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Live foraminifera from the open slope between Grand Rhône and Petit Rhône Canyons (Gulf of Lions, NW Mediterranean)

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ABSTRACT

We present an ecological study of live (Rose Bengal stained) foraminifera from 6 deep-sea stations sampled on the open slope between the Grand Rhône Canyon and the Petit Rhône Canyon (eastern part of the Gulf of Lions, NW Mediterranean). The 6 stations describe a bathymetric transect from ~350 to ~2000 m depth. The main objective of our study is to investigate the changes of the foraminiferal density, composition and microhabitat along this transect in response to the physico-chemical conditions at and below the sediment–water interface. All our observations underline the general meso-oligotrophic character of our inter-canyon open-slope setting where low-quality organic matter originating from both marine and continental sources settles. The input of organic matter at the sediment–water interface leads to a classical succession of redox reactions within the sediment. The shallowest station (~350 m) appears as an active sedimentary environment, where coarse sediments characterized by lower-quality organic matter and biogenic material accumulate. The 550-m-deep station presents bioturbated sediments with the highest concentration of labile organic compounds. The deeper stations, between about 750 and 2000 m deep, show decreasing sedimentation rates with water depth and are characterized by a background of low-quality organic matter. The foraminiferal changes recorded along the bathymetric transect are related to a complex association of physico-chemical parameters. We think that the quality of organic matter in the surficial sediment, as expressed by the lipid concentration, is the major parameter controlling the foraminiferal distribution at our open-slope stations. From the 550- to the 2000-m-deep station, the foraminiferal standing stocks and diversity decrease with depth, as a result of the increasing scarcity of labile organic compounds at the sediment–water interface. Oxygen concentration and penetration depth and the intensity of bioturbation seem to play only a secondary ecological role. Other, putative hydro-sedimentary processes (winnowing by strong bottom currents, sand-bed deposition) appear as additional parameters controlling the foraminiferal community structure. At the 350-m-deep station, the live foraminiferal fauna can be considered as a non-equilibrium assemblage thriving in frequently disturbed and

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food-impoverished sediments. At the 745- and 980-m-deep stations, the occurrence of suspensivorous epibenthic/epilithic species suggests the presence of strong bottom-water current velocities and the related suspension of organic particles.

1. Introduction

Knowledge about the ecology of deep-sea benthic foraminifera has improved considerably during the two last decades, mainly as a result of the increased demand for information from the paleoceanographical community. This information on benthic foraminiferal ecology was needed for the improvement of benthic proxies (e.g. Gooday, 2003; Jorissen et al., 2007). Ecological studies based on in-situ collection allowed understanding of how the major physico-chemical parameters control the spatial and temporal dynamics of live (Rose Bengal stained) foraminiferal communities (e.g. Corliss, 1985; Gooday, 1988; Mackensen and Douglas, 1989; Corliss and Emerson, 1990; Jorissen et al., 1998; Jannink et al., 1998; van der Zwaan et al., 1999; Kitazato et al., 2000; Fontanier et al., 2002; Schönfeld, 2002; Licari et al., 2003; Hess et al., 2005; Eberwein and Mackensen, 2006; Langezaal et al., 2006; Fontanier et al., 2006; Schumacher et al., 2007; Koho et al., 2007). On the basis of these studies, it appears that the density, composition and vertical distribution of live foraminiferal faunas in the sediment are constrained by organic-matter fluxes derived from primary production, bottom and pore-water oxygenation, sedimentary processes and current velocity at the sediment–water interface (see reviews by Gooday, 2003 and Jorissen et al., 2007). These conclusions based on in-situ observations are largely confirmed by culture experiments (e.g. Heinz et al., 2002; Geslin et al., 2004; Langezaal et al., 2004; Ernst and van der Zwaan, 2004; Nomaki et al., 2005; Ernst et al., 2005). Temporal and spatial dynamics of deep-sea foraminifera are controlled mainly by the organic-matter flux reaching the sea floor (e.g. Altenbach and Sarnthein, 1989; Herguera and Berger, 1991). Densities of hard-shelled foraminifera are generally much lower in oligotrophic basins than in upper-slope areas with high organic-matter export fluxes. Consequently, if the often diverse soft-shelled component (Nozawa et al., 2006) is ignored, then live foraminiferal faunas from oligotrophic settings are often less diverse than those from eutrophic areas (e.g. Jorissen et al., 1998; Fontanier et al., 2002; Licari et al., 2003; Eberwein and Mackensen, 2006). In terms of vertical distribution, foraminiferal faunas from oligotrophic environments are concentrated at the sediment–water interface to take optimal advantage of the scarce organic detritus exported to the sea floor. In environments where high organic-matter fluxes at the sediment–water interface allow the burial of fresh organic matter in deeper sediment layers, some foraminiferal taxa occupy deeper microhabitats. Consequently, the composition of foraminiferal fauna changes according to the trophic levels at the sea floor (Jorissen et al., 1995). After phytoplankton blooms, foraminiferal faunas may respond to seasonal organic-matter supply by a density increase. This response generally leads to the dominance of a number of small-sized opportunistic species that are able to feed on ephemeral phytodetritus, freshly deposited at the sediment–water interface (e.g. Gooday, 1988; Kitazato et al., 2000; Fontanier et al., 2003, 2006; Langezaal et al., 2006). Areas where very high organic-matter fluxes induce severe oxygen depletion in pore and bottom waters are more complex. In such settings, the vertical distribution of foraminiferal faunas below the sediment–water interface is limited by the oxygen penetration depth (OPD), and only some highly tolerant taxa are able to persist at or below the zero-oxygen boundary (e.g. Sen Gupta and Machain-Castillo, 1993; Jannink et al., 1998; Bernhard and Sen Gupta, 1999; Schönfeld, 2001; Schumacher et al., 2007).

Living foraminiferal faunas from canyon systems have been poorly studied, despite the fact that canyons represent complex biotopes where the sedimentary dynamics and organic-matter focusing results in very unusual ecological conditions compared to open-slope environments (Jorissen et al., 1994; Schmiedl et al., 2000; Anschutz et al., 2002; Hess et al., 2005; Fontanier et al., 2005; Koho et al., 2007).

The Gulf of Lions (NW Mediterranean) presents a continental margin that is incised by a succession of canyons separated by narrow open-slope areas (Berné and Gorini, 2005). Complex hydro-sedimentary processes induce a preferential focusing of organic carbon (OC) in the canyon systems, and consequently, less organic matter is deposited at the open-slope areas between the canyons (Buscail et al., 1990, 1997; Buscail and Germain, 1997). Schmiedl et al. (2000) found more abundant and diverse living (Rose Bengal stained) foraminifera in organic-matter-enriched sediments from the axis of Lacaze-Duthiers Canyon (western part of the Gulf of Lions) than in organic-matter-depleted slope sediments. In this paper, we present an ecological study of live (Rose Bengal stained) foraminifera from 6 deep-sea stations sampled on the open slope between the Grand Rhône Canyon and the Petit Rhône Canyon (eastern part of the Gulf of Lions) (Fig. 1). At 200 m depth, this open slope is only ~4 km wide. At 1500 m depth, it is more than 30 km wide. The 6 stations describe a bathymetric transect from about 350 to 2000 m depth. Following the observations of Buscail et al. (1990), Buscail and Germain (1997) and Buscail et al. (1997), the continental slope area is characterized by (1) a lower-OC flux compared to adjacent canyons and (2) a predominance of low-quality organic compounds. The investigation of our 6 stations during the *BEHEMOTH* cruise in September 2006 provided a large environmental data set, which allowed us to investigate the main ecological characteristics of the live foraminiferal faunas sampled in our inter-canyon open-slope area. The main objectives of our study are: (1) to present and to discuss

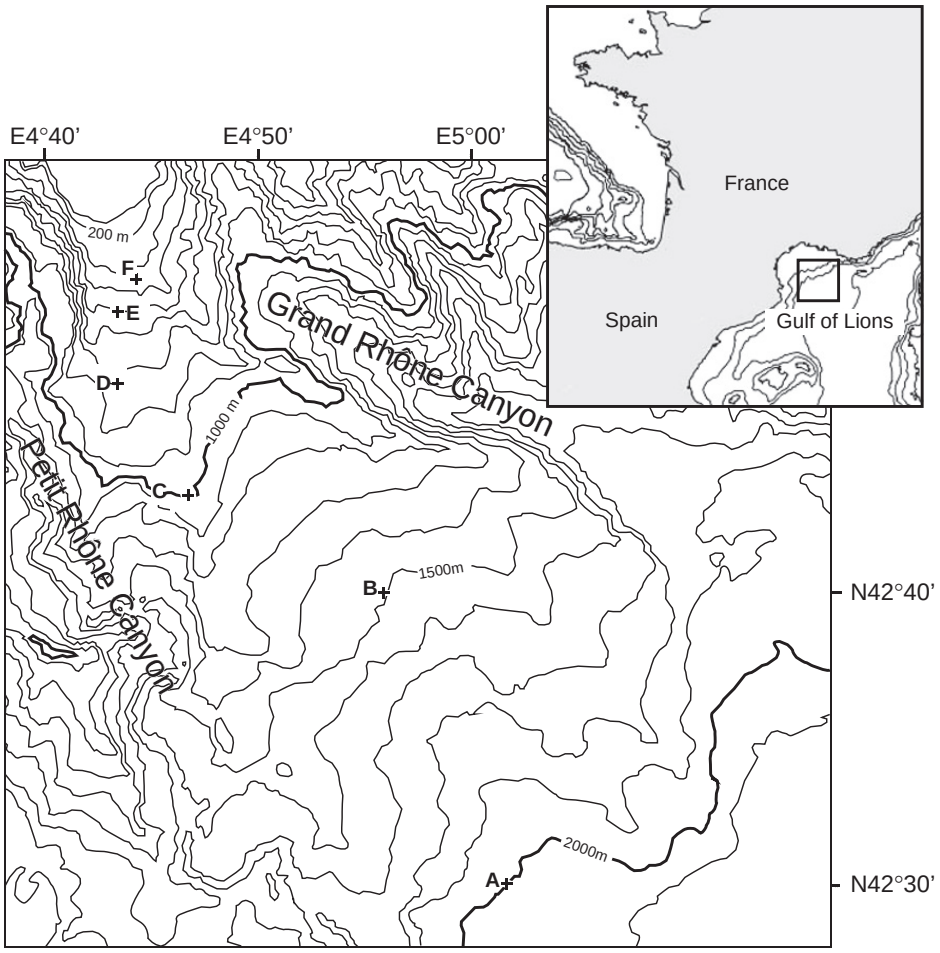

Fig. 1. Study area, bathymetry and geographical position of stations A, B, C, D, E and F. This map was kindly provided by S. Berné and L. Maltese (IFREMER). Note the location of the Grand Rhône and the Petit Rhône Canyons.

the changes of the foraminiferal density and composition along our 6-stations bathymetrical transect, (2) to compare the faunal succession with our set of physico-chemical data and (3) to explain the microhabitat changes in response to the physico-chemical conditions at and below the sediment–water interface. Concerning environmental parameters, we focus on bottom-water and pore-water oxygenation, redox element concentration in the sediment (nitrate, nitrite, ammonia), organic matter (TOC content, C:N ratio, $\delta^{13}C$, lipid, sugar and amino acid (AA) concentrations) and sedimentary features (sedimentation and bioturbation rate, grain-size distribution).

2. Material and methods

2.1. Study area

The Gulf of Lions margin consists of a large crescent-shaped continental shelf incised by sub-marine canyons separated by narrow stretches of open continental slope (Berné and Gorini, 2005) (Fig. 1). The surface waters, down to ~200 m, exhibit important changes in temperature and salinity, related to the seasons, the coastal input of riverine freshwater and the impact of lower-salinity Atlantic water (Millot, 1990; Béthoux et al., 2002). Below the surface waters spreads the Levantine Intermediate Water (LIW), which is characterized by a salinity maximum (~38.5) and a temperature maximum (>13 °C). In winter, dry and cool winds blowing from northern continental areas induce dense shelf water cascading downslope (Millot, 1990; Béthoux et al., 2002; Canals et al., 2006). This dense water forms the Western Mediterranean Deep Water (WMDW) (Millot, 1990; Béthoux et al., 2002; Canals et al., 2006). The WMDW occurs below the LIW with a diffusive boundary at 500–800 m (Béthoux et al., 2002). It is generally characterized by a rather homogeneous temperature (12.7–12.9 °C) and salinity (38.40–38.45) (Send et al., 1999; Béthoux et al., 2002). The winter vertical mixing leads also to the upward transport of nutrients from intermediate waters into the surface layers and a relatively high annual primary production compared to the more oligotrophic eastern Mediterranean Sea (Diaz, 2000). Bosc et al. (2004) estimated a total annual primary production between 180 and 204 $g\,C\,m^{-2}\,yr^{-1}$.

