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The influence of seasonal processes on geochemical profiles and foraminiferal assemblages on the outer shelf of the Bay of Biscay

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Abstract

Benthic foraminifera are widely used tools to reconstruct paleoenvironments. They reflect bottom water oxygen concentrations and organic carbon flux. To increase their accuracy as proxies, seasonal variability of foraminiferal populations from the outer shelf of the Bay of Biscay (150 m water depth) was followed over a 3-year period. The selected area is characterized by seasonal variation in organic matter deposition. A strong interaction between organic detritus input, macrofaunal bioturbational activity, the degree of separation of redox zones and the reproduction, growth and migrational response of benthic foraminifera was found. During periods of high labile organic matter input, as occurs during spring bloom conditions, the redox zonation was not well established. Different organic degradation pathways occurred at the same depth intervals in the sediment. Shallow infaunal species reacted in response to the high nutrient content with rapid growth (*Bolivina subaenariensis*) or reproduction (*Epistominella vitrea, Bolivina seminuda, Bolivina dilatata/spathulata*). Infaunally living foraminifera, *Chilostomella oolina* and to lesser extent *Nonion scaphum*, migrated to the sediment surface in reaction the increase organic matter input to the seafloor. This migration could have been induced by the more intensive overlapping of redox zones that were perhaps better separated vertically in winter. However, this migration could also have been triggered by the occurrence of fresh phytodetritus in the sediment, becoming even available in slightly deeper sediment level due to the increased bioturbation activity.

Keywords: Benthic foraminifera; Seasonal response; Phytoplankton; Microhabitat; Redox zonation; Europe; France; Bay of Biscay

1. Introduction

Foraminifera form a significant part of the benthic fauna in marine environments. Together with bacteria, foraminifera are responsive on short

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time scales (i.e. days/weeks) to any type of pertubation. For example, they are the first meiofaunal group reacting to an increased organic matter input to the sediment surface, which was found by Pfannkuche and Soltwedel (1998) at the Goban Spur in the N.E. Atlantic (135–4500 m water depth). Due to this rapid response, foraminifera show strong seasonal variability in standing stock (Lutze, 1968; Ohga and Kitazato, 1997; Murray and Alve, 2000; Jannink, 2001; Fontanier et al., 2003) and to a lesser degree also in their faunal composition and depth distribution in the sediment (Barmawidjaja et al., 1992; Ohga and Kitazato, 1997, Kitazato et al., 2000, Fontanier et al., 2003). Due to a higher intensity of the seasonal inputs of organic matter in bathyal and shallower systems, fluctuations of foraminiferal faunas are more easily generated in these areas compared to abyssal depths (Gooday and Rathburn, 1999). This current study will contribute to our knowledge of the effect of seasonal organic matter inputs on the foraminiferal standing stock.

In marine sediments the pore water redox stratification has been attributed to organic matter oxidation coupled to a corresponding vertical succesion of microbial respiratory pathways (Froelich et al., 1979). In most areas, a seasonal change in the organic matter input is correlated to a change in the thickness of the oxygenated layer at the surface of the sediment column. A shoaling of the oxygen containing layer may be caused by an increased oxygen demand due to the degradation of organic matter, by seasonal stratification of the water column resulting in lower bottom water oxygen concentrations, or by a combination of these phenomena (Ohga and Kitazato, 1997; Duijnstee, 2001; Hyacinthe et al., 2001; Jannink, 2001).

Such changes in the oxygenated zone will subsequently trigger changes in deeper redox zones. Due to the coupling of redox processes and bacterial activities the changes in redox conditions will induce changes in bacterial occurrences and activities in these deeper redox zones as well (Laanbroek, 1990; Koretsky et al., 2005). In horizontally heterogeneous sediment columns, which may be due to macrofaunal burrows, a three-dimensional mosaic of temporally and spatially fluctuating redox environments may occur. These conditions may lead to the co-existance of multiple organic carbon degradation pathways in specific sediment intervals (Canfield and Des Marais, 1991; Koretsky et al., 2005).

These redox patterns and their corresponding bacterial processes have been suggested to influence microhabitat selection by foraminifera (Jorissen et al., 1998; Van der Zwaan et al., 1999; Fontanier et al., 2002). However, at an upper slope station in the Bay of Biscay, the variability of the organic matter flux to the sediment surface over the year seems to be too low in comparison with the stock of labile organic matter present in the upper sediment to induce significant fluctuations of the early diagenetic processes in the upper sediment over the year (Fontanier et al., 2003). These authors suggest that foraminiferal migration and reproductive behaviour in this area is independant of redox gradients but should rather be triggered by changes in the trophic conditions (i.e. the presence of bacterial pools; quantity and quality of organic remains). Infaunally living species were found to migrate to the sediment surface in reaction to an increased phytodetritus event (Fontanier et al., 2003). This phenomenon was earlier described for infaunal species by Barmawidjaja et al. (1992) and Kitazato et al. (2000).

Several experimental designs have been employed in attempts to separate the effects of shifts in redox zonation and food supply on foraminiferal microhabitat distribution. Some experiments have focussed on the effect of shifts in redox zonation (Moodley and Hess, 1992; Alve and Bernhard, 1995; Boom and Rutten, 1997; Rutten and Boom, 1997; Moodley et al., 1997, 1998; Duijnstee, 2001; Ernst, 2002; Geslin et al., 2004), whereas other studies concentrated on the effect of a changing food input (Heinz et al., 2001, 2002; Jannink, 2001). Ernst (2002) studied the effect of both redox shifts and food supply. Results obtained from these experiments are not conclusive. Although most studies suggest that oxygen depletion is the most important regulating factor for the vertical migration of foraminifera (Duijnstee, 2001; Ernst, 2002; Geslin et al., 2004), the results on experimental food addition were less straightforward. While enhanced reproduction is reported in all studies (Jannink, 2001; Heinz et al., 2001, 2002; Ernst, 2002) the outcome differed considerably with respect to the number of species that react to the food impulse. The study of Ernst (2002) suggested that the combination of food and oxygen is important. In his study, some species better survived prolonged periods of anoxia when high doses of food were present. These results may indicate the interdependency of several factors controlling foraminiferal survival and activity. Heinz et al. (2002) showed that when different types of food particles were presented, the reaction differed between taxa. This outcome was confirmed by results obtained by Suhr et al. (2003) who showed that different foraminiferal species have different feeding strategies, and consequently, may have different nutritional values for other organisms. Therefore, not only the quantity, but also the quality of the organic matter serving as food for the foraminifera appears to have a large impact on foraminiferal ecology.

The outcome of experiments as described above is important. Foraminifera are increasingly used as tools for paleo-reconstructions, not only as proxies on paleotemperature, but also with respect to bottom water oxygen concentrations and organic matter flux (Van der Zwaan et al., 1999). The proxy value of foraminifera strongly depends on an accurate knowledge of their ecology. Increased knowledge of the food requirements of specific species of foraminifera is essential, since it may enable us to use these highly responsive micro-organisms to precisely study temperal variability of present and past marine ecosystems.

In this study, temporal variation of foraminiferal assemblages was followed over a 3-year period at an outer shelf station in the Bay of Biscay. One of the aims of this research is to precisely study the effect of organic matter on the redox zonation and the effect both have on foraminiferal migration within the sediment.

In two earlier papers, the results of similar studies obtained for 550 and 1000 m deep upper slope stations are presented (Fontanier et al., 2003, 2005). Although the succession of redox zones was surprisingly stable over the studied period, the foraminiferal faunas showed important fluctuations of density and composition over time. The two upper slope stations studied by Fontanier et al. (2003, in press) are situated in a mesotrophic context, whereas our outer shelf station is much closer to the coast and experiences a much higher organic input (Hyacinthe et al., 2001; Fontanier et al., 2002). As a consequence, the succession of redox zones at our station is much more compressed, and the seafloor is inhabited by an entirely different set of benthic foraminiferal species. In this paper, we will investigate whether the responses to seasonal and interannual variability in our eutrophic outer shelf context follow the same patterns as those observed at the earlier described upper slope.

2. Material and methods

2.1. Setting

The station sampled for this study is located at the outer shelf, in the Bay of Biscay (France) at 150 m water depth (43°42′93″N, 1°43′10″W) (Fig. 1). This station is referred to as station D. The Bay of Biscay is a semi-enclosed basin characterised by a relatively homogeneous water mass. Circulation in the upper water mass (0–500 m) seems to be disconnected from the North Atlantic current and is generally weak (Tréguer et al., 1979). The station at 150 m water depth is just at the diffusive boundary between the surface waters, characterised by seasonal variations in mixing, thermocline depth and continental runoff, and sub-surface waters (Tréguer et al., 1979). According to Henaf (1973) an isohaline boundary exists between the coastal and oceanic water, and exchange between these two seems to be of little importance. At station D bottom water temperature (11.9 °C) and salinity (35.6) are constant throughout the year (Ogawa and Tauzin, 1973).

