluta (Cushman), 1923	Jones (1994), pl.62, Figs. 13-16
Eggerella bradyi (Cushman), 1911	Jones (1994), pl. 47, Figs. 4-7
Eggerella scabra (Williamson), 1858	Jones (1994), pl. 47, Figs. 15-17
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), 1839	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 orbicularis (sensu Parker, Jones and Brady), 1865	Jones (1994), pl. 115, Fig. 6
Gyroidina umbonata (Silvestri), 1898	Parker (1958). pl. 3, Fig. 19 and 20
Haplophragmoides bradyi (Robertson), 1891	Schiebel (1992), pl. 7, Fig. 1a
Hoeglundina elegans (d'Orbigny), 1826	Phleger et al.(1953), pl. 9, Fig. 24 and 25
Hormosina globulifera Brady, 1879	Jones (1994), pl. 39, Figs. 1-4, 6
Hyalinea balthica (Schroeter), 1783	Jones (1994), pl. 112, Fig. 1 and 2
Karreriella bradyi (Cushman), 1911	Jones (1994), pl. 41, Figs. 1-4
Lagenammina pseudodifflugiformis Nogan, 1964	Nogan (1964), pl.1, Fig.1
Lenticulina gibba (d'Orbigny), 1839	Hess (1998), pl.13, Fig. 1
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
Nonionella turgida (Williamson), 1858	Jones (1994), pl. 109, Figs. 17-19
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
Paratrochammina challengeri Brönnimann and Whittaker, 1988	Jones (1994), pl. 35, Fig. 10
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 murrhina (Schwager), 1866	Hess (1998), pl.9, Fig. 1
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
Reophax bilocularis Flint, 1899	Hess (1998), pl.2, Fig. 13 and 14
Reophax guttiferus Brady, 1881	Jones (1994), pl. 31, Fig. 10-15
Reophax micaceus Eerland, 1934	Schiebel (1992), pl. 8, Fig. 7
Reophax scorpiurus Montfort, 1808	Loeblich and Tappan (1988), pl. 44, Figs. 1-3
Rhabdamina cornuta (Brady), 1879	Jones (1994), pl. 22, Fig. 11 and 13
Robertinoides bradyi (Cushman and Parker), 1936	Jones (1994), pl. 50, Fig. 18
Rotamorphina? Involuta (Parker), 1958	Parker (1958), pl. 4, Figs. 28-30
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
Spirophtalmidium acutimargo (Brady), 1884	Jones (1994), pl.10, Fig. 13
Stainforthia fusiformis (Williamson), 1858	Schiebel (1992), pl. 2, Fig. 10
Technitella legumen Norman, 1878	Jones (1994), pl.25, Figs. 8-10
Textularia earlandi Parker, 1952	Timm (1992), pl.3, Fig. 1a-b
Thurammina albicans Bradyi, 1879	Jones (1994), pl.37, Figs. 2-7
Thurammina papillata Bradyi, 1979	Jones (1994), pl.36, Figs. 7-18
Trifarina angulosa (Williamson), 1858	Jones (1994), pl. 74, Fig. 17 and 18
Trifarina bradyi Cushman, 1923	Jones (1994), pl. 67, Figs. 1-3
Trifarina pauperata (Heron-Allen and Earland), 1932	Schiebel (1992), pl. 3, Fig. 3
Triloculina tricarinata d'Orbigny, 1826	Hess (1998), pl.9, Fig. 10
Trochammina globigeriniformis (Parker and Jones), 1865	Timm (1992), pl.4, Fig. 2a-b
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