The Rhône River is the main source of the terrigeneous material, accounting for about 80% of the overall riverine input into the Gulf of Lions (Durrieu de Madron et al., 2000). Along the slope, near-bottom sediments may be

advected by (1) dense water cascading in winter, (2) meandering of slope currents or (3) bottom Ekman transport related to the surface water cyclonic circulation, with a preferential transport of inorganic material into the canyon systems (Durrieu de Madron and Panouse, 1996; Durrieu de Madron et al., 1999, 2000; Monaco et al., 1999; Canals et al., 2006). In our study area, the sedimentation rates in the open-slope environments decrease with increasing water depth, from ~0.12 cm yr^{-1} at 200 m depth to ~0.01 cm yr^{-1} at 2500 m depth (Buscail et al., 1997; Zuo et al., 1997; Miralles et al., 2005). Organic material reaching the sea floor may originate from a variety of sources including riverine input, suspended shelf sediments or marine biological production (Buscail and Germain, 1997; Durrieu de Madron et al., 2000). Lateral export of suspended particulate organic matter from the shelf to the slope induces a focusing of labile organic material in canyon systems (Buscail et al., 1990, 1997; Buscail and Germain, 1997; Durrieu de Madron et al., 2003; Canals et al., 2006). Finally, more than 50% of the total carbon (TC) deposited on the continental shelf deposits is exported to the adjacent slope (Buscail et al. 1990), with a pronounced depocenter in the muddy sediments found in the canyon areas at mid-slope (500–1500 m depth). These sediments have an organic carbon content (TOC) of 0.6–0.9% DW (Buscail and Germain, 1997). Buscail and Germain (1997), emphasizing that the open-slope area separating the Petit Rhône and Grand Rhône canyons (our study area) has a lower organic carbon content (TOC = 0.5% DW).

2.2. Sediment sampling

In the present paper, we investigated 6 stations on the open slope separating the Grand Rhône Canyon and the Petit Rhône Canyon (Fig. 1 and Table 1). These stations form a bathymetric transect from ~350 to ~2000 m depth. The shallowest site (station F, 343 m) is bathed by the LIW. Stations E (552 m) and D (745) are positioned in the diffusive boundary layer separating the LIW and the WMDW. Stations C (980 m), B (1488 m) and A (1987 m) are bathed by the WMDW. Sediment samples were collected with a classical Barnett multicorer (Barnett et al., 1984). Each core has a surface area of about 72 cm^2. The multicorer allowed sampling of the first dm of the sediment, the overlying bottom waters and a comparatively undisturbed sediment–water interface.

2.3. Geochemical analysis

2.3.1. Oxygen concentration of pore water and bottom water

Overlying water was collected immediately after core recovery for dissolved O_2 concentration measurements by the Winkler titration method (Grasshoff et al., 1983). Bottom-water oxygen concentration (3 replicates) and temperature data are presented in Table 1. Profiles of O_2 in the sediment pore water were performed on board using polarographic oxygen microelectrodes (Unisense®) provided with a built-in reference and an internal guard cathode (Revsbech, 1998). The O_2 microelectrodes had tip outer diameters of 100 μm, a stirring sensitivity of <1%, a 90% response time of 10 s and a current drift of less than 1% per hour. The sensors were operated with a motor-driven micromanipulator, and the sensor current was measured with a picoamperemeter connected to an A–D converter (Unisense®), which transferred the signals to a PC (Revsbech and Jørgensen, 1986). The profiling procedure was as follows: the O_2 sensor penetration speed was ~70 s mm^{-1}, the waiting time was 15 s at each increment step and 5 readings were taken every 3 s and then averaged. A two-point linear calibration of microelectrodes was achieved between the bottom-water oxygen concentration estimated by Winkler titration and the anoxic zone of the sediment. The core temperature was maintained at in-situ temperature using a refrigerating device. At each site, 4 oxygen profiles were produced in the same core (5 mm apart) in order to obtain information on spatial variability. At station B (1488 m), we performed only one oxygen profile. Since we did not reach the zero-oxygen boundary in the first 10 cm of the sediment at stations A and B (1987 and 1488 m depth, respectively), we extrapolated the OPD (where dissolved oxygen concentrations reach zero) by using a second-order polynomial regression performed on the oxygen profiles.

Table 1
Water depth, geographical position, bottom-water temperature, bottom-water salinity, bottom-water oxygenation and oxygen penetration depth for our six stations

Station	Depth (m)	Latitude (N)	Longitude (E)	Multicorer deployments	Duplicate cores for foraminiferal analysis	Bottom-water temperature (°C)	Bottom-water oxygenation (μmol l^{-1})	Oxygen penetration depth (mm)
F	343	42°52.34′	4°42.93′		BTF1			
	350	42°52.32′	4°42.43′	3	BTF2	14	198.5 ± 1.3	20.5 ± 3.3
	352	42°50.31′	4°44.41′		(NO_3^-, NO_2^-, NH_4^+)			
E	552	42°48.78′	4°43.21′	2	BTE1*, BTE2*	13.7	197.3 ± 0.3	57.2 ± 4.5
D	745	42°46.66′	4°43.91′	2	BTD1*, BTD2*	13.5	206.3 ± 0.7	36.5 ± 1.6
C	980	42°43.18′	4°46.58′	2	BTC′3, BTC′4	13.4	214.6 ± 1.9	50.7 ± 6.3
B	1488	42°38.83′	4°56.03′	1	BTB1, BTB2	13.4	216.0 ± 0.6	141.5 ± 0.0
A	1987	42°28.25′	5°00.61′	1	BTA1, BTA2	13.3	219.3 ± 1.0	197.0 ± 11.0

The number of multicorer deployments per station is also mentioned. Note that a single asterisk indicates that duplicate cores were collected from two different multicorer deployments.

2.3.2. Nitrate, nitrite and ammonia analyses

At each station, a second core was sliced in thin horizontal sections (every 0.5 cm for the top 2 cm, 1 cm below down to 10 cm depth and every 2 cm below 10 cm) within $1\frac{1}{2}$ h. For every level a sub-sample was immediately sealed in a pre-weighed vial and frozen under an inert atmosphere (N_2) for further analyses of porosity and chemistry of the solid fraction. Another 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. In the laboratory, porosity was determined by comparison of the weights of wet and freeze-dried sediment. Interstitial water compounds were analyzed by techniques adapted for small volumes (Anschutz et al., 1999; Hyacinthe et al., 2001). Finally, dissolved nitrate, nitrite and ammonia were measured by flow injection analysis according to Anderson (1979) and Hall and Aller (1992). Precisions are $\pm 0.5\,\mu mol\,l^{-1}$ for NO_3^-, $\pm 0.1\,\mu mol\,l^{-1}$ for NO_2^- and ±5% for NH_4^+.

2.4. Sedimentological analyses

2.4.1. Granulometry

At each station, we collected a sub-sample (~20 cc) of the first cm of a third core (also investigated for organic-matter analysis; see below). Grain sizes (D_{10}, Q_{50} and D_{90}) were measured with a Malvern Laser Diffraction Particle Sizer (type 2600).

2.4.2. Sedimentation and bioturbation rates

A fourth core was dedicated entirely to the determination of ^{234}Th, ^{210}Pb and ^{226}Ra activities using a low-background, high-efficiency, well-shaped γ-detector (Schmidt et al., 2007). The measurements of the uppermost sediment layers had to be completed within 1 month of sampling because of the rapid decay of ^{234}Th. Excess ^{234}Th and ^{210}Pb were calculated by subtracting the activity supported by their respective parent isotopes from the total activity in the sediment, and then by correcting ^{234}Th values for radioactive decay that occurred between sample collection and counting (this correction is not necessary for ^{210}Pb because of its longer half-life). Based on the assumption of a constant flux and constant sediment accumulation rate (referred to as the CF:CS method), the decrease of $^{210}Pb_{xs}$ activity with depth makes it possible to calculate a sedimentation rate (Schmidt et al., 2007). The compaction effect is not considered, and the sediment accumulation rates correspond to maximum values. Taking into account its very short half-life (24.1 days) and the relatively low sedimentation rates (far below $1\,cm\,yr^{-1}$), $^{234}Th_{xs}$ should be present only at the sediment–water interface. However, all the profiles show penetration to variable depths, which indicates efficient mixing of the upper sediments, usually referred to as bioturbation (D_b). The simplest way to derive D_b from $^{234}Th_{xs}$ profiles is to assume bioturbation as a diffusive process occurring at a constant rate within a surface mixed layer under steady state (Schmidt et al., 2001, 2002).

2.5. Biogeochemical analyses

For each station, we collected a sub-sample (~36 cc) from the first cm of the third core in order to perform various analyses on the organic matter. Chemical compounds were analyzed using milled, freeze-dried sub-samples. Total nitrogen (TN), TC and OC concentrations were measured on homogenized, precisely weighed samples in an automatic CN-analyzer LECO 2000. OC contents were measured after removal of the carbonate fraction by acidification with 2 N HCl (overnight, at 50 °C) (Cauwet et al., 1990). Extensive testing at CEFREM showed long-term precision for TOC and TN of about 0.02%. Total organic matter (TOM) of marine origin was determined by multiplying the OC concentrations by 1.8 (Gordon, 1970). Total AAs were assayed by a colorimetric method on the fraction hydrolyzed by 6 N HCl for 16 h at 110 °C. Absorption of the products resulting from the AA–ninhydrin reaction was measured at 570 nm using a Beckman spectrophotometer (precision of 15%) (Stevenson and Cheng, 1970). Total lipids were measured by a colorimetric method after extraction with a 2/1 (V:V) chloroform–methanol mixture. Absorption of the products was measured at 520 nm with a Beckman spectrophotometer (precision of 10%) (Barnes and Blackstock, 1973). Total carbohydrates (TCHO) were determined with the colorimetric 2,4,6-tripyridyls-triazine (TPTZ)-method described by Myklestad et al. (1997). Hydrosoluble sugars are sugars that have been previously released in a Milli-Q water solution at 90 °C (1 h) before the TPTZ procedure. Sub-samples of surface sediments were collected for carbon-stable isotopic analysis of organic matter ($\delta^{13}C$). Sediments were first acidified (HCl, 2 N) to remove carbonates before being combusted in an Elemental Analyzer (Eurovector EA300) interfaced with an Isoprime (GVI) isotopic ratio mass spectrometer. Typical reproducibility of analyses was ±0.1‰ for $\delta^{13}C$.

2.6. Foraminiferal faunal analysis

For faunal analysis, two duplicate cores were sliced horizontally for each station; every 0.5 cm from the sediment–water interface down to 4 cm depth, every cm between 4 and 10 cm depth (Table 1). Sediments were stored in 500-cm^3 bottles, which were filled with 95% ethanol containing $1\,g\,l^{-1}$ Rose Bengal stain. Rose Bengal staining is commonly used to identify live foraminifera (Walton, 1952; Murray and Bowser, 2000). Onboard the ship, all samples were gently shaken for several minutes to obtain a homogeneous mixture. In the laboratory, they were sieved through 63- and 150-μm mesh screens, and the sieve residues were stored in 95% ethanol. Stained foraminifera belonging to the >150 μm size fraction were sorted in wet samples and stored in Plummer slides. One problem with this technique is the fact that Rose Bengal may stain the protoplasm of dead foraminifera, which may be relatively well preserved for a considerable period of time under the anoxic conditions that generally prevail deep in the sediment (Corliss and Emerson, 1990; Bernhard, 2000). As a consequence, a strict application

of the staining criteria is usually easy in superficial samples but may become more subjective in deeper levels. In all cases, we applied our staining criteria very strictly (all chambers except the last one stained bright pink) and compared doubtful individuals with perfectly stained individuals of the same species found in more superficial sediment layers. Non-transparent agglutinated and miliolid taxa were broken on many occasions for inspection of the interior of the test. Most live foraminifera were identified to species level (see Appendix for taxonomic references). Fragments of branch-like agglutinating foraminifera (such as *Hyperammina*) were not included in the quantitative analyses. We calculated Shannon index H (log base e) and Evenness index E (Hayek and Buzas, 1997) as described in Murray (2006). In order to describe the vertical distribution of the total faunas or individual taxa, we calculate the Average Living Depth (ALD_x, Jorissen et al., 1995), which allows a rapid characterization of the microhabitat patterns. 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. The criteria used for the calculation of the ALD_{10} are described in Fontanier et al. (2002). In order to investigate whether or not the spatial variability between duplicate cores at a single station obscures the spatial variability of live (stained) foraminiferal faunas along our bathymetric transect, a cluster analysis (Ward's method) was applied for the 12 duplicate cores. We used the arcsinus values of square root "pi" for all taxa recorded in each core. The "pi" value is the relative abundance (%) of one species divided by 100. A tree diagram was constructed according to the Ward's method based on the squared Euclidean distances between all duplicate cores.