Vertical mixing is induced by wind and waves, while internal waves in the vicinity of the shelf break may strongly enhance mixing across the thermocline. Stratification of the water layers is well established in early June and deepens until September (Wollast and Chou, 2001). In autumn a still pronounced thermocline separates two water masses in which nutrients are regenerated from organic matter degradation. During winter, under the action of winds, the mixed layer starts to deepen due to increased wave action; progressive enrichment of nutrients is observed in the superficial waters (Tréguer et al., 1979).

In the southern part of the Bay of Biscay chlorophyll-*a* values were found to be highest in March, April, September and October (Fernandez and Bode, 1991). Prymnesiophytes are present throughout the year and often the dominating group of phytoplankton (Wollast and Chou, 2001). The prymnesiophytes are mainly composed of coccolithophores which exhibit a seasonal succession (Beaufort and Heussner, 1999; Lampert, 2001). During spring bloom, however, diatoms are most abundant (Lampert, 2001; Wollast and Chou, 2001). The spring bloom leads to rapid phytoplankton growth, and exhaustion of silicon may occur rapidly. By wind action silicon is re-supplied to the surface layer, leading to a pulse-like bloom period,

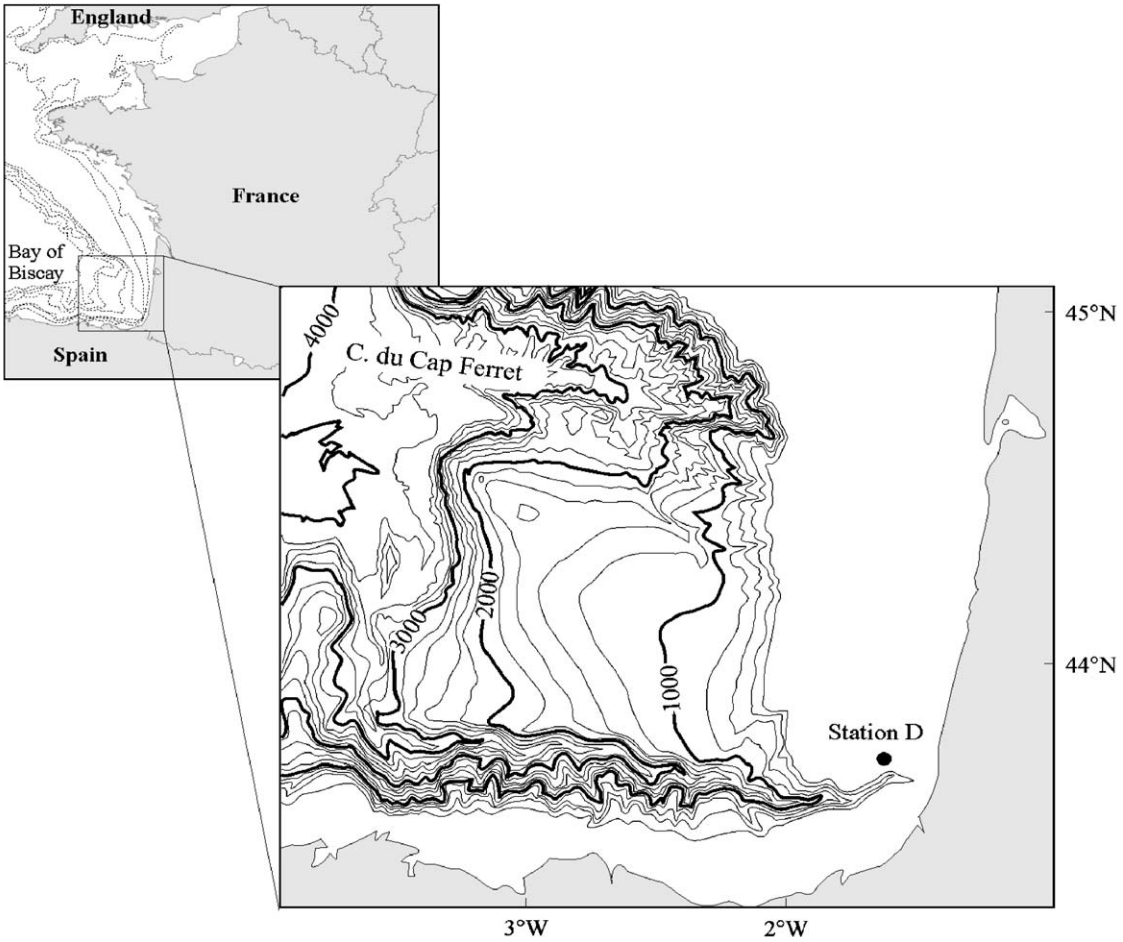


Fig. 1. Sample area 43°41′93N, 1°43′10W.

in which the individual peaks in phytoplankton growth last only a few days (Tréguer et al., 1979). During spring and throughout summer the photic layer is depleted in nutrients due to phytoplankton uptake (Tréguer et al., 1979).

Due to this lack of nutrients in the surface water during summer, the highest chlorophyll-*a* concentrations were found deeper at 30–40 m. Minor upwelling events have been observed in summer (Froidefond et al., 1996). The upwelling results in large coccolithophores blooms (Holligan et al., 1983; Fernandez et al., 1993; Beaufort and Heussner, 1999).

An autumn bloom was described at the BIOTRANS site in the North Atlantic Ocean, northwest of the sample area, to occur at a depth of 30–50 m in 1998. This bloom was mainly composed of autotrophic dinoflagellates, with smaller amounts of diatoms (Sellmer et al., 1998).

The study site is situated about 50 km north of the Adour and 250 km south of the Gironde rivers. The Gironde had an average yearly flux of 1.100 m^3s^{-1} over the years 1990–1997 (Schäfer et al., 2002). A seasonal increase occurs in the flux of this river. For the Gironde a maximum of ~5000 m^3s^{-1} was found in February 1998 and a minimum of ~100 m^3s^{-1} in the summer months of 1998. During spring, the flux was ~3,250 m^3s^{-1} in 1999. The increased run-off of this river in spring and autumn might also lead to an increase of nutrients in the water. Normally, the impact of the Gironde river on the study area is probably minor since in the absence of wind the Gironde plume flows northwards along the coast. However, the prevailing wind direction may drastically influence the spreading of the plume (Froidefond et al., 2002, and references therein). The Adour river has a mean discharge of 350 m^3s^{-1} (Brunet and Astin, 1999). Although little is know about the interannual variation of the discharge of the Adour river, as other rivers it is expected to show seasonal variability in flux (Coynel et al., 2005). Due to the overall northward-directed currents in the southern part of the Bay of Biscay, the Adour river as well as the small mountainous rivers in the Pyrenean area are important contributors to the total suspended matter input by rivers. According to Maneux et al. (1999), these coastal rivers are together responsible for 52% of the total suspended load into the coastal zone.

The organic matter is characterised by its high degradability at all depths and is intensely decomposed after arrival at the seafloor. Almost no organic carbon is preserved in the shelf sediments (0.1 g cm^{-2} y^{-1}) (Wollast and Chou, 2001; Duchemin et al., 2005). Profiles of ^{210}Pb and C_{org}, together with the observation of burrows indicate that the sediments are strongly bioturbated down to a depth of 30 cm (Hyacinthe et al., 2001).

2.2. Sampling

The station was sampled nine times in the period between October 1997 and June 1999. With a few exceptions due to bad weather, the station was sampled every 2 or 3 months over that period. Two more samples were taken in April 2000, and in April 2001. The exact dates of sampling are listed in Table 1. Cores were sampled with a classical Barnett multi-tube corer (Barnett et al., 1984); each tube had a surface area of 72 cm^2 (diameter: 9.6 cm).

2.3. Geochemistry

Bottom waters derived from the multi-tube cores were collected as soon as possible in order to measure dissolved oxygen using the Winkler titration method (Strickland and Parson, 1972). On board cores were kept at in situ temperature to measure the pore-water oxygen concentration. This was done with a cathode type mini-electrode (Revsbech, 1983; Helder and Bakker, 1985; Revsbech and Jørgensen, 1986). These analyses were duplicated and finished within half an hour after sampling. For further analyses, the cores were sliced in 0.5 cm slices (for the top 2 cm of the sediment column), 1 cm for the intermediate depth and still deeper in slices of 2 cm, all within 1 h of the oxygen measurements.