3. Results

3.1. Bottom and pore-water oxygen concentration

Along our 6-stations bathymetric transect, the bottom-water oxygen concentration increases gradually with water depth with values ranging from $199 \pm 1\,\mu mol\,l^{-1}$ at station F (~350 m) to $219 \pm 1\,\mu mol\,l^{-1}$ at station A (1987 m) (Table 1). Pore-water oxygen profiles at all stations show a classical decrease in the sediment (Figs. 2a–7a). At station F, oxygen profiles show a mean OPD of ~20 mm below the sediment–water interface (Fig. 2a). At station E (552 m), the OPD is ~57 mm. Note that two oxygen profiles (1 and 2) exhibit a clear sub-surface increase between 35 and 45 mm depth, which may be related to the presence of oxic microenvironments related to observed burrows (Fig. 3a). From station D (745 m) to station A (1987 m), the OPD increases from ~37 to ~200 mm (Table 1). Finally, our results show a significant correlation between OPD into the sediment and water depth along the whole bathymetric transect (Table 6a).

3.2. Nitrate, nitrite and ammonia in pore water

For stations F, E, D and C, nitrate profiles exhibit a strong decrease in the topmost centimeters of the sediment, from 15 to 20 $\mu mol\,l^{-1}$ at depth to values lower than 10 $\mu mol\,l^{-1}$ at the sediment–water interface (Figs. 2b–5b). Below the maximum, nitrate concentration decreases more or less

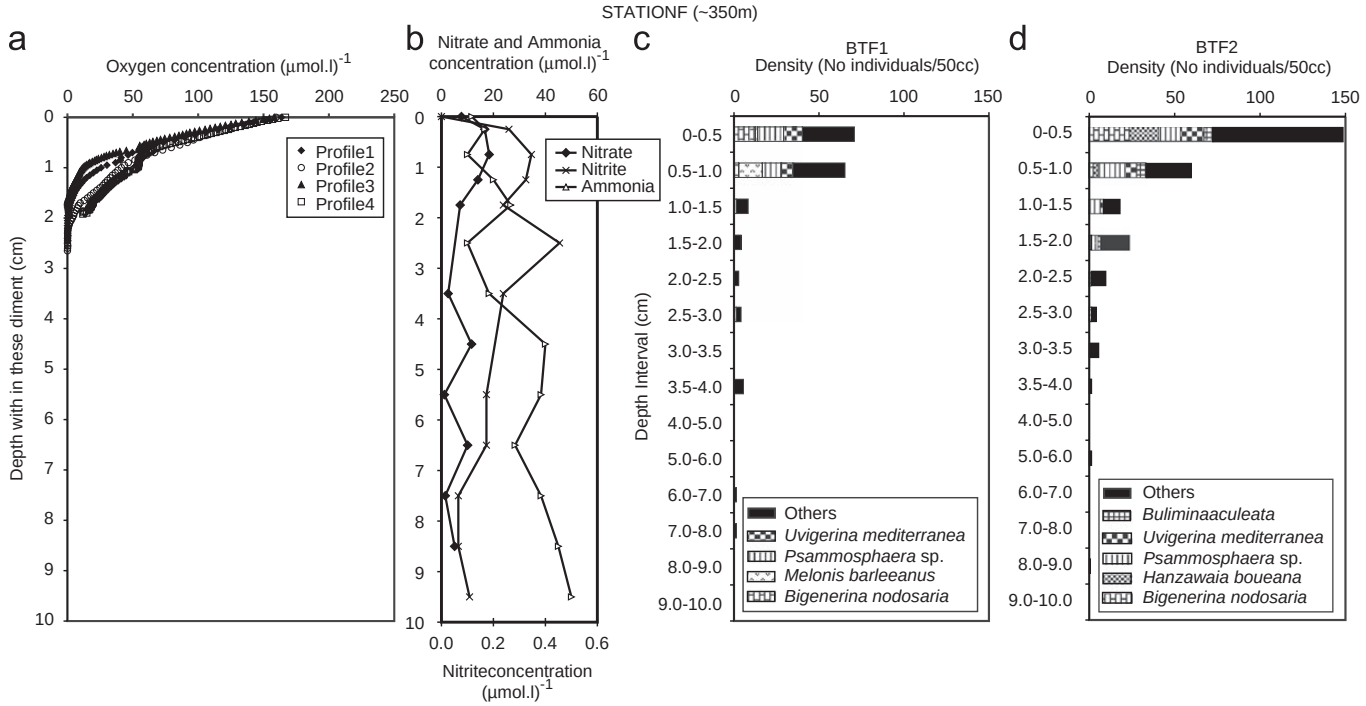

Fig. 2. Station F, water depth is ~350 m. (a) Oxygen profiles; (b) nitrate, nitrite and ammonia concentrations in the pore water; (c) foraminiferal distribution (number of individuals >150 µm fraction found in each level, standardized for a 50 cm^3 sediment volume) for both duplicate cores BTF1 and BTF2. Only taxa with a percentage higher than 5% are presented.

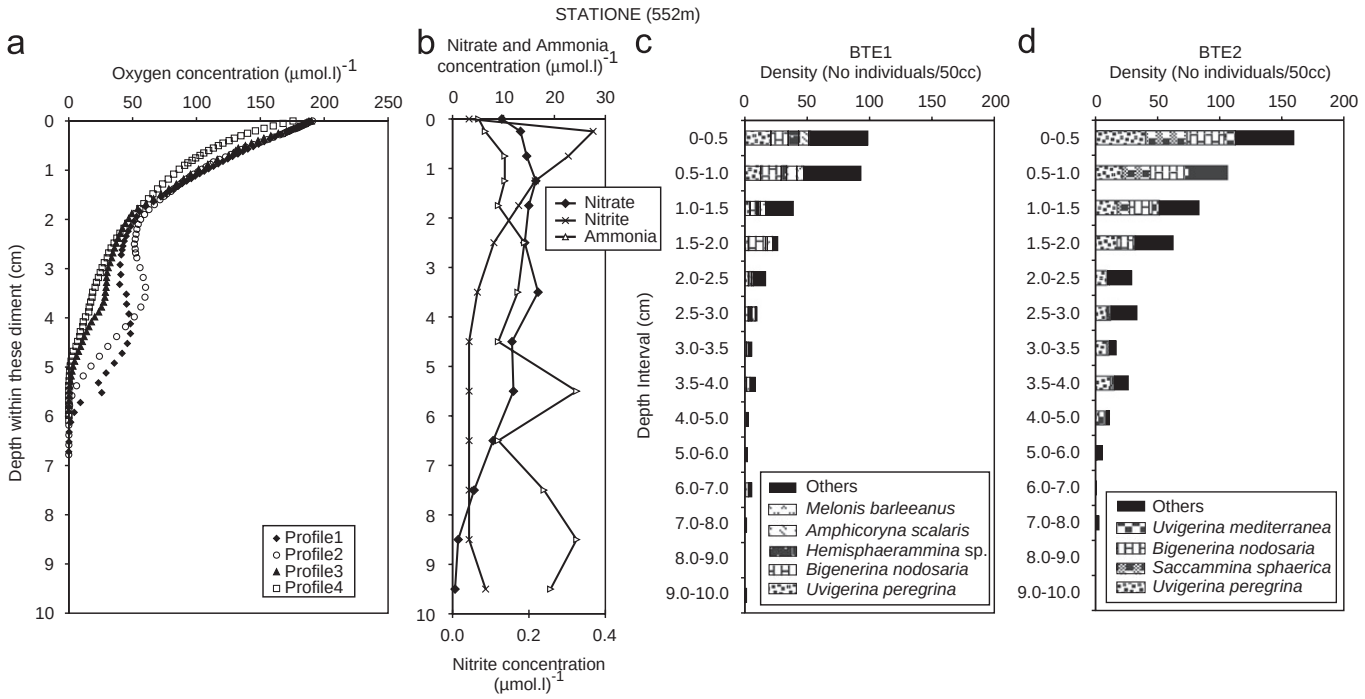

Fig. 3. Station E, water depth is 552 m. (a) Oxygen profiles; (b) nitrate, nitrite and ammonia concentrations in the pore water; (c) foraminiferal distribution (number of individuals >150 µm fraction found in each level, standardized for a 50 cm^3 sediment volume) for both duplicate cores BTE1 and BTE2. Only taxa with a percentage higher than 5% are presented.

Table 2
Main sedimentary features along our 6-station bathymetric transect

Station	Depth (m)	Sedimentary features (0–1 cm)					Sedimentation rate ($cm\,yr^{-1}$)	Bioturbation D_b ($cm^2\,yr^{-1}$)
		D_{10} (µm)	Q_{50} (µm)	D_{90} (µm)	Lithology	Sieve residues (>150 µm)		
F	343	2.79	122.78	310.73	Silty sand	Sand, Glauconite and Bioclasts	–	–
E	552	nd	nd	nd	nd	Bioclasts	–	2.963
D	745	1.58	6.77	26.92	Clayey silt	Abundant bioclasts (Pteropod)	0.077	0.541
C	980	1.41	5.99	29.24	Clayey silt	Abundant bioclasts (Pteropod)	0.067	1.334
B	1488	1.53	7.72	130.75	Sandy silt	Abundant bioclasts (Pteropod)	0.062	0.188
A	1987	1.93	22.37	255.82	Sandy silt	Very abundant bioclasts (Pteropod)	0.032	–

D_{10}, Q_{50} and D_{90} were calculated for the first cm of sediment for stations A, B, C, D and F. No values are available for station E ("nd"). Simple characterisations of sieve residues (>150 µm) are given. Sedimentation rates were successfully calculated for stations A, B, C and D. For stations E and F, excess ^{210}Pb activity ($^{210}Pb_{xs}$) at the sediment–water interface was lower than in deeper sediment layers, and the calculation of a sedimentation rate was not possible.

gradually. Inversely, ammonia concentration increases to deeper sediment layers with values higher than 20 µmol l^{-1} in deeper intervals. For stations F, E, D and C, nitrite concentrations are below the detection limit at the sediment–water interface and show a sub-surface maximum (>0.2 µmol l^{-1}). At stations B and A, nitrate, nitrite and ammonia profiles are more erratic and do not show a clear trend with depth in the sediment (Figs. 6b and 7b).

3.3. Sedimentary features

Station F (343 m) is characterized by silty sands enriched in glauconitic compounds (mainly foraminiferal inner moulds) and bioclasts (Table 2). Station E (552 m) is characterized by a high abundance of various bioclasts. Stations D (745 m), C (980 m), B (1488 m) and A (1987 m) are characterized by clayey or sandy silts with numerous pteropod fragments (Table 2). On the basis of the vertical profiles of excess ^{210}Pb ($^{210}Pb_{xs}$), maximum sedimentation rates were successfully calculated for stations D, C, B and A revealing sedimentation rates decreasing from the shallower station D (745 m, 0.077 $cm\,yr^{-1}$) to the deeper station A (1987 m, 0.032 $cm\,yr^{-1}$) (Table 2). The ^{234}Th in excess was always at significant levels (30–105 mBq g^{-1}) in the surface sediment. With its short half-life (24.1 days), this observation shows the presence of freshly deposited particles at the water–sediment interface at all stations. The general trend in ^{234}Th-derived

bioturbation rates is a rapid decrease with increasing depth (Table 2), as often reported for continental slope environments (Schmidt et al., 2002). The highest value ($\sim$3 $cm^2\,yr^{-1}$) is obtained at station E, in agreement with the aforementioned presence of microenvironments related to burrows.

3.4. Particulate organic matter

Along our bathymetric transect, the TOC content of the first cm of the sediment ranges from 0.46% to 0.80% (DW) with the lowest value recorded at the shallowest station F (343 m) and the highest values recorded at stations D and C (respectively 745 m and 980 m) (Table 3). The $\delta^{13}C$ of particulate organic-matter ranges from −22.85‰ to −23.89‰ with a significant positive correlation with water depth (Tables 6a and b). The C:N ratio is minimal at station C (980 m) with a value of 11.40 and maximal at station F (343 m) with a value of 15.96. The lipids concentration is minimal at station F (343 m) with a value of 0.098 $mg\,g^{-1}$, whereas it is higher at stations E (552 m) and D (745 m) with respective concentrations of 0.263 and 0.191 $mg\,g^{-1}$ (Table 3). The total sugar and AA concentrations are maximal at station E (552 m) with respective values of 4.645 and 1.946 $mg\,g^{-1}$, whereas the concentrations are lower at stations F (343 m), B (1488 m) and A (1987) (Table 3). The sum of lipids, sugars and AAs is considered as labile organic matter. The sediment at stations E, D and C is rich in labile OM (5–7 $mg\,g^{-1}$); values at stations A and B are two times poorer ($<3\,mg\,g^{-1}$) (Table 3).