From each individual slice, a subsample was immediately sealed in a pre-weighed vial, flushed with N_2 and frozen for analyses of porosity and chemistry of the solid fraction. Another subsample was taken to analyse the pore water. These samples were flushed with N_2 and centrifuged (5000 rpm, 20 min). Interstitial water compounds were analysed by techniques adapted for small volumes (Anschutz et al., 1999). An aliquot was filtered and acidified with ultrapur HNO_3 for dissolved Fe and Mn analysis (Hyacinthe et al., 2001). Nitrate and nitrite were measured by flow injection analysis (FIA; Anderson, 1979).

Table 1
Exact dates of samplemoments

Sample name	Date
October 1997	26
January 1998	30
June 1998	08
July 1998	23
October 1998	17
December 1998	08
January 1999	23
April 1999	19
June 1999	24
April 2000	25
April 2001	18

2.4. Primary production

For analysis of primary production, satellite images recorded by the SEAWiFS satellite were used. Chlorophyll-*a* concentration maps created from these images are published online by the Joint Research Center (European Commission). From these maps chlorophyll-*a* concentrations were extracted. Unfortunately remote sensing data on chlorophyll-*a* concentration can not be used straightforward in shallow water environments as the reflectance is caused by chlorophyll-*a* and by suspended matter. Satellite images from deeper-water areas are much more reliable as less suspended matter is present there. Therefore SeaWiFS data of the deep-sea area of the Bay of Biscay (550 and 1000 m water depth) were used to study the variation in chlorophyll-*a* throughout the sample period (Fontanier et al., 2003, 2005).

2.5. Foraminifera

For foraminiferal analyses, a core was sliced in 0.25 cm slices for the top centimeter, 0.5 cm slices for the 1–4 cm interval and 1 cm slices from 4 to 10 cm. In April 2000 and April 2001 duplicate cores were analysed for foraminiferal numbers. In each case, a large sea-urchin was found in one of the cores. Since those cores may have been strongly influenced by bioturbation, they were not used for the study of temperal variability of the foraminiferal fauna. The slices of sediment were stored in bottles (500 cm^3) filled with a mixture of ethanol (95%) and Rose Bengal stain (1 gl^{-1}). In order to get a homogeneous mixture, samples were gently but well shaken and stored. Before analysis, samples were sieved over 150 and 63 μm meshes. The two fraction sizes were stored in 95% ethanol until microscopic analysis, providing this was done within a month after sieving. Otherwise, the samples were dried.

Microscopical analysis was performed in an ethanol–water mixture (50%). Only foraminifera with a clear pink or red colour were counted as living. Foraminifera larger than 150 μm were collected from the total sediment interval down to 10 cm depth. For the size fraction 63–150 μm only the fauna of a core sampled in January 1999 was analysed to a depth of 10 cm. In the case of all the other cores, only the top cm was studied. Numbers were standardised to a volume of 50 cm^3.

The average living depth is used to define migrational patterns, it is calculated as follows (after Jorissen et al., 1995):

$$ALD_X = 1/n_j \sum n_{ij} d_{ij},$$

where x = lower boundary of deepest sample, j = species, i = class interval, d_i = mean depth of class i and n is total number of the species j.

To summarize the most important (i.e. defining) patterns in the assemblage, a larger number of relatively abundant taxa was included in a principal component analysis, without log-transformation, using Canoco (version 4.0, Ter Braak and Smilhauer, 1998). To obtain information on the abundance of individual species as well as their contribution to the total population we employed absolute densities as well as relative abundances (percentage data). In order to distinguish between seasons, each core was given a score of 1 for the season in which it was sampled, and a score of zero for the other three seasons. These scores were added independently of the data in the PCA diagram. The species used in the analyses were selected by listing the 15 most abundant species at each sampling event. All species that were found to be among the most abundant species during at least two sample events were entered in the analysis.

Since our data from the smaller size fraction are restricted to the top cm layer, for both size fractions only samples from this interval were included. Such a focussing on the fauna in the topmost centimeter seems judicious since several papers (Gooday, 1996; Pfannkuche and Soltwedel, 1998; Rathburn et al., 2001; Fontanier et al., 2003) suggest that responses to seasonal variability of phytodetritus input are mainly taking place in the topmost centimeter of the sediment.

3. Results

3.1. Geochemistry

All geochemical data are presented in Fig. 2. The results show that bottom water oxygen concentrations were relatively stable throughout the year. Also, the depth distribution of oxygen in the sediment was fairly constant, and reached in most cores a depth of 5 mm. In some cases oxygen was found slightly deeper, such as in October 1997 and October 1998 where it was present down to about 8 mm. At other times it was found slightly shallower, such as in April 1999, June 1999, April 2000 and April 2001 when only the top 3–4 mm contained free oxygen. However, these differences over time were rather small.

In nearly all cores nitrate and nitrite concentrations were found to be highest at the sediment surface. Only in January 1999 was the concentration of nitrate and nitrite highest just below the sediment surface.

Deeper in the sediment, an increase in dissolved iron (Fe^{2+}) and manganese (Mn^{2+}) was observed. The available results are shown in Fig. 2. In October 1998, December 1998, April 1999 and June 1999, the highest Fe^{2+} concentration was found to co-occur with the highest Mn^{2+} concentration. In January 1999, and April 2000 the highest Fe^{2+} concentration occurred somewhat deeper in the sediment than the highest Mn^{2+} concentration. In July 1998 and April 2001, the patterns were not so clear. In July 1998, the highest Fe^{2+} concentration was found deeper in the sediment than the highest Mn^{2+} concentration, but the Fe^{2+} concentration was also relatively high at shallow depths (0.5–2 cm). In April 2001, both Fe^{2+} and Mn^{2+} concentrations were relatively high from 4.5 to 10 cm. However, the increase in Fe^{2+} started at 2 cm depth, whereas the increase in Mn^{2+} started at the sediment surface.

Summarising the geochemical results, we can conclude that the distribution of redox species follows approximately the well-established depth sequence of diagenetic reactions governed by the preferential use of the electron acceptor that yields the highest amount of free energy for the bacterially mediated oxidation of organic matter. Oxygen is reduced near the sediment–water interface, followed by the reduction of nitrate and manganese oxide, then reactive iron oxide, which produce dissolved iron (Fe^{2+}) and manganese (Mn^{2+}) observed in the vertical profiles (Froelich et al., 1979, Postma and Jakobsen, 1996). However, at station D, where the relative positions of reducing and oxidising sediment components was influenced by strong bioturbation (Hyacinthe et al., 2001), the time sequence of redox reactions does not always translate to a similarly recognisable depth sequence. The bioturbated sediment can be thought of as an environment where the distribution of oxidants and reductants