3.5. Diversity, density and vertical distribution of live foraminiferal faunas ($>150\,\mu m$)

Along the bathymetric transect, the species richness ranges from 18 to 61 species, in cores BTB2 and BTE2, respectively (Table 4). Lower foraminiferal diversity is recorded at the deeper stations B (1488 m) and A (1987 m), whereas higher diversity characterizes the

Table 3
Analyses of the particulate organic matter in the first cm at the 6 stations of our bathymetric transect

Station	Depth (m)	Particulate organic matter (0–1 cm)								
		TOC (%)	$\delta^{13}C$ (‰)	C:N	Lipids ($mg\,g^{-1}$)	Hydrosoluble sugars ($mg\,g^{-1}$)	Total sugars ($mg\,g^{-1}$)	Amino acids ($mg\,g^{-1}$)	Labile organic matter ($mg\,g^{-1}$)	Labile organic matter (% TOM)
F	343	0.46	−23.69	15.96	0.098	0.246	2.127	0.914	3.139	37.9
E	552	0.66	−23.89	11.50	0.263	0.226	4.645	1.946	6.854	57.4
D	745	0.80	−23.75	12.23	0.191	0.157	3.588	1.107	4.886	34.1
C	980	0.80	−23.74	11.40	0.160	0.206	4.101	1.625	5.886	40.9
B	1488	0.56	−23.59	12.51	0.158	0.077	1.684	0.724	2.566	25.3
A	1987	0.55	−22.85	13.75	0.165	0.163	1.518	1.044	2.726	27.3

Measurements of organic carbon content (TOC), $\delta^{13}C$, C:N ratio, and lipid, hydrosoluble sugar, total sugar and amino acid concentrations are presented. Labile organic matter concentrations are indicated ($\sum$lipid, total sugar and amino acid concentrations). Percentages of labile OM related to total organic matter (TOM) are also presented.

Table 4
Main features of live (stained) foraminiferal faunas of all duplicate cores for the 6 stations (Density (*D*), specific richness (*S*), Shannon index (*H*), Evenness index (*E*), community ALD_{10})

Station	Depth (m)	Duplicate cores	Foraminiferal density (Nbr./core)	Specific richness (*S*)	Shannon index (*H*)	Evenness index (*E*)	Community ALD_{10} (cm)
F	343	BTF1	120	40	2.37	0.27	0.97
	350	BTF2	198	43	2.49	0.28	0.80
E	552	BTE1	232	48	3.10	0.46	1.46
		BTE2	401	61	2.64	0.23	1.53
D	745	BTD1	129	34	2.29	0.29	1.04
		BTD2	190	50	2.98	0.39	1.26
C	980	BTC′3	137	40	2.89	0.45	0.67
		BTC′4	83	28	2.84	0.61	0.97
B	1488	BTB1	91	31	2.72	0.49	0.61
		BTB2	51	18	2.35	0.58	0.54
A	1987	BTA1	87	28	2.89	0.64	0.34
		BTA2	55	24	2.15	0.36	0.42

shallower station E (552 m) (Tables 4). Intermediate values of species richness (between 28 and 50 taxa) are recorded at stations F (~350 m), D (745 m) and C (980 m). The Shannon and Evenness indices exhibit no obvious bathymetric trend. The foraminiferal density follows the same trends as those described previously for the species richness. Lower densities are recorded at stations B (1488 m) and A (1987 m) with values ranging between 51 and 91 individuals per core (72 cm^2 surface area, 10 cm long) (Table 4). The highest densities of our bathymetric transect are observed in both replicate cores from station E with 232 and 401 individuals per core (72 cm^2 surface area, 10 cm long) (Table 4). The foraminiferal density is well correlated with the species richness, the concentration of lipids and the percentage of labile organic compounds (Tables 7a and b). The foraminiferal faunas in both replicate cores of station E penetrate deeply into the sediment and present maximal ALD_{10} values for the whole bathymetric transect (1.46 and 1.53 cm) (Figs. 3c and d; Table 4). Shallower foraminiferal communities ($ALD_{10} < 0.61$ cm) are observed at stations B and A, where faunas are strongly concentrated in the first half cm of sediment, and do not occur below 1.5 cm (Figs. 6c,d and 7c,d and Table 4). Finally, the ALD_{10} values are significantly positively correlated with the foraminiferal density and species richness (Table 7a and b).

3.6. Composition of foraminiferal faunas (>150 μm)

3.6.1. Station F (343–350 m)

In duplicate cores BTF1 and BTF2, live foraminiferal faunas are dominated by the non-fossilizing agglutinated taxon *Psammosphaera* spp. (see Appendix; Figs. 2c and d). This taxon represents respectively 16% and 14% of the fauna in cores BTF1 and BTF2. *Bigenerina nodosaria* and *Uvigerina mediterranea* compose about 10% of the living faunas. *Melonis barleeanus* represents between 5% and 10%. *Hanzawaia boueana* and *Bulimina aculeata* represent respectively 7% and 6% of the living fauna in core BTF2. In core BTF1, these two species are almost absent. All aforementioned taxa occupy shallow infaunal microhabitats with the exception of *M. barleeanus*, which shows an intermediate infaunal microhabitat (Table 5). *Chilostomella oolina*, which is infrequent (about 4%), occurs in a deep infaunal microhabitat. Its maximal density is found at 3.5–4 cm in core BTF1 and at 2–2.5 cm in core BTF2 (see Appendix).

3.6.2. Station E (552 m)

Foraminiferal faunas in both duplicate cores BTE1 and BTE2 are dominated by *Uvigerina peregrina* (13 versus 27%) and *B. nodosaria* (18 versus 16%) (see Appendix; Figs. 3c and d). *Saccammina sphaerica*, *U. mediterranea*, *M. barleeanus* and *Amphicoryna scalaris* are secondary species with relative abundances of between 3% and 13%. Most of these abundant taxa occur in the first 2 cm of sediment. Only *M. barleeanus* occupies an intermediate infaunal microhabitat (Table 5, see Appendix). Many species that exhibit a clear maximum at the sediment surface (e.g. *U. peregrina*, *U. mediterranea*, *A. scalaris*) have a very wide depth range and can be found to a considerable depth in the sediment (see Appendix).

3.6.3. Station D (745 m)

Foraminiferal faunas in both duplicate cores BTD1 and BTD2 are dominated by *U. mediterranea* (about 15%) and *B. nodosaria* (6% and 20%, respectively) (see Appendix; Figs. 4c and d). *U. peregrina* represents 10% of the living fauna in core BTD2, whereas *Planulina ariminensis*, *Gyroidina orbicularis* and *Crithionina mamilla* are relatively abundant in core BTD1. *U. mediterranea*, *U. peregrina* and *G. orbicularis* spread from the sediment–water interface down to intermediate infaunal microhabitats, whereas the other dominant taxa occur in shallow infaunal microhabitats (Table 5). *M. barleeanus* is the only other taxon showing a tendency to occupy deeper sediment layers.

3.6.4. Station C (980 m)

In duplicate cores BTC′3 and BTC′4, *U. mediterranea* (about 20%) and *G. orbicularis* (about 8%) are dominant species (see Appendix; Figs. 5c and d). In core BTC′4, *Rosalina bradyi* has a relative abundance of 16% (13 individuals). Rather surprisingly, it is absent in core BTC′3. *M. barleeanus* and *U. peregrina* are both secondary species that occur with percentages lower than 10% in both cores. Most of these species occupy shallow infaunal habitats with the exception of *G. orbicularis* and *M. barleeanus*, which show a tendency to prefer intermediate infaunal microhabitats (Table 5).

3.6.5. Station B (1488 m)

In duplicate cores BTB1 and BTB2, *U. peregrina* (17% and 30%, respectively), *Ammolagena clavata* (14% and 8%) and *G. orbicularis* (3% and 16%) are the dominant species (see Appendix; Figs. 6c and d). *U. mediterranea* (about 7% in both cores) is a secondary species. *Thurammina albicans* and *Hoeglundina elegans* are both relatively abundant (7%) in core BTB1. All these taxa occupy shallow infaunal microhabitats (Table 5).

3.6.6. Station A (1987 m)

In duplicate cores BTA1 and BTA2, *Ammobaculites agglutinans* (18% and 6%, respectively) and *Reophax bilocularis* (13% and 8%) are dominant taxa (see Appendix; Figs. 7c and d). *U. peregrina*, *H. elegans*, *Lagenammina tubulata* and *Nodellum membranaceum* are secondary species with percentages lower than 10%. All these taxa occupy very shallow infaunal microhabitats ($ALD_{10} < 0.5$ cm, Table 5).

3.7. Comparison of living foraminiferal faunas from duplicate cores

The cluster analysis (Ward's method) of the foraminiferal faunas recorded in our 12 cores is illustrated by a tree diagram (Fig. 8), which shows clearly that both duplicate cores from stations A, B, D, E and F match in rather well-constrained sub-clusters (see the sub-clusters 1, 2, 3, 4 and 5 in Fig. 8). Only

Table 5
Average living depth (ALD_{10}) of foraminiferal species and (between parentheses) the number of individuals on which the calculation is based

Station:	F		E		D		C		B		A		Microhabitat
Depth (m):	343	350	552		745		980		1488		1987		
Duplicate cores:	BTF1	BTF2	BTE1	BTE2	BTD1	BTD2	BTC′3	BTC′4	BTB1	BTB2	BTA1	BTA2	
Taxa (>5 individuals/core):	ALD_{10}		ALD_{10}		ALD_{10}		ALD_{10}		ALD_{10}		ALD_{10}		
Anphicoryna scalaris			1.04 (17)	1.20 (11)									SI
Bulimina aculeata		0.98 (11)											SI
Bulimina inflata						0.55 (5)							SI
Bulimina marginata				2.60 (5)									DI
Chilostomella oolina	3.25 (5)	1.86 (9)											DI
Cibicides ?lobatulus		1.61 (7)											SI/II
Gavelinopsis praegeri		0.33 (6)											SI
Gyroidina orbicularis			1.75 (5)		1.03 (9)		1.07 (11)	1.25 (6)		0.88 (8)			SI/II
Hanzawaia boueana		0.32 (14)											SI
Hoeglundina elegans		0.35 (5)							0.92 (6)		0.25 (5)		SI
Melonis barleeanus	0.75 (12)	1.68 (7)	2.78 (20)	1.92 (12)	0.89 (7)	1.08 (6)		0.92 (6)					II
Planulina ariminensis					0.81 (9)								SI
Rosalina bradyi								0.40 (13)					SI
Uvigerina auberiana		0.25 (5)											SI
Uvigerina mediterranea	0.49 (13)	0.47 (16)	1.95 (10)	2.17 (25)	1.21 (27)	1.23 (28)	0.54 (28)	1.28 (13)	0.75 (5)				SI/II
Uvigerina peregrina		0.35 (5)	0.72 (31)	1.71 (108)		1.34 (19)	0.30 (10)		0.55 (15)	0.28 (15)	0.25 (8)		SI
Biloculinella sp. 1			4.70 (5)										DI
Pyrgo depressa			0.83 (6)										SI
Quinqueloculina seminula		0.89 (7)											SI
Free agglutinated sp. 66							0.25 (7)						SI
Ammobaculites agglutinans										0.38 (16)	0.45 (5)		SI
Ammolagena clavata									0.29 (13)				SI
Crithionina mamilla		0.25 (6)		0.65 (5)	0.25 (12)	1.04 (7)							SI
Hemisphaerammina sp.			0.50 (10)	0.75 (5)		0.56 (8)							SI
Hippocrepinella alba				1.58 (6)									SI/DI
Lagenammina tubulata											0.25 (7)		SI
Psammosphaera sp.	0.46 (19)	0.79 (28)											SI
Recurvoides spp.			0.25 (5)	1.95 (11)									SI/II
Reophax bilocularis											0.25 (11)	0.25 (7)	SI
Reophax dentaliniformis			0.50 (6)	1.42 (6)									SI/II
Saccammina sphaerica			0.60 (10)	0.67 (50)									SI
Thurammina albicans									0.58 (6)				SI
Tritaxis fusca		0.39 (7)					0.25 (9)						SI
Bigenerina nodosaria	0.34 (11)	0.38 (20)	1.15 (41)	0.90 (63)	0.50 (12)	0.98 (37)	0.55 (5)						SI
Nodellum membranaceum								2.05 (5)					II
Total fauna	0.97 (120)	0.80 (197)	1.46 (232)	1.53 (401)	1.04 (129)	1.26 (190)	0.67 (137)	0.97 (83)	0.61 (91)	0.54 (51)	0.34 (87)	0.42 (56)	

Only occurrence of >5 individuals is shown. Microhabitat patterns are summarized as shallow infaunal (SI), intermediate infaunal (II) or deep infaunal (DI) taxa.