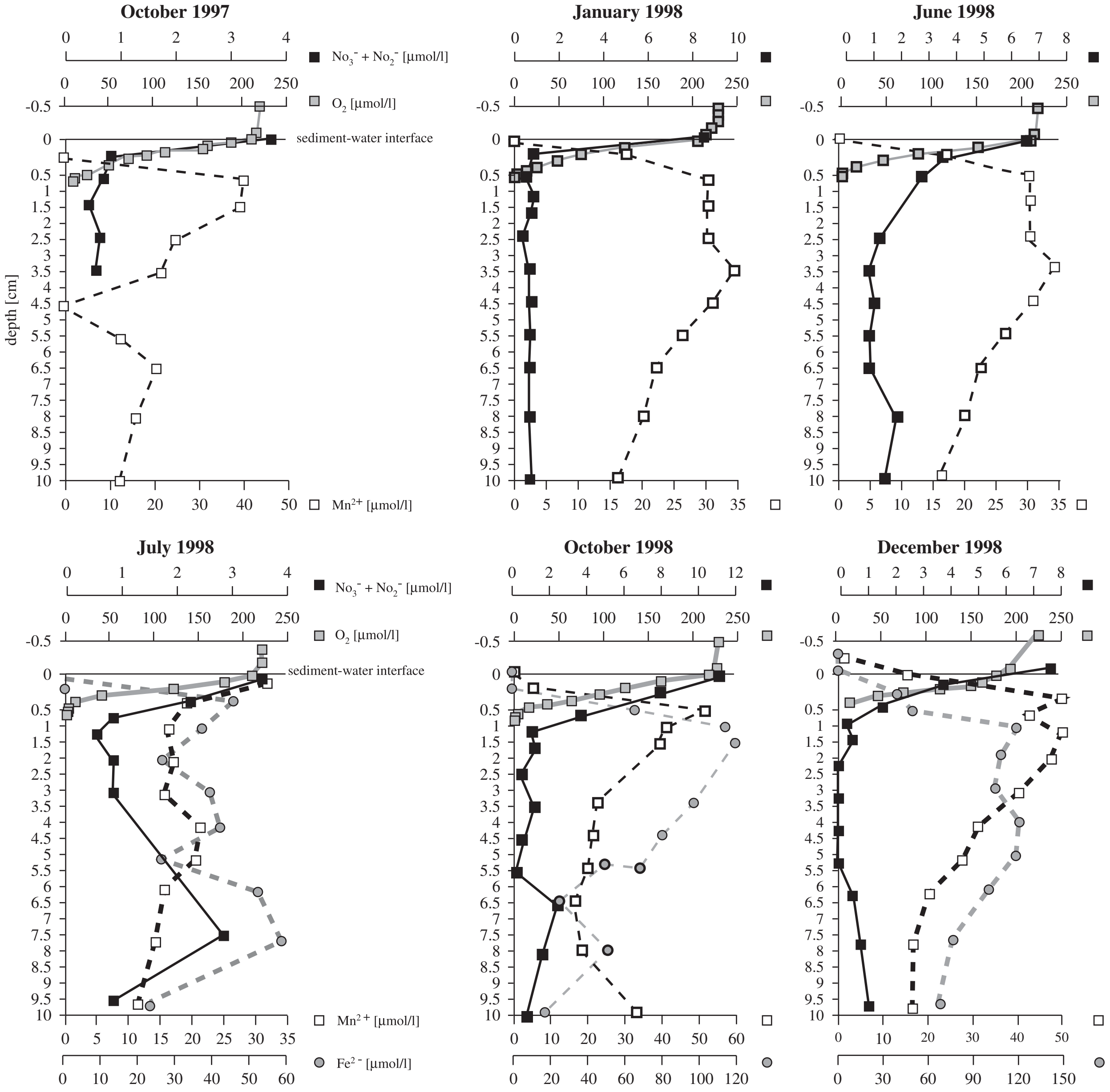


Fig. 2. Composite figure showing porewater conditions (summed Nitrate (NO_3^-) and Nitrite (NO_2^-), disolved manganese (Mn^{2+}) and dissolved iron (Fe^{2+})) as far as available.

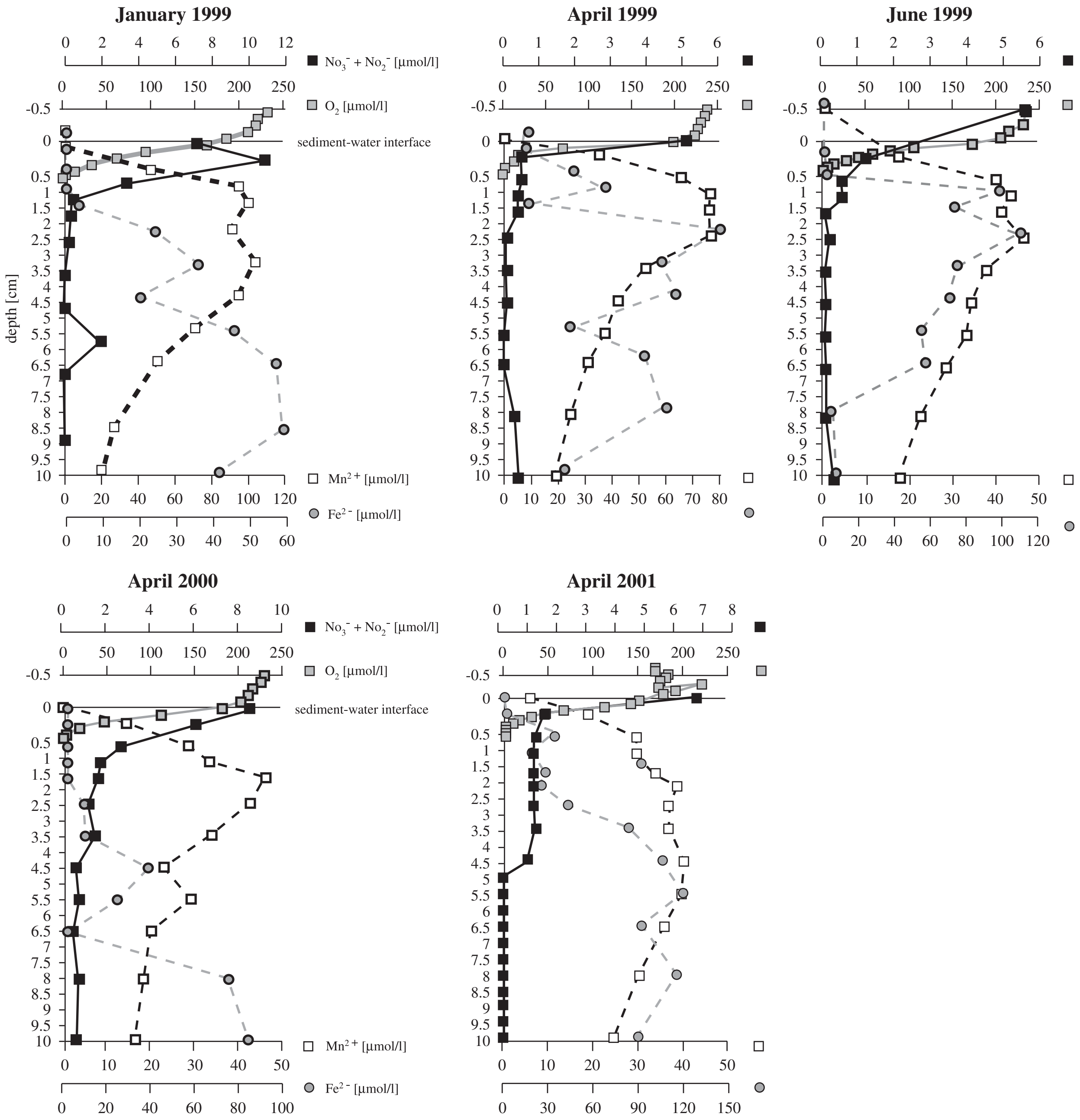


Fig. 2. (*Continued*)

evolves towards a steady state, without necessarily achieving it before the next event disrupts the process. Vertical profiles of redox species are therefore likely to represent a transient state rather than a steady state. The changes with time of vertical profiles observed at station D illustrate the dynamic nature of diagenesis in bioturbated sediments, as thoroughly described by Hyacinthe et al. (2001). With the exception of January 1999, denitrification was observed in the superficial sediment interval, where oxic degradation occurs. For the deeper redox zones, a well-established vertical zonation, with iron reduction positioned below manganese reduction, was only found in the months January 1999 and April 2000. It should be noted, however, that for manganese and iron data are not available for all months. January 1999 is the only sampling event were a consistent succession of redox zones occurred with depth.

3.2. Primary production

Sea surface chlorophyll-*a* concentrations measured at stations located where the water depths are 1000 and 550 m are shown in Fig. 3. The patterns at the two stations are similar, although values are slightly different. Because the chlorophyll-*a* concentrations at the deeper stations are similar, we believe that this pattern can be extrapolated to our station at 150 m. For the period September 1997 until December 2001, four clear peaks in Chlorophyll-*a* were found, in March/April 1998, March 1999, March 2000 and March 2001. In the years 1999 and 2001 a secondary chlorophyll-*a* peak was found in May/June. In 2000 this secondary peak was found in June, which was even more pronounced than the primary peak of April 2000.

3.3. Foraminiferal densities

The absolute number of foraminifera found at each sample event is given in Fig. 4. For the $>150\,\mu$m fraction the total number of foraminifera found in the 10 cm deep sediment core, with a surface area of 72 cm^2, is shown. For the 63–150 μm fraction the total number of foraminifera in the first centimeter of sediment is shown, also for a surface of 72 m^2. Generally, the number of foraminifera was much higher in the smaller size fraction. Total foraminiferal densities ($>150\,\mu$m) varied from ~800 to ~3050 specimens per 72 cm^2, 10 cm deep core, and from ~300 to ~12,400 individuals in the topmost cm of 72 cm^2 cores in the 63–150 μm fraction. In both size fractions maximum numbers were found for the months June 1999 and April 2001.