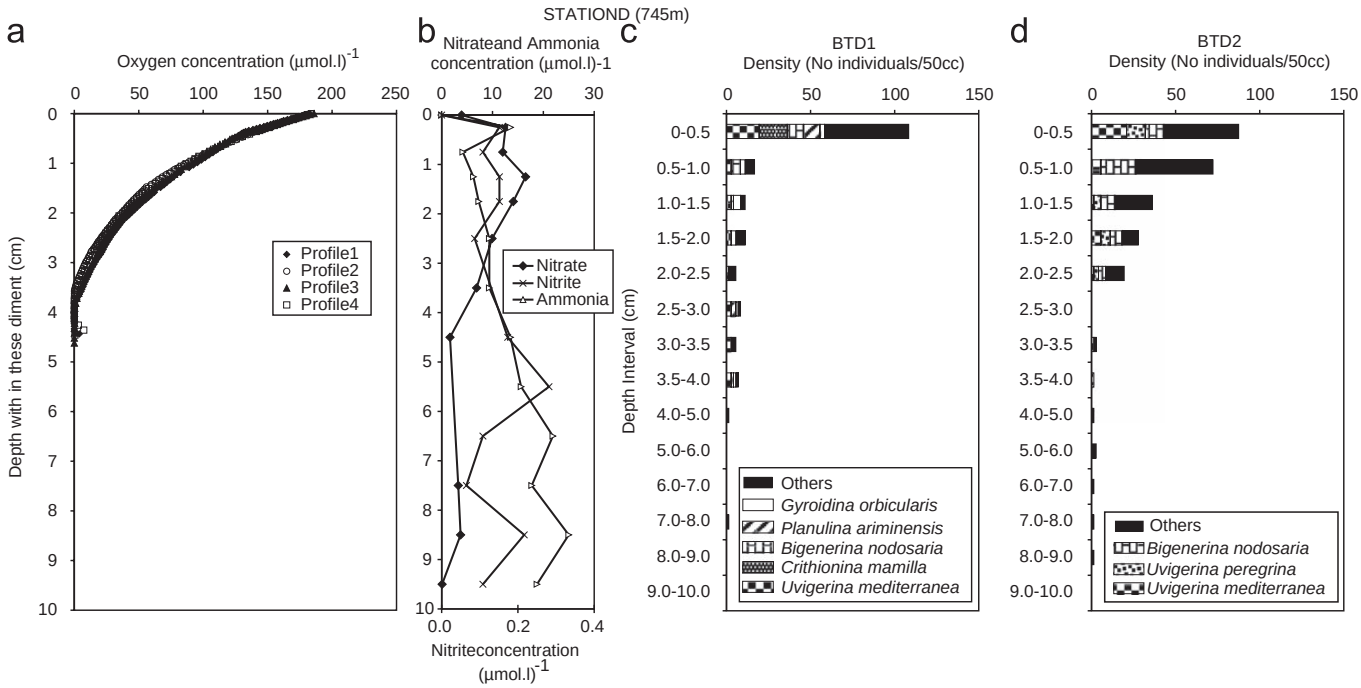

Fig. 4. Station D, water depth is 745 m. (a) Oxygen profiles; (b) nitrate, nitrite and ammonia concentrations in the pore water; (c) foraminiferal distribution (number of individuals >150 µm fraction found in each level, standardized for a 50 cm^3 sediment volume) for both duplicate cores BTD1 and BTD2. Only taxa with a percentage higher than 5% are presented.

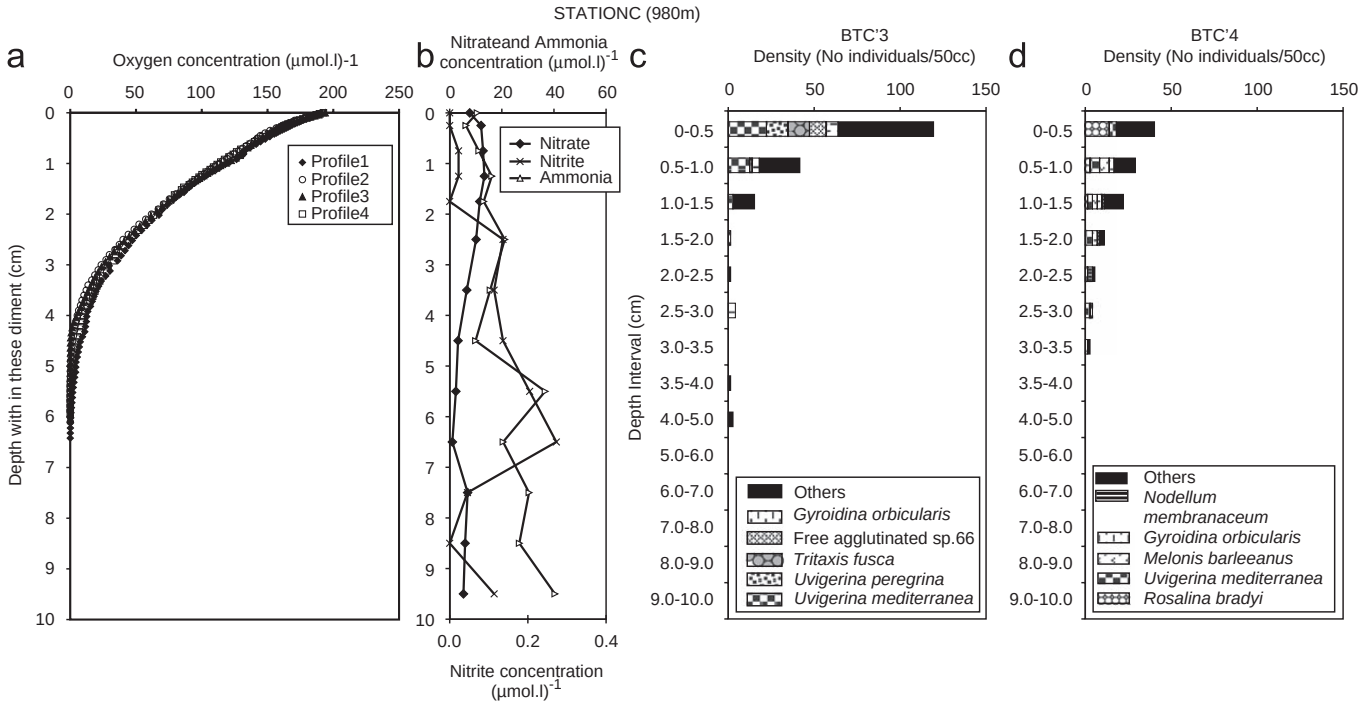

Fig. 5. Station C, water depth is 980 m. (a) Oxygen profiles; (b) nitrate, nitrite and ammonia concentrations in the pore water; (c) foraminiferal distribution (number of individuals >150 µm fraction found in each level, standardized for a 50 cm^3 sediment volume) for both duplicate cores BTC′3 and BTC′4. Only taxa with a percentage higher than 5% are presented.

cores BTC′3 and BTC′4 from station C (980 m) are not grouped in a single cluster, but match with the cores from the adjacent and shallower station D (745 m) in cluster 3. Our results suggest that the spatial variability recorded by cores at a single station does not significantly obscure the larger-scale spatial variability.

4. Discussion

4.1. Sedimentary features along the bathymetric transect

The sedimentation rates from station C (745 m; ~0.08 cm yr^{-1}) down to station A (1987 m; ~0.03 cm yr^{-1}) are in

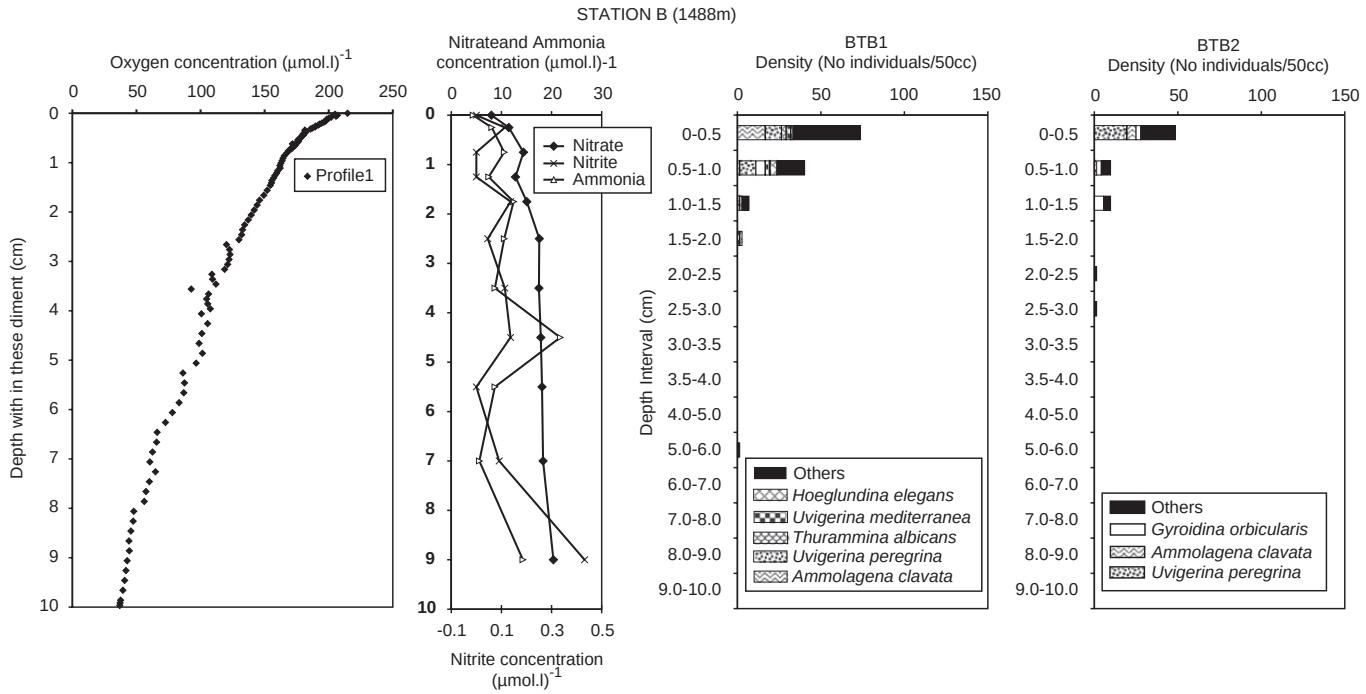

Fig. 6. Station B, water depth is 1488 m. (a) Oxygen profile; (b) nitrate, nitrite and ammonia concentrations in the pore water; (c) foraminiferal distribution (number of individuals >150 µm fraction found in each level, standardized for a 50 cm^3 sediment volume) for both duplicate cores BTB1 and BTB2. Only taxa with a percentage higher than 5% are presented.

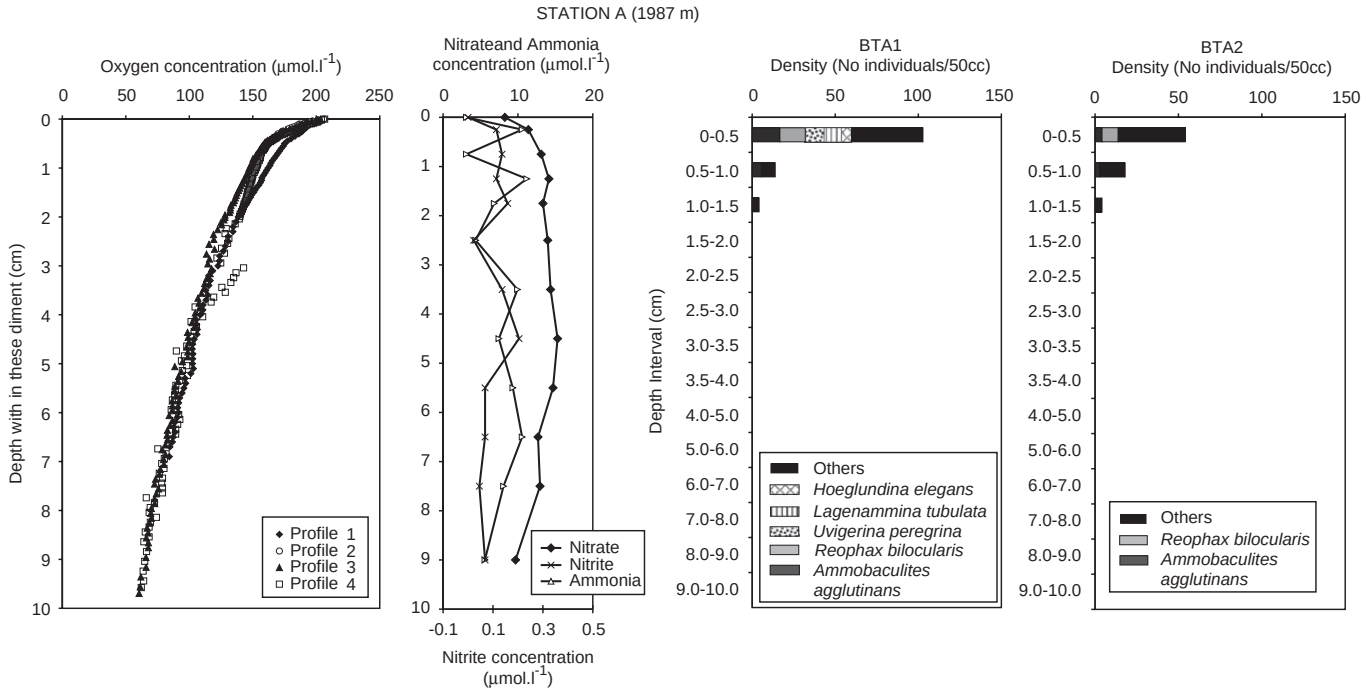

Fig. 7. Station A, water depth is 1987 m. (a) Oxygen profiles; (b) nitrate, nitrite and ammonia concentrations in the pore water; (c) foraminiferal distribution (number of individuals >150 µm fraction found in each level, standardized for a 50 cm^3 sediment volume) for both duplicate cores BTA1 and BTA2. Only taxa with a percentage higher than 5% are presented.

agreement with those determined by Zuo et al. (1997) and Buscail et al. (1997) for different stations located in the same bathymetric range on the open slope between the Grand Rhône Canyon and the Petit Rhône canyon (values between ~0.12 and ~0.03 cm yr^{-1}). Logically, the deeper the stations are, the scarcer the terrigeneous input from shelves and continental areas becomes. For station E (552 m depth), no sedimentation rate could be calculated because the $^{210}Pb_{xs}$ profile in the first cm of the sediment exhibits an erratic pattern. This is probably due to the

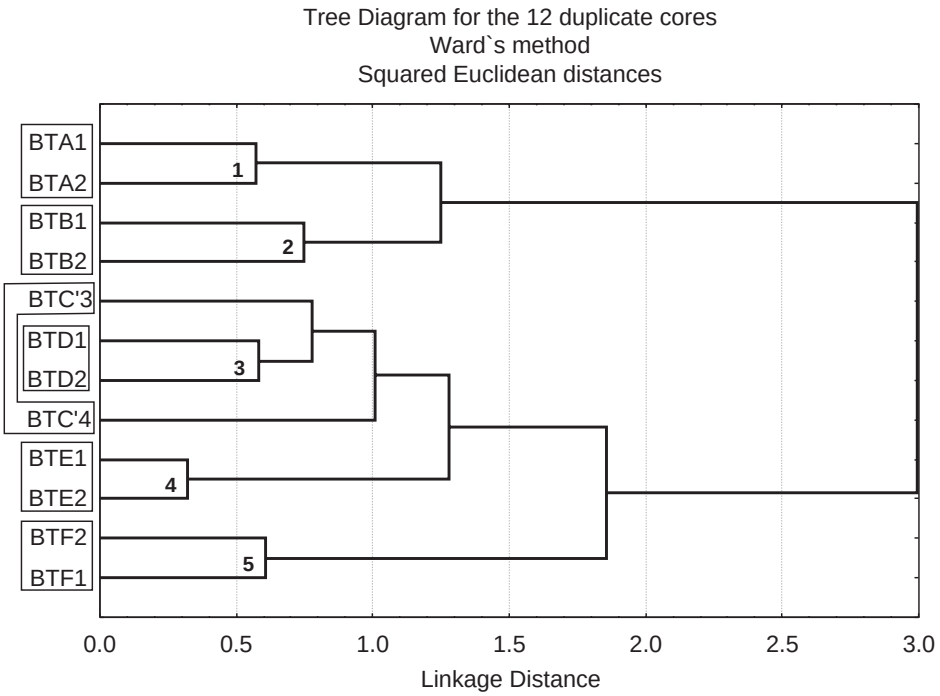

Fig. 8. Tree diagram realized according to Ward's method based on the squared Euclidean distances between all duplicate cores. Clusters 1, 2, 3, 4 and 5 are discussed in discussion.

enhanced bioturbation (high ^{234}Th–D_b) observed in the cores sampled at this site. The oxygen profiles underline the effect of bioturbation on sediment heterogeneity (Fig. 3a). The 350-m-deep station F appears as a "sedimentary" exception along our bathymetric transect. The abundance of coarse sediment (silty sands; $Q_{50} = 122.78\,\mu m$), the presence of glauconitic components (mainly inner moulds of benthic foraminifera) in the 10-cm long cores (BTF1 and BTF2) and the lower value of $^{210}Pb_{xs}$ for the first cm of sediment ($18\,mBq\,g^{-1}$ for the 0–0.5 cm interval) are all indications of an admixture of reworked sediment. On the one hand, this sandy substrate could be related to the erosion of outer-shelf relict sands by dense water cascading (e.g. turbidity flow) (Gaudin et al., 2006). On the other hand, the coarse sediment observed at station F may result from intense winnowing by strong bottom currents. Another observation in agreement with the reworked or winnowed nature of the sediment deposited at our station F is the lower quality of organic matter in the first cm of sediment (Table 3). The particulate organic matter yields the highest C:N ratio (15.96) recorded along our bathymetric transect suggesting the admixture of degraded organic compounds (Fenchel and Jørgensen, 1977; Meyers, 1994, 1997; Harmelin-Vivien et al., 2008).

4.2. Particulate organic matter along our bathymetric transect

Elevated TOC contents (0.80% DW) are recorded at the mid-slope stations D (745 m) and C (980 m), suggesting that these sites function as a depocenter for clayey silts enriched in organic matter (Tables 2 and 3). Along the bathymetric transect, the C:N ratio of particulate organic matter is always above 10, suggesting the dominant burial of organic detritus with a low nutritional value (Fenchel and Jørgensen, 1977; Meyers, 1994, 1997; Harmelin-Vivien et al., 2008). The relatively high bottom-water temperature ($>13\,^{\circ}C$) in our study area, the low sedimentation rates and the long residence times at the sediment–water interface (via suspension) are probably responsible for an enhanced mineralization of labile organic compounds in the water column and at the sediment–water interface (Buscail and Germain, 1997). The carbon isotopes of particulate OC (ranging from −23.89‰ to −22.85‰) suggest that organic detritus is a mixture of marine and terrestrial organic compounds. According to Darnaude et al. (2004) and Tesi et al. (2007), marine organic matter has a mean $\delta^{13}C$ of about −22.00‰ in the Gulf of Lions, compared to $\delta^{13}C$ values of −28.00‰ for the terrestrial organic detritus discharged by the Rhône River (Kerhervé P., unpublished data; Tesi et al., 2007; Harmelin-Vivien et al., 2008). Station E (552 m) has the most food-rich station of the bathymetric transect, with high concentrations of labile organic compounds (lipids, AAs and sugars).

4.3. Biogeochemical relationships

The progressive deepening of OPD from the 343-m-deep station F to the 1987-m-deep station A may reflect a decrease of oxygen consumption in the sediment in response to a reduced input of labile organic matter. When station F, characterized by deposition of sandy sediment and reworked organic matter, is excluded from the statistical analyses (Table 6b), labile organic-matter concentration (sum of lipids, AAs and sugars) is well

Table 6
Pearson's correlation coefficients between main physico-chemical parameters along the bathymetric transect

	Depth (m)	Bottom-water temperature (°C)	Bottom-water oxygenation ($\mu mol\,l^{-1}$)	Oxygenation penetration depth (mm)	TOC (% dw)	$\delta^{13}C$ (permil)	C:N ratio	Total sugars ($mg\,g^{-1}$)	Hydrosoluble sugars ($mg\,g^{-1}$)	Lipids ($mg\,g^{-1}$)	Amino acids ($mg\,g^{-1}$)	Labile organic matter ($mg\,g^{-1}$)	Labile organic matter (% TOM)
(a) Pearson coefficients with 6 stations													
Depth (m)	1.00												
Bottom-water oxygenation ($\mu mol\,l^{-1}$)	**−0.83**	1.00											
Bottom-water temperature (°C)	**0.91**	**−0.89**	1.00										
Oxygenation penetration depth (mm)	**0.96**	−0.69	0.76	1.00									
TOC (% dw)	−0.13	−0.43	0.11	−0.33	1.00								
$\delta^{13}C$ (permil)	**0.85**	−0.51	0.67	**0.85**	−0.39	1.00							
C:N ratio	−0.10	0.57	−0.20	0.00	**−0.81**	0.33	1.00						
Total sugars ($mg\,g^{-1}$)	−0.59	0.13	−0.48	−0.64	0.74	−0.70	−0.67	1.00					
Hydrosoluble Sugars ($mg\,g^{-1}$)	−0.67	0.68	−0.67	−0.62	−0.02	−0.29	0.27	0.47	1.00				
Lipids ($mg\,g^{-1}$)	−0.06	−0.22	−0.23	0.01	0.49	−0.26	−0.75	0.67	0.00	1.00			
Amino acids ($mg\,g^{-1}$)	−0.36	0.06	−0.37	−0.35	0.54	−0.41	−0.61	**0.89**	0.57	0.72	1.00		
Labile organic matter ($mg\,g^{-1}$)	−0.53	0.11	−0.45	−0.56	0.71	−0.64	−0.68	**0.99**	0.50	0.71	**0.94**	1.00	
Labile organic matter (% TOM)	−0.68	0.48	−0.74	−0.59	0.27	−0.62	−0.33	**0.84**	0.72	0.61	**0.90**	**0.87**	1.00
(b) Pearson coefficients with 5 stations (F is out)													
Depth (m)	1.00												
Bottom-water temperature (°C)	−0.86	1.00											
Bottom-water oxygenation ($\mu mol\,l^{-1}$)	0.87	−0.99	1.00										
Oxygenation penetration depth (mm)	**0.95**	−0.66	0.69	1.00									
TOC (% dw)	−0.72	0.28	−0.35	**−0.89**	1.00								
$\delta^{13}C$ (permil)	**0.92**	−0.75	0.71	**0.89**	−0.63	1.00							
C:N ratio	0.88	−0.67	0.63	**0.88**	−0.68	**0.93**	1.00						
Total sugars ($mg\,g^{-1}$)	**−0.93**	0.77	−0.79	**−0.91**	0.75	−0.79	**−0.88**	1.00					
Hydrosoluble sugars ($mg\,g^{-1}$)	−0.53	0.50	−0.54	−0.50	0.49	−0.25	−0.49	0.79	1.00				
Lipids ($mg\,g^{-1}$)	−0.68	**0.94**	**−0.94**	−0.45	0.10	−0.49	−0.45	0.67	0.59	1.00			
Amino acids ($mg\,g^{-1}$)	−0.68	0.69	−0.68	−0.59	0.45	−0.49	−0.70	0.88	**0.94**	0.71	1.00		
Labile organic matter ($mg\,g^{-1}$)	**−0.89**	0.78	−0.79	−0.84	0.68	−0.73	−0.85	**0.99**	0.85	0.71	**0.93**	1.00	
Labile organic matter (% TOM)	−0.78	0.87	−0.85	−0.64	0.38	−0.62	−0.74	**0.89**	0.83	0.87	**0.96**	**0.94**	1.00

The variables are: station depth, bottom-water temperature, bottom-water oxygenation, oxygen penetration depth, organic carbon content of the first cm of sediment (TOC), carbon isotopic ratio of organic matter ($\delta^{13}C$), C:N ratio, and total sugar, hydrosoluble sugar, lipid, amino acid and labile organic matter concentrations and percentage of labile OM related to total organic matter. In (a), coefficients were calculated with data from all stations (A, B, C, D, E and F). In (b), station F was excluded from statistics, since it represents a singular sedimentary environment characterised by mass deposition of sands with very low quality organic matter. Bold values are significant at the 0.05 threshold level.

correlated with water depth ($r=-0.89$, $p<0.05$). OPD shows a significant negative correlation with the OC content and with the concentration of total sugars (respectively $r=-0.89$ and $r=-0.91$, $p<0.05$). This suggests that in "normal" open-slope environments (without sand-bed deposition or strong winnowing) the organic-matter content does have a direct effect on the oxygen consumption in the sediment (e.g. Hyacinthe et al., 2001). Nitrate, nitrite and ammonia profiles at stations F, E, D and C (Figs. 2b, 3b, 4b and 5b) show a normal succession of redox reactions within the sediment (Froelich et al., 1979). At the deeper stations A (1987 m) and B (1488 m), nitrate, nitrite and ammonia do not exhibit a clear concentration gradient in the 10-cm-long cores, indicating limited redox reactions in the topmost sediment. Finally, the input of organic matter (even with a low nutritional value) at the sediment–water interface is responsible for a classical succession of redox reactions within the sediment, where oxygen and nitrate are preferentially used for its degradation. Redox gradients are steeper at the shallower stations than at the deeper sites, reflecting the higher input of (more or less degraded) organic matter and increased mineralization within the sediment. At the deepest sites, profiles with low gradients underline the oligotrophic character of the upper sediment layers.

4.4. Live foraminiferal faunas and environmental controls

4.4.1. Major trends

Foraminiferal density is well correlated with species richness (Table 7a and b). The highest foraminiferal standing stocks (~315 ind./core) and the highest diversity (48–61 species and Shannon diversity index of 2.64–3.10) are both recorded at station E (552 m) (Table 4). From station E (552 m) to station A (1987 m), species richness and foraminiferal density progressively diminish (Fig. 9a). Highly diverse and abundant foraminiferal faunas are generally observed on the upper slope where the organic-matter flux is high (e.g. Corliss, 1991; Jorissen et al., 1998; Fontanier et al., 2002; Licari et al., 2003; Eberwein and Mackensen, 2006). In the oligotrophic lower-slope environments, both foraminiferal standing stocks and diversity indices are lower. In our study area, the decrease of density and specific richness with depth is probably a consequence of the increasing poverty of labile organic matter (Table 4). The significant positive correlation coefficients between foraminiferal density/specific richness and lipid concentration in the upper sediment (Table 7b and Fig. 9b) suggest that organic-matter quality plays a prominent role in controlling the foraminiferal community structure. Lipids (and AAs) are considered by Grémare et al. (2002, 2003) as the most labile organic compounds, which control the abundance and biomass of benthic meio- and macrofauna in the Gulf of Lions.