Total densities differed between months, and were for all cores positioned in one of the upper three sediment intervals (Fig. 5, left-hand column). The highest densities were found in April 2001 (0–0.25 cm: ~4000 individuals per 50 cm^3), June 1999 (0–0.25 cm: ~2500/50 cm^3) and April 2000 (0–0.25 cm: ~2000/50 cm^3). Lowest maximal densities, between 500 and 700 specimens per 50 cm^3, were found in January, June, July, October and December 1998; in July and October in the topmost interval, and in the other 3 months in the second or third sediment interval. In October 1997, January 1999 and April 1999 intermediate maximal densities (between 900 and 1600 individuals per 50 cm^3) were found in one of the two topmost sediment layers.

The maximum densities in June 1999, April 2000 and April 2001 were mostly caused by a strong peak in the number of specimens in the 0–0.25 cm layer, and to a lesser extent in the 0.25–0.5 cm and deeper layers. Spring maxima were mainly due to very high densities of *Bolivina subaenariensis* in the topmost sediment layer. The higher numbers of specimens in the $>150\,\mu$m fraction found in October 1997, October 1998, June 1999, and January 1999, on the contrary, were not due to *Bolivina subaenariensis* but rather to a relatively high number of specimens of both *Valvulineria bradyana* and *Chilostomella oolina*.

Densities for individual species in the size fraction $>150\,\mu$m, given as numbers per 50 cm^3 for each depth level, are shown in Fig. 5 (centre column). The four most important species, *B. subaenariensis*, *V. bradyana*, *Nonion scaphum* and *C. oolina*, that always represented more than 75% of the total population, are shown separately. All other species are lumped together in the ‘rest’ group, which includes *Bulimina marginata*, *Cassidulina carinata*, *Clavulina cylindrica*, *Nouria polymorphinoides* and *Uvigerina peregrina*.

B. subaenariensis bloomed in the topmost sediment interval in April 2001 (~2000 specimens per 50 cm^3), April 2000 (~1500/50 cm^3) and June 1999 (~900/50 cm^3) whereas it was present in much lower densities in October 1997 (~50/50 cm^3), January 1999 (~30/50 cm^3) and December 1998 (~20/50 cm^3).

In June 1999, all specimens of *B. subaenariensis* were inconclusively stained and important parts of the tests were not filled by protoplasm. Since those inconclusively stained specimens probably died in the weeks or month(s) prior to sampling (Corliss and Emerson, 1990), they are indicative of the presence of a rich living fauna earlier in spring. Even if those inconclusively stained specimens were probably dead at the time of sampling, we nevertheless decided to retain them in our analyses, in order to represent these rich spring faunas. They are therefore included in Fig. 5.

The maximal density of *V. bradyana*, also consistently situated in the topmost 0.5 cm, varied in most cores from 50 to 250 individuals per 50 cm^3. Highest densities were observed in January 1999 (~850/50 cm^3 at 0.25–0.5 cm), October 1997 (~450/50 cm^3 at 0–0.35 cm) and June 1999 (~400/50 cm^3 at

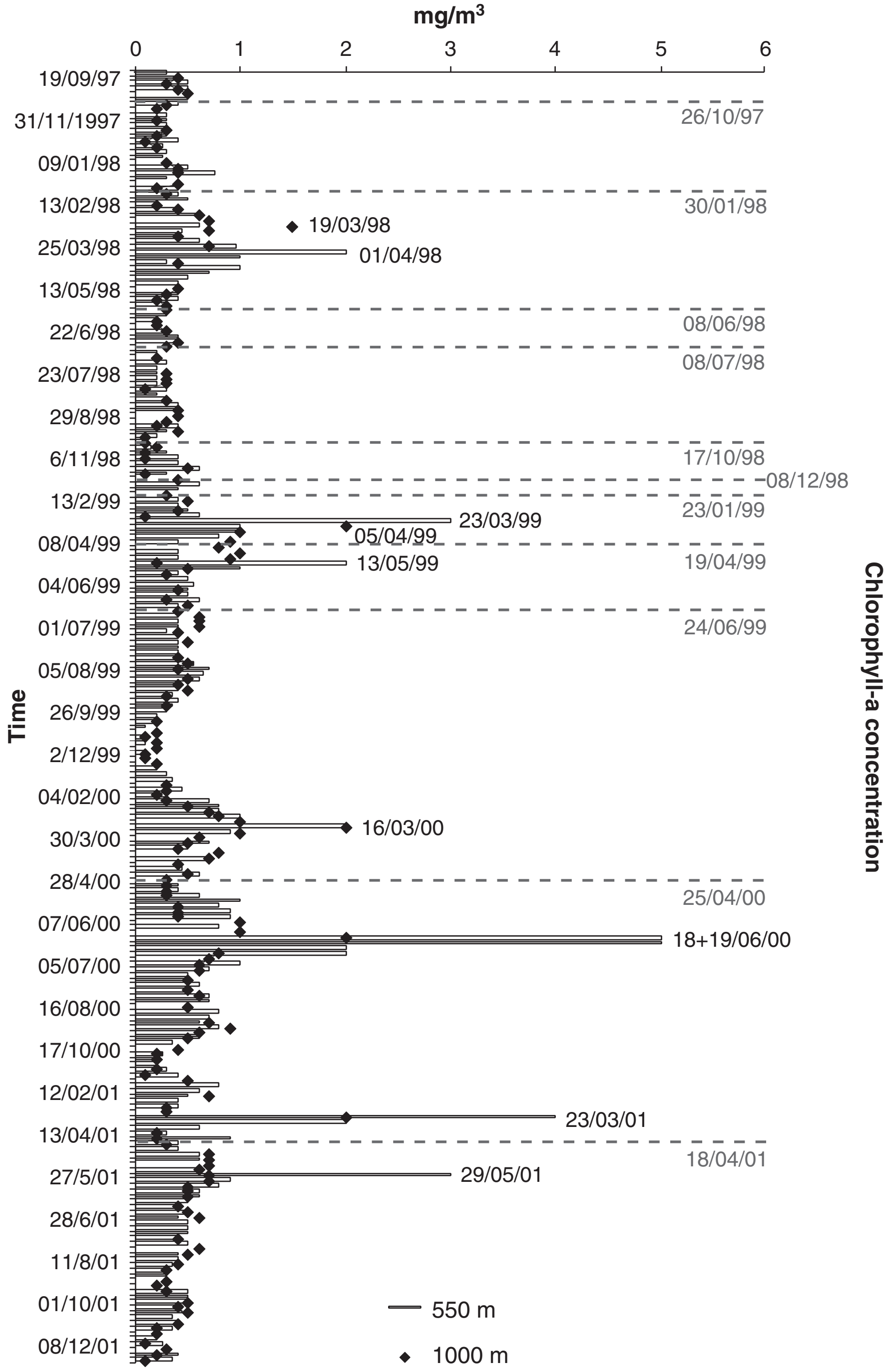


Fig. 3. Sea surface chlorophyll-*a* concentrations, as measured from satellite images. Dashed lines indicate sampling events.

0–0.5 cm). Other taxa living in the upper sediment layers had either maximal densities in April 2001 (*B. marginata* ~250/50 cm^3 and *C. carinata* ~200/50 cm^3, both at 0–0.25 cm), or in October 1997 (*C. cylindrica* ~500/50 cm^3 at 0–0.35 cm), or in October 1998 (*U. peregrina* ~100/50 cm^3).

Since the number of foraminifera is maximal in the top sediment layers, the trends in deeper sediment layers are rather obscured in the left-hand column of Fig. 5, and therefore we added separate figures for the two most abundant intermediate to deep infaunal species in the >150 μm fraction,

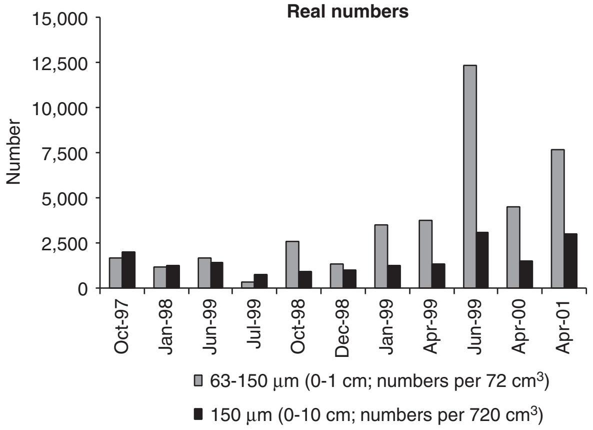


Fig. 4. Total foraminiferal numbers (unstandardised) in two size fractions. For the 63–150 µm size fraction the numbers are summed over 0–1 cm sediment depth, and for the size fraction $>150\,\mu m$ the number are summed over 0–10 cm sediment depth.

N. scaphum and *C. oolina* (Fig. 5, centre column). Both show a rather similar depth distribution pattern, with a continuous presence from the top down to five centimetre depth, except for October 1998 when *N. scaphum* is absent in the first centimeter, and resided much deeper in the sediment than *C. oolina*. A similar pattern, with *N. scaphum* penetrating much deeper into the sediment than *C. oolina*, is found in June 1999.

Highest densities of *C. oolina* were found in October 1997 ($\sim 300/50\,cm^3$ in the 0.35–0.75 cm layer), in June 1998 ($\sim 225/50\,cm^3$ at 0.5–0.75 cm) and in January 1998 ($\sim 200/50\,cm^3$ at 0.5–0.75 cm). For *N. scaphum* highest densities were found in April 2001, with about 350 individuals per $50\,cm^3$ in the top 0.25 cm. In all other cores the maximum density of *N. scaphum* specimens occurred deeper in the sediment; a maximum value of $\sim 300/50\,cm^3$ was observed in June 1999 at 0.75–1 cm depth.

The average living depth (ALD) of *N. scaphum* and *C. oolina* is shown in Fig. 5e. This figure shows that both species reside rather deep in January 1999. In this month *N. scaphum* has an average living depth of 4.11 cm, and the average living depth of *C. oolina* is 3.13 cm. *C. oolina* has a shallower average living depth in all other months, whereas *N. scaphum* is found deepest in October 1998 with an average living depth of 4.30 cm. *N. scaphum* is also found relatively deep in June 1999 and April 2000, with average living depths of respectively, 2.8 and 2.66 cm. The shallowest average living depths of *C. oolina* are found in June 1998 (0.97 cm), July 1998 (0.93 cm), June 1999 (1.09 cm) and April 2000 (0.63 cm). For *N. scaphum*, shallowest average living depths are found in June 1999 (1.68 cm), July 1998 (1.67 cm), April 1999 (1.68 cm) and April 2001 (1.59 cm). Also *Nouria polymorphinoides* occurred slightly deeper in the sediment; a highest maximal density of $\sim 100/50\,cm^3$ was found in April 2001 at 0.25–0.75 cm (see Appendix 2).

The densities of the main species occurring in the 63–150 µm size fraction are shown in Fig. 5, right-hand column. Five abundant species, *Bolivina dilatata/spathulata*, *Bolivina seminuda*, *Bolivina subaenariensis*, *Bulimina marginata/aculeata* and *Epistominella vitrea*, that always represent more than 50% of the total population, are shown separately. All other species are lumped together in the 'rest' group. Only the core sampled in January 1999 was studied down to 10 cm depth. The results (Appendix 1) show that a very large part of the population (~80%) lived in the upper centimeter of sediment; the number of specimens found deeper than 1 cm in the sediment is very small in comparison to the numbers found in the topmost cm. In all other months the population inventoried in the 0–1 cm level lived predominantly in the top half cm of the sediment. Therefore, we decided to limit the study of all other cores to the topmost centimeter.

In this small size fraction, highest maximal densities were found in the topmost level in June 1999 ($\sim 15{,}000/50\,cm^3$) and April 2001 ($\sim 12{,}500/50\,cm^3$). The density maxima were, as in the $>150\,\mu m$ fraction, predominantly caused by an increase of foraminiferal numbers in the uppermost half cm of the sediment.

At all sampling times, *B. subaenariensis* was the most frequent taxon. In all cores sampled in autumn, winter and in April 1999 and April 2000, it accounts for 60–80% of the total assemblage. In these months it is accompanied by relatively small populations of *Bulimina marginata/aculeata* and *Textularia porrecta*. In all June and July samples, as well as in April 2001, *B. subaenariensis* accounted only for 30–40% of the fauna. Although the overall faunal density was much higher in June 1999 and April 2001 than in all other months (Fig. 5), the absolute density (4000–5000 specimens per $50\,cm^3$) of *B. subaenariensis* was similar to that observed in January 1999, April 1999 and April 2000. Therefore, the extremely high faunal densities of June 1999 and April 2001 were caused by a strong frequency increase of other taxa. The most conspicuous one was *E. vitrea*, found in the topmost

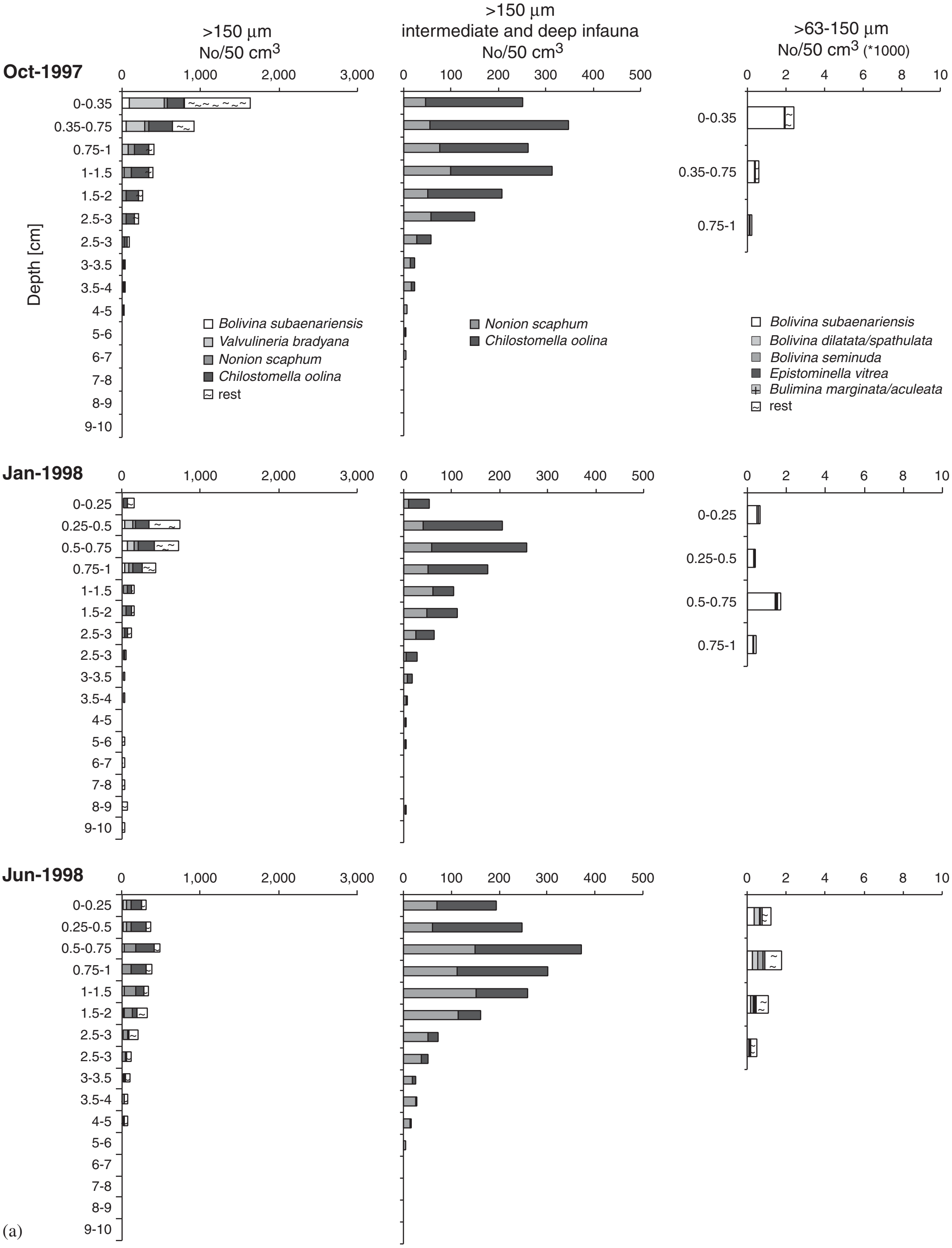


Fig. 5. Depth profiles of the most abundant species. Numbers are standardized for 50 cm^3. The left-hand column shows total abundance, the middle column shows the abundance of the two intermediate to deep infaunal foraminifera, *Nonion scaphum* and *Chilostomella oolina*, and the right-hand column shows the abundance of the 63–150 μm fraction. (e) shows the Average Living Depth (ALD) of *Nonion scaphum* and *C. oolina*.