4.4.2. Compositional changes

The trophic gradient along our bathymetric transect is also illustrated by gradual changes in the composition of the foraminiferal faunas (Fig. 10). At station E (552 m), and to a lesser extent at station D (745 m), Uvigerinids (*U. peregrina* and *U. mediterranea*), *B. nodosaria*, *A. scalaris*, *M. barleeanus* and *S. sphaerica* appear to benefit from deposits rich in labile organic matter. In many ecological studies, these taxa have been described as meso-eutrophic species living in outer-shelf and/or upper-slope environments with moderate-to-high organic-matter fluxes (e.g. Corliss, 1991; Schönfeld, 1997; Jorissen et al., 1998; de Rijk et al., 2000; Fontanier et al., 2002; Licari et al., 2003; Eberwein and Mackensen, 2006). Furthermore, uvigerinids (*U. peregrina* and *U. mediterranea*) and *M. barleeanus* have been described in the western Mediterranean Sea as living in upper-slope environments characterized by a labile organic-matter flux of 2.5 g C m^{-2} yr^{-1} (Altenbach e t al., 1999; de Rijk et al., 2000). This flux level has been considered as a major ecological boundary between oligotrophic and meso-eutrophic benthic environments (de Rijk et al., 2000). Therefore, the density increase of *U. peregrina*, *U. mediterranea* and *M. barleeanus* from station A (1987) to station E (552 m) suggests an increase of exported labile organic matter with decreasing water depth. The gradual impoverishment towards the deeper stations B (1488 m) and A (1987 m) is underlined by (1) the shallow infaunal distribution of the benthic foraminiferal faunas, (2) the relative abundance of agglutinated species (*A. clavata*, *A. agglutinans*, *L. tubulata*, *R. bilocularis*, *T. albicans*) and (3) the occurrence of species commonly described as deep-sea oligotrophic taxa, such as *H. elegans* and *A. clavata* (e.g. Corliss, 1991; Harloff and Mackensen, 1997; Schönfeld, 1997; Jorissen et al., 1998; Fontanier et al., 2002; Licari et al., 2003; Nigam et al., 2004; Eberwein and Mackensen, 2006).

4.4.3. Foraminiferal microhabitats

Density and species richness are also positively correlated with the microhabitat of the whole foraminiferal assemblage (depicted by ALD_{10}; Table 7a and b and Fig. 11). At stations B (1488 m) and A (1987 m), foraminiferal faunas, which are characterized by low-standing stocks and low species richness, are strongly concentrated in the first half cm of the sediment where fairly low concentrations of labile organic compounds (lipids, AAs, sugars) are recorded (Table 3). Conversely, at station E (552 m) where relatively high concentrations of labile organic compounds (lipids, AAs, sugars) accompany a large quantity of low-quality organic detritus (Table 3), some representatives of the highly diverse foraminiferal faunas dwell in deeper sediment layers (Table 5). Here, infaunal microhabitats are occupied by low-standing stocks of intermediate and deep infaunal taxa (*M. barleeanus*, *Globobulimina* spp., *Chilostomella* spp.). These species are generally abundant in organic-matter-enriched sediments (e.g. Corliss, 1991; Jorissen et al., 1998; Kitazato et al., 2000; Schmiedl et al., 2000; Fontanier et al., 2002, 2005; Licari et al., 2003). Such relationships between microhabitat (diversity, density) and organic-matter supply at the sediment–water interface have previously been considered in the TROX-model of Jorissen et al. (1995). In oligotrophic settings, low-diversity and low-density foraminiferal faunas are concentrated at the well-oxygenated sediment–water interface to optimize acquisition of scarce food deposits (Jorissen et al., 1995).

Table 7
Pearson's correlation coefficients between the major foraminiferal patterns and the main physico-chemical parameters along the bathymetric transect

	Foraminiferal density (Nbr./core)	Specific richness (S)	Shannon index (H)	Evenness index (E)	Community ALD_{10} (cm)
(a) Pearson coefficients with 6 stations					
Foraminiferal density (Nbr./core)	1.00				
Specific richness (S)	**0.96**	1.00			
Shannon index (H)	0.53	0.48	1.00		
Evenness index (E)	−0.65	−0.78	0.16	1.00	
Community ALD_{10} (cm)	**0.94**	**0.96**	0.59	−0.65	1.00
Depth (m)	−0.70	**−0.83**	−0.24	0.80	−0.80
Bottom-water temperature (°C)	0.56	0.65	−0.20	**−0.86**	0.50
Bottom-water oxygenation ($\mu mol\,l^{-1}$)	**−0.85**	**−0.91**	−0.14	**0.91**	**−0.83**
Oxygenation penetration depth (mm)	−0.55	−0.73	−0.31	0.68	**−0.73**
TOC (% dw)	0.16	0.23	0.75	0.18	0.40
$\delta^{13}C$ (permil)	−0.61	−0.67	−0.49	0.43	−0.79
C:N ratio	−0.24	−0.14	**−0.84**	−0.44	−0.36
Total sugars ($mg\,g^{-1}$)	0.73	0.76	**0.90**	−0.25	**0.84**
Hydrosoluble sugars ($mg\,g^{-1}$)	0.59	0.69	0.27	−0.62	**0.50**
Lipids ($mg\,g^{-1}$)	0.68	0.54	0.72	−0.03	**0.64**
Amino acids ($mg\,g^{-1}$)	0.73	0.68	**0.92**	−0.10	0.68
Labile organic matter ($mg\,g^{-1}$)	0.75	0.75	**0.93**	−0.21	**0.82**
Labile organic matter (% TOM)	**0.93**	**0.90**	0.72	−0.47	**0.86**
(b) Pearson coefficients with 5 stations (F is out)					
Foraminiferal density (Nbr./core)	1.00				
Specific richness (S)	**0.97**	1.00			
Shannon index (H)	0.68	0.72	1.00		
Evenness index (E)	−0.80	−0.86	−0.30	1.00	
Community ALD_{10} (cm)	**0.94**	**0.98**	0.71	−0.84	1.00
Depth (m)	−0.79	−0.88	−0.77	0.71	**−0.95**
Bottom-water temperature (°C)	**0.97**	**0.94**	0.64	−0.78	**0.96**
Bottom-water oxygenation ($\mu mol\,l^{-1}$)	**−0.97**	**−0.97**	−0.61	0.87	**−0.98**
Oxygenation penetration depth (mm)	−0.59	−0.73	−0.75	0.57	**−0.82**
TOC (% dw)	0.25	0.46	0.61	−0.37	0.52
$\delta^{13}C$ (permil)	−0.61	−0.66	−0.69	0.45	−0.80
C:N ratio	−0.59	−0.65	**−0.88**	0.29	−0.74
Total sugars ($mg\,g^{-1}$)	0.79	0.87	**0.93**	−0.59	**0.88**
Hydrosoluble sugars ($mg\,g^{-1}$)	0.66	0.71	0.82	−0.43	**0.59**
Lipids ($mg\,g^{-1}$)	**0.98**	**0.93**	0.56	−0.80	0.88
Amino acids ($mg\,g^{-1}$)	0.79	0.80	**0.94**	−0.42	0.72
Labile organic matter ($mg\,g^{-1}$)	0.82	**0.88**	**0.95**	−0.57	0.87
Labile organic matter (% TOM)	**0.93**	**0.91**	**0.89**	−0.58	0.86

The biotic variables are foraminiferal density, specific richness, Shannon diversity index, evenness index and assemblage ALD_{10}. For each station, we used mean values calculated on both replicate cores. The abiotic variables are station depth, bottom-water temperature, bottom-water oxygenation, oxygen penetration depth, organic carbon content of the first cm of sediment (TOC), carbon isotopic ratio of organic matter ($\delta^{13}C$), C:N ratio, total sugar, hydrosoluble sugar, lipid, amino acid and labile organic matter concentrations and percentage of labile OM related to total organic matter. In (a), coefficients were calculated with data from all stations. In (b), station F was excluded from the statistics. Bold values are significant at the 0.05 threshold level.

In our study area, such conditions prevail clearly at stations B (1488 m) and A (1987 m). The foraminiferal penetration in the sediment should be maximal in meso-eutrophic settings, where the combination of availability of labile organic matter in the deeper sediment and a deeper oxygen penetration allow a maximal vertical distribution of the fauna (Jorissen et al., 1995). Different specialized taxa occupy shallow, intermediate and deep infaunal micohabitats within the sediment, thus constituting a highly diverse and relatively dense foraminiferal fauna (Jorissen et al., 1995). Such conditions are apparently reached at the 552-m-deep station E. However, closer inspection of the data shows that some of the taxa present in deeper layers are usually limited to the upper sediment layer (such as *U. peregrina*, *U. mediterranea* and *A. scalaris*) (e.g. Corliss, 1991; Jorissen et al., 1998; Schmiedl et al., 2000; Fontanier et al., 2002, 2003, 2006; Licari et al., 2003; Eberwein and Mackensen, 2006). This suggests that these taxa: (1) have been passively transported by active bioturbation or (2) live in the direct vicinity of abundant burrows observed in the deeper sediment layers.

Fig. 12 is a synthetic scheme illustrating the changes of the foraminiferal composition and the foraminiferal microhabitat along our bathymetric transect. Major physico-chemical parameters are also depicted. As suggested above, we show that the faunal variability is related to a complex association of physico-chemical parameters. The lipids concentration in the upper sediment (0–1 cm) is probably the major parameter controlling the foraminiferal distribution along our open-slope stations. The OPD and the intensity of bioturbation seem to play secondary ecological roles. As presented below,

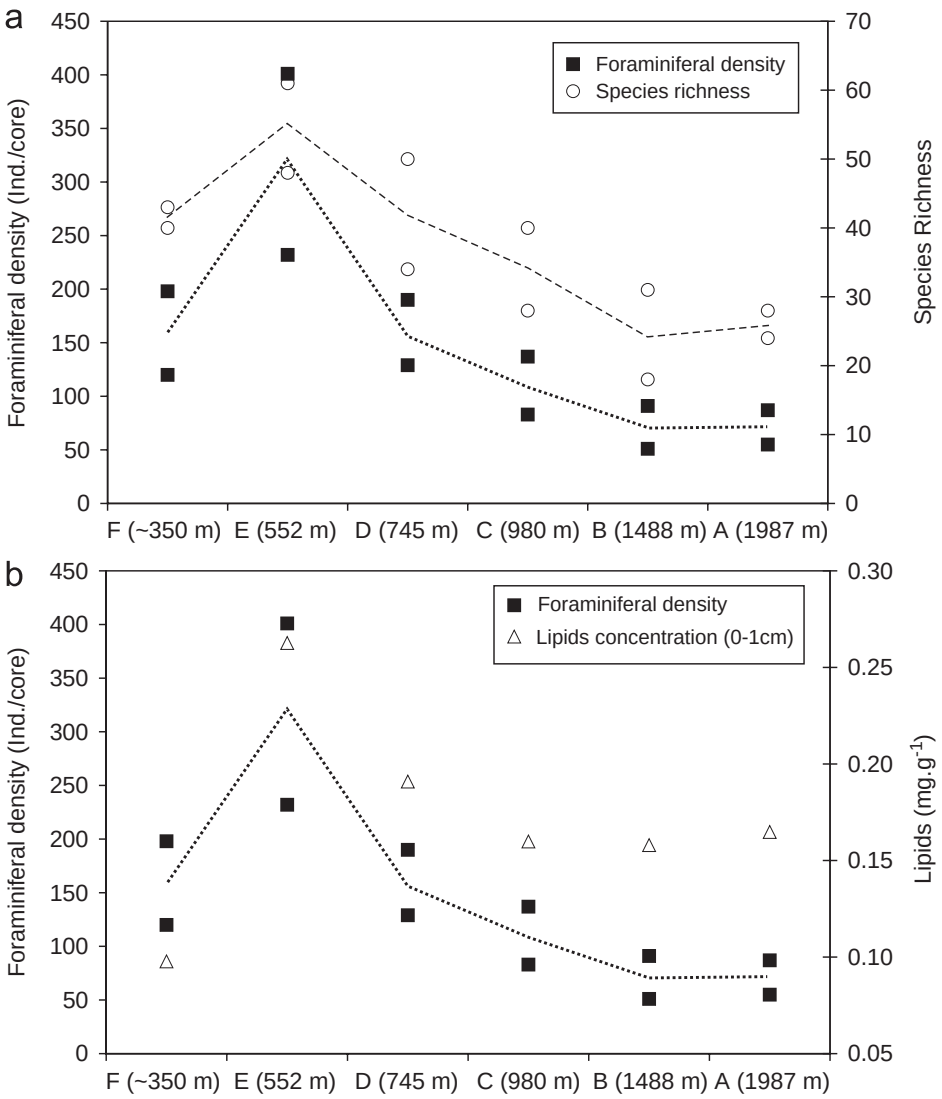

Fig. 9. (a) Foraminiferal density and species richness for the 12 cores collected at our 6 stations. The dotted line represents the mean values of foraminiferal density at each station. The dashed line represents the mean values of foraminiferal species richness; (b) foraminiferal density and lipid concentration in the upper sediment (0–1 cm) for the 12 cores collected at our 6 stations. The dotted line represents the mean values of foraminiferal density.

other hydro-sedimentary processes at the sediment–water interface may be significant parameters controlling foraminiferal dynamics at some of the stations.