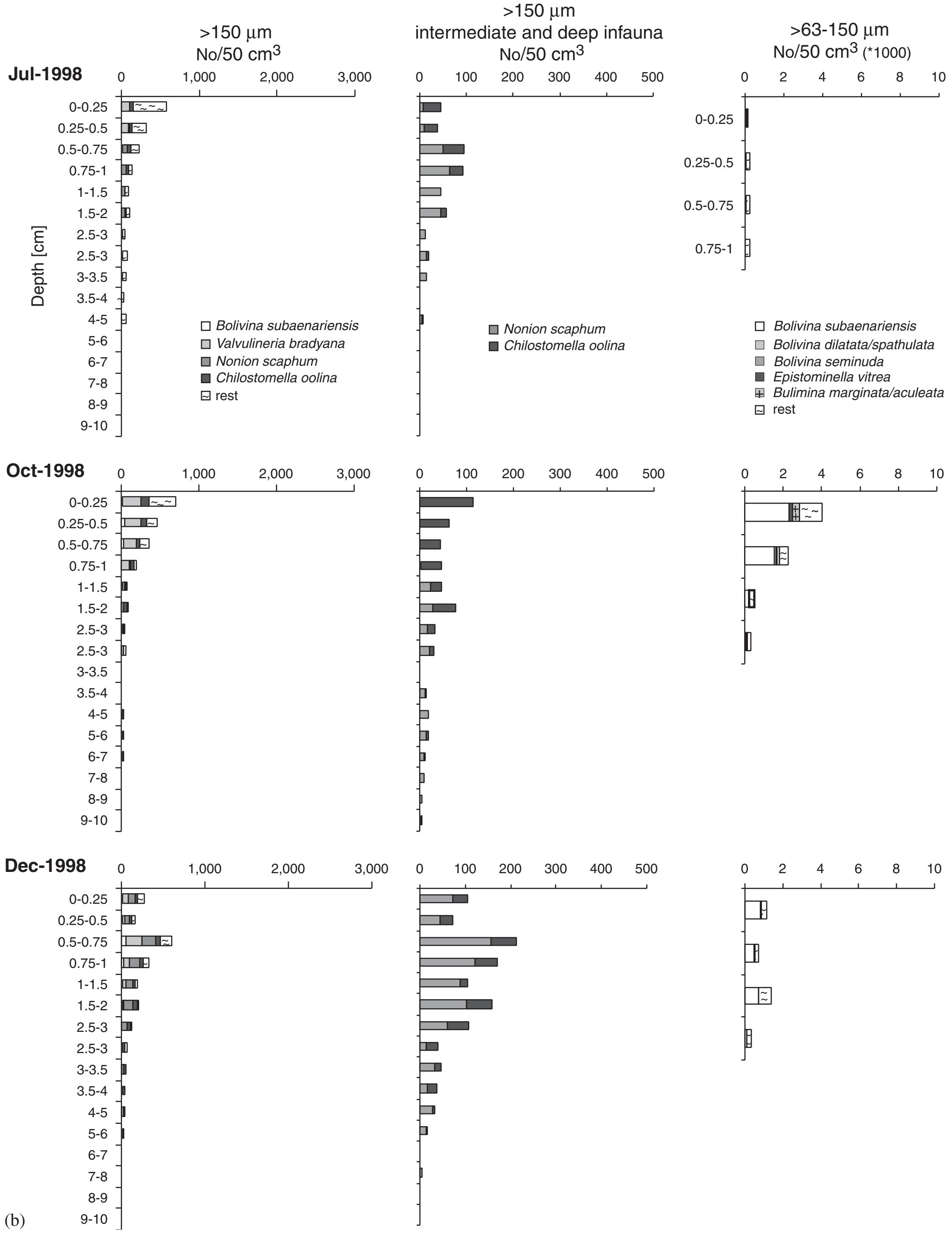
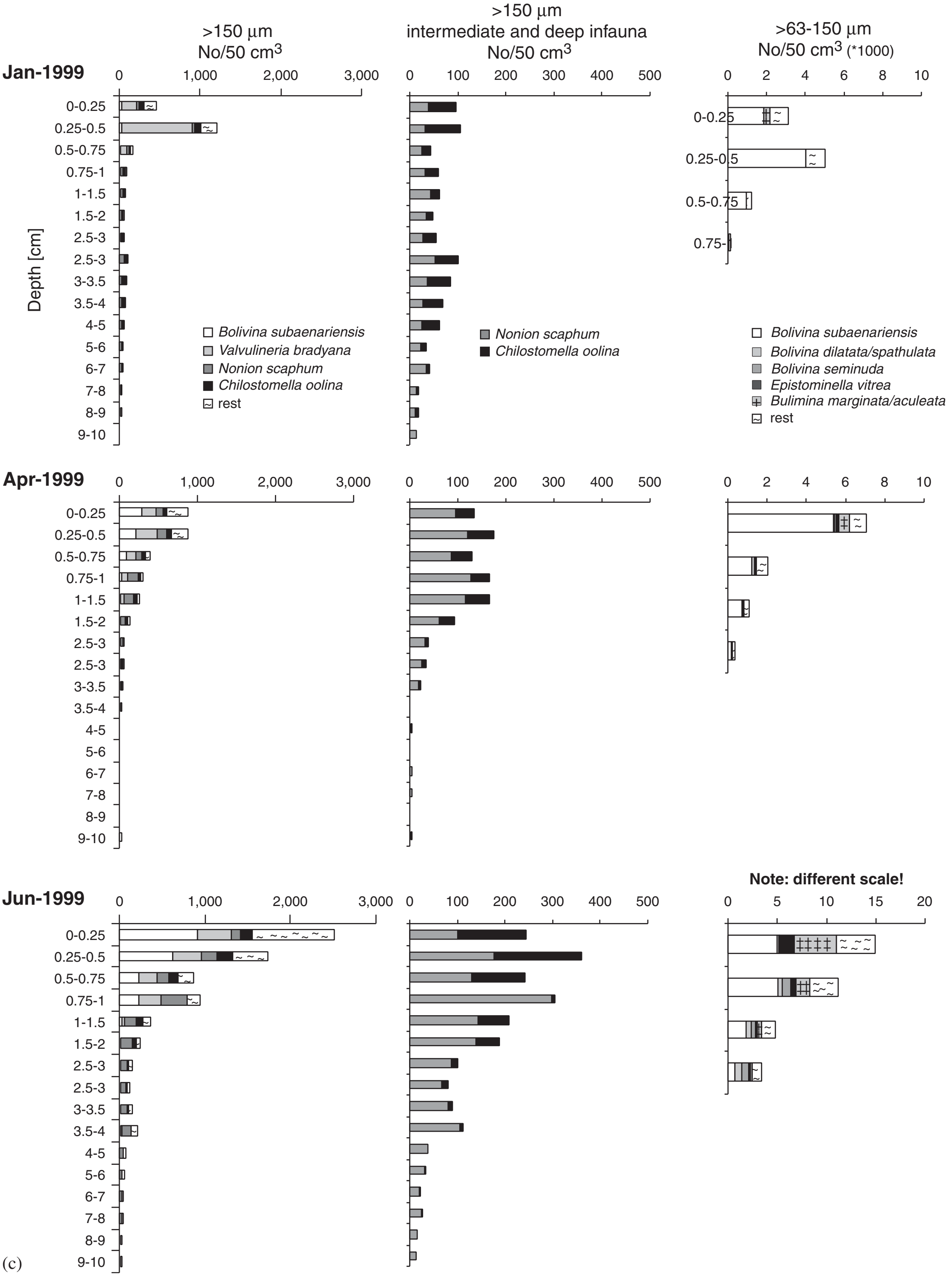


Fig. 5. (*Continued*)

layer with densities of ~3000/50 cm^3 in April 2001 and ~1500/50 cm^3 in June 1999, but almost absent in all other months. *B. marginata/aculeata* (~3700/50 cm^3 in June 1999 and ~900/50 cm^3 in April 2001) also showed maximal frequencies in these 2 months. *B. seminuda* (700–800/50 cm^3 at 0.25–0.75 cm) and