4.4.4. Peculiar faunas at station F (~350 m)

The foraminiferal community at the 350-m-deep station F is dominated by few taxa, living mainly in the first cm of the well-oxygenated sandy sediment (*Psammosphaera* spp., *B. nodosaria*, *U. mediterranea*) (Fig. 9). *Psammosphaera* spp., which is the dominant species at this site, agglutinates its test with large sand particles. Therefore, it may be well adapted to live or to colonize repeatedly deposited coarse sediments or strongly winnowed sea floor. Such an assumption is in agreement with the observation at the HEBBLE (High Energy Benthic Boundary Layer Experiment) Site off Nova Scotia (40°27′N, 62°20′W, 4815–4825 m depth) where coarsely grained agglutinated *Psammosphaera* and *Saccammina* are able to live in high-energy or otherwise stressed environments (Kaminski, 1985). Rather surprisingly, the meso-eutrophic taxa *B. nodosaria* and *U. mediterranea* have an absolute frequency slightly lower than the values observed at the deeper station E (552 m). Their relatively low-standing stocks may reflect the lower quality of organic matter deposited at this site. Consequently, the foraminiferal fauna found at station F looks like a non-equilibrium fauna living in a disturbed and nutrient-deficient setting (compare Alve, 1999). A comparable situation has been described in active canyons where turbidity flows or strong bottom currents generate sediment instability and ecological disequilibria (Jorissen et al., 1994; Hess et al., 2005; Koho et al., 2007).

4.4.5. Foraminifera typical of high current velocities

At stations D (745 m) and C (980 m), the occasional presence of live (stained) species such as *P. ariminensis* and *R. bradyi* is interesting (Fig. 9). *P. ariminensis* has been described by various authors (e.g. Lutze and Thiel, 1989; Schönfeld, 1997, 2002) as an epibenthic/epilithic species

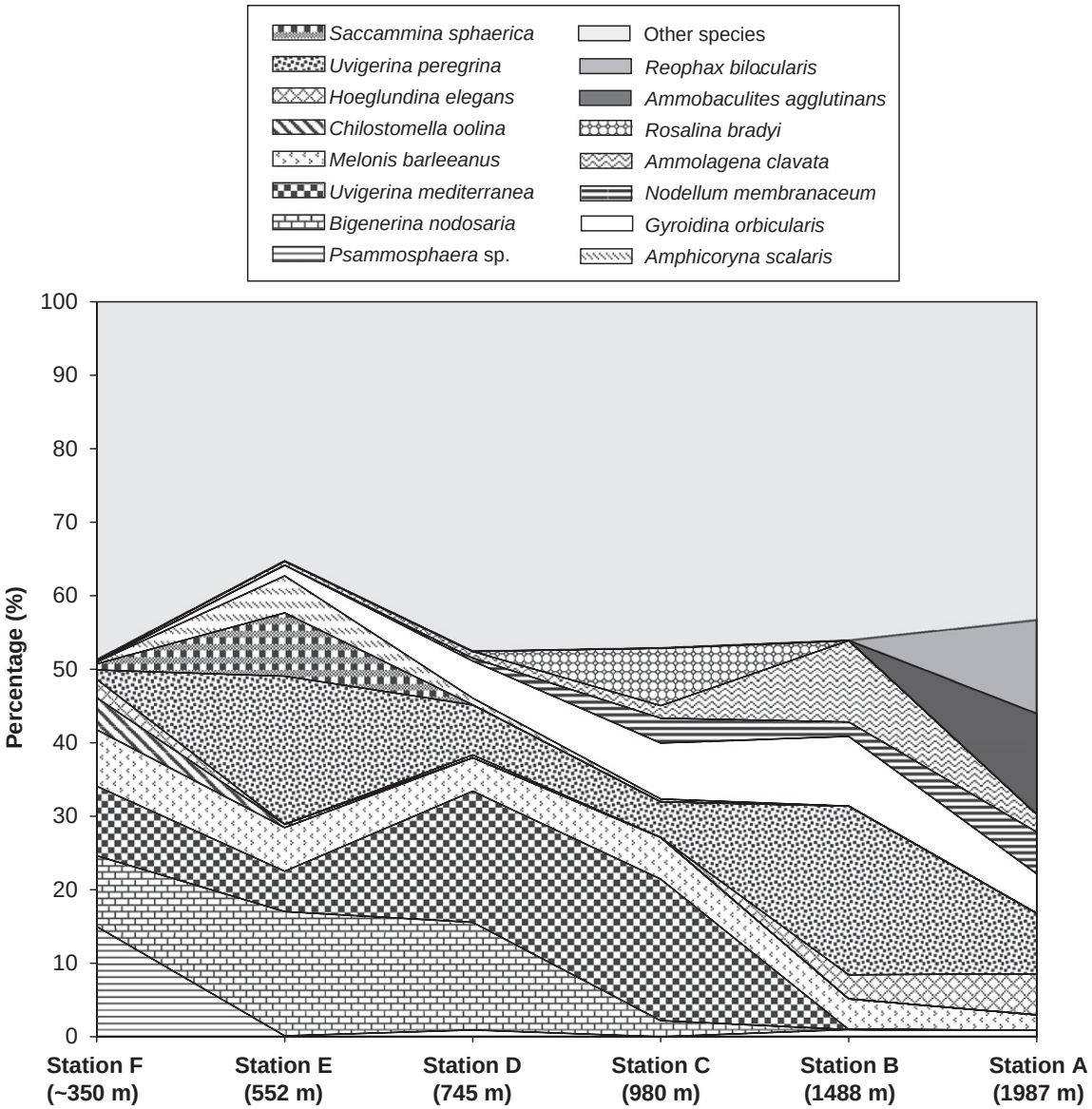

Fig. 10. Percentages of some dominant species (>5%) along our 6-station bathymetric transect. Note that we have also illustrated the relative abundance of *Chilostomella oolina*, although this species is not dominant at our stations. Note also that we plotted the mean percentage values calculated for each station on the basis of the duplicate cores.

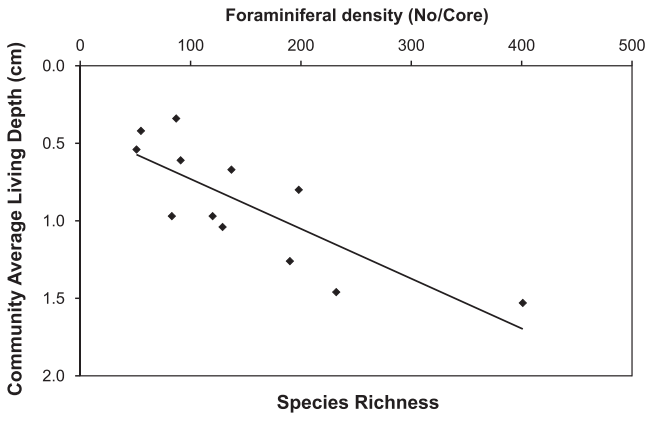

Fig. 11. Average living depth (ALD_{10}) of foraminiferal community versus foraminiferal density for the 12 cores collected at our 6 stations.

able to live on elevated substrate in high-energy environments. Therefore, these authors considered it as a suspension feeder thriving in water masses with relatively elevated current velocities. *R. bradyi* is commonly described as an epiphytic/epilithic taxon living in shelf and upper-slope environments (e.g. Jorissen, 1987; Ferraro and Molisso, 2000). At both of our stations, we recorded representatives of both species attached to various bioclastic fragments in the first half cm interval. This suggests that also in our open-slope environment, these taxa live as suspension feeders at the sediment–water interface.

5. Conclusions

This investigation provides a consistent environmental data set, and its interpretation allows us to investigate

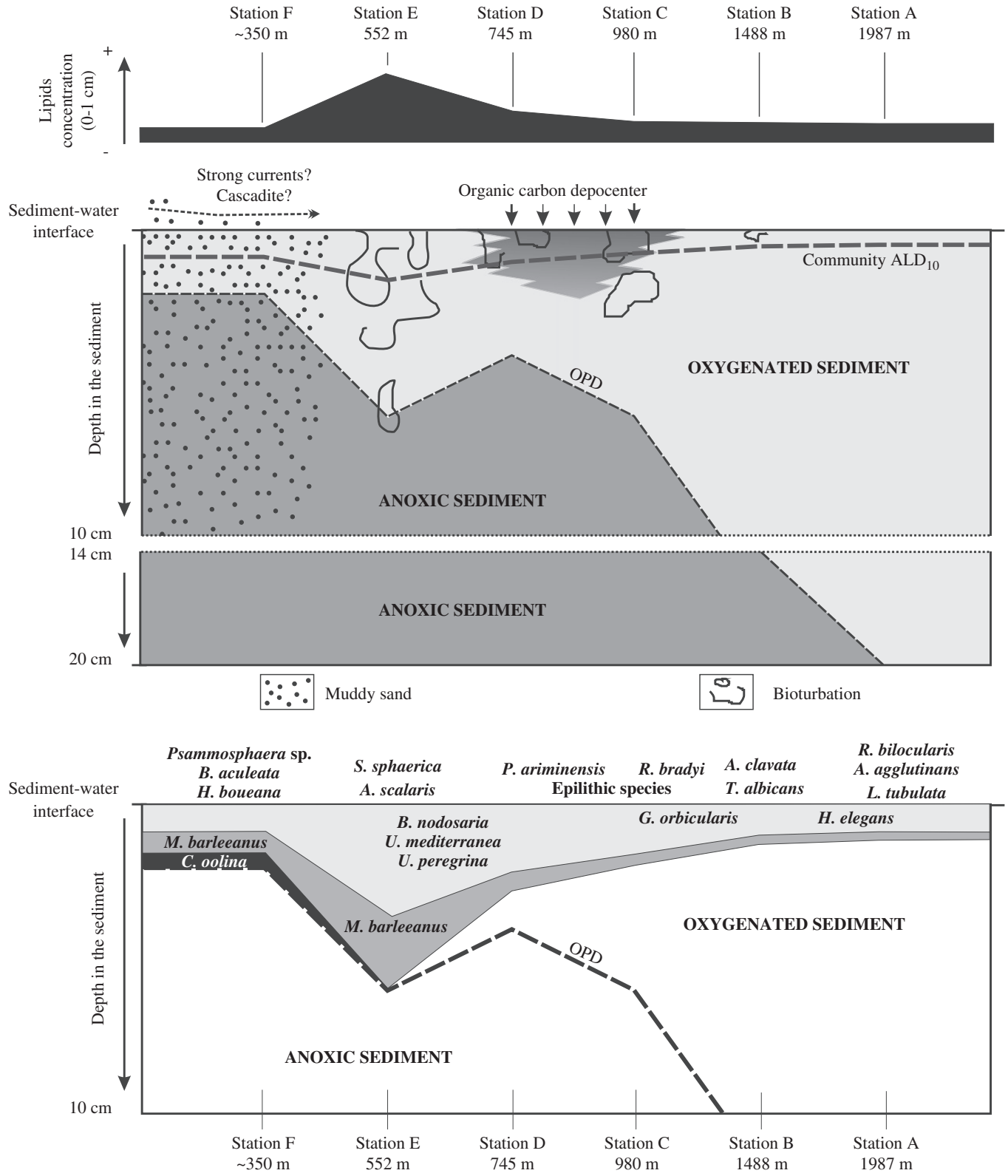

Fig. 12. Synthetic scheme illustrating the changes of (1) the foraminiferal composition and (2) the microhabitat of dominant species along the bathymetric transect. Major physico-chemical parameters are presented in a simplified way in the upper panel: lipid concentration in the upper sediment (0–1 cm), oxygen penetration depth (OPD), bioturbation and hydro-sedimentary processes.

major aspects of ecology of live foraminiferal faunas. All our observations underline the general meso-oligotrophic conditions prevailing on this inter-canyon open slope. All stations are characterized by well-oxygenated bottom waters and the input of low-quality organic matter originating from both marine and continental sources. In

some cases, organic-matter deposition seems partly related to complex hydro-sedimentary processes (sand-bed deposition, suspension or winnowing by strong bottom currents). In other cases, more labile organic compounds (lipids and, in a lesser degree, AAs and sugars) concentrate in the upper sediment. The significant positive correlation coefficients between foraminiferal density, specific richness, microhabitat and lipids concentration in the upper sediment suggest a prominent role of organic-matter quality as a structuring parameter of the foraminiferal community structure.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr.2008.07.003.

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