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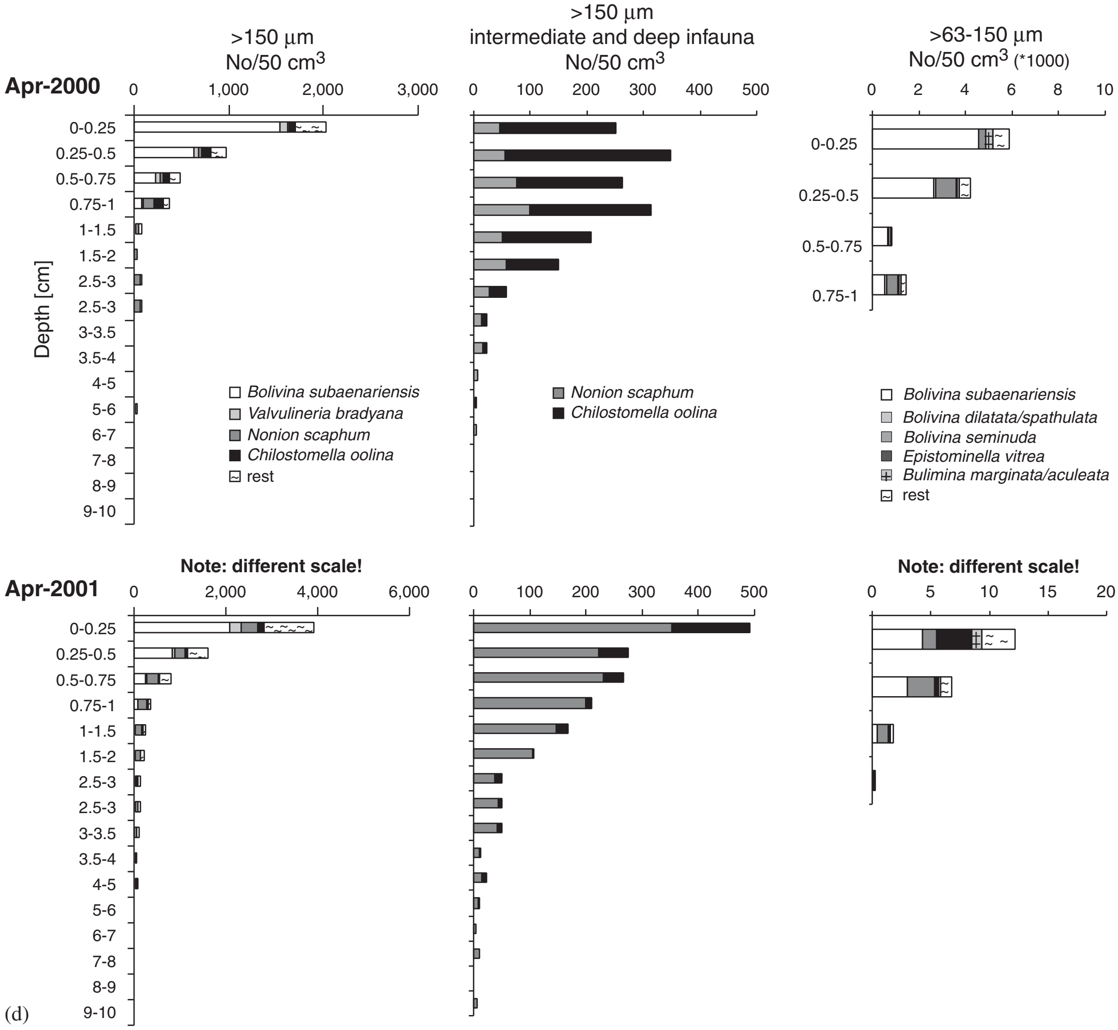

Fig. 5. (*Continued*)

C. carinata (~600/50 cm^3 at 0–0.25 cm in April 2001) are other taxa responsible for the density peaks in April 2001 and June 1999.

3.4. Principal component analysis

In both principal component analyses (absolute density and percentage data) performed on the >150 µm fraction the first two axes explain around 75% of the variation. Results obtained for the absolute density data are shown in Fig. 6a. In this diagram, based on standardized absolute frequencies (numbers/50 cm^3), nearly all taxa correlate with summer and spring conditions, because overall faunal densities were maximal in those seasons. No species correlate with autumn and winter since for all stations absolute numbers were low in those seasons. For this reason, the analysis was repeated using percentage data (Fig. 6b), which should discriminate between species peaking in spring and species that show only a minimum variability of density over the year, and that are relatively enriched (their percentage increases) in winter/autumn.

In the PCA diagram based on absolute densities, *B. subaenariensis*, *N. polymorphinoides* and *N. scaphum* show the clearest correlation to spring and summer, suggesting that their absolute numbers increased more than those of other taxa during these seasons (Fig. 6a). In the PCA diagram based on the percentage data, *B. subaenariensis* still strongly correlates with spring, confirming its percentage increase in this season. *N. scaphum*, on the contrary, now shows a much clearer correlation with summer

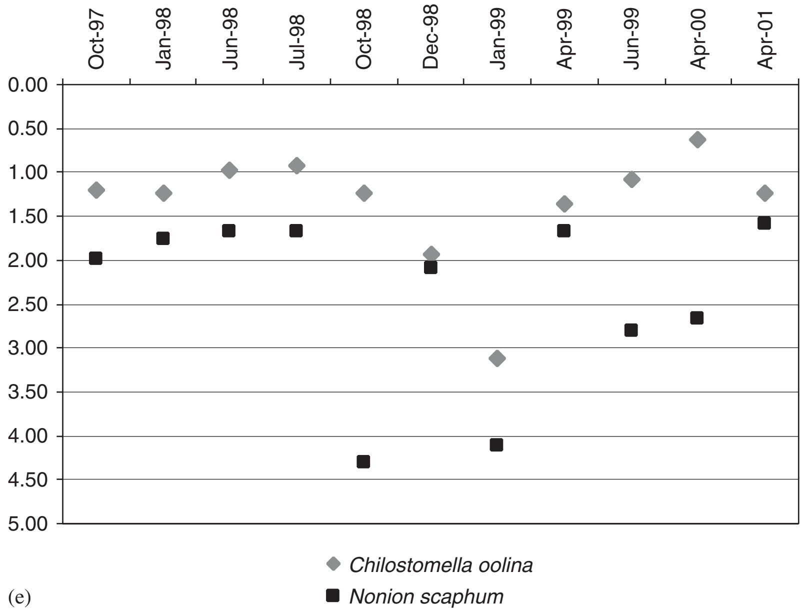

Fig. 5. (*Continued*)

(Fig. 6b). Also *C. oolina* is related to summer (Fig. 6b). However, it should be kept in mind that *N. scaphum* and *C. oolina* are both intermediate infaunal species and results obtained from the first cm give only a partial picture of their overall distribution. The correlation with summer is probably indicative of a high percentage of adult individuals in the topmost cm. This may be due to growth, but may also be due to migration to more superficial sediment layers.

V. bradyana, *B. alata* and *C. cylindrica* show a correlation with autumn and winter (Fig. 6b). Apparently, their absolute density decreased less in autumn/winter than that of other taxa, causing a relative frequency increase, in a season when most densities were decreasing.

A similar PCA analysis was performed on the most abundant taxa of the 63–150 μm fraction (Table 2, Fig. 7a and b). Again, both absolute densities and percentage data were analysed; in both diagrams the first two axes explained over 70% of the variation. The selection of species to be entered in the diagram was performed in the same way as for the larger size fraction. Selected species are listed in Table 2.

Rather surprisingly, in the 63–150 μm size fraction *B. subaenariensis* did not show the correlation with spring that was observed in the >150 μm size fraction (Fig. 7a and b). This is explained by the fact that its absolute density was relatively stable, and its relative frequencies were even minimal in spring and summer. In contrast, other species, such as *B. dilatata*, *B. seminuda*, *C. carinata* and *E. vitrea*, that are correlated to spring and summer in both diagrams, showed a strong increase in absolute as well as relative frequency. The large-sized infaunal species *N. scaphum* and *C. oolina* correlate to summer in the percentage-based diagram of the 63–150 μm size fraction, suggesting the presence of juvenile specimens in the topmost sediment layer in this season.

4. Discussion

4.1. Geochemistry and primary production patterns

Summarizing the geochemical results, we can conclude that the distribution of redox species follows approximately the well-established depth sequence of diagenetic reactions governed by the preferential use of the electron acceptor that yields the highest amount of free energy for the bacterially mediated oxidation of organic matter. Oxygen is reduced near the sediment–water interface, followed by the reduction of nitrate and manganese oxide, then reactive iron oxide, which produce dissolved iron (Fe^{2+}) and manganese (Mn^{2+}) observed in the vertical profiles (Froelich et al., 1979; Postma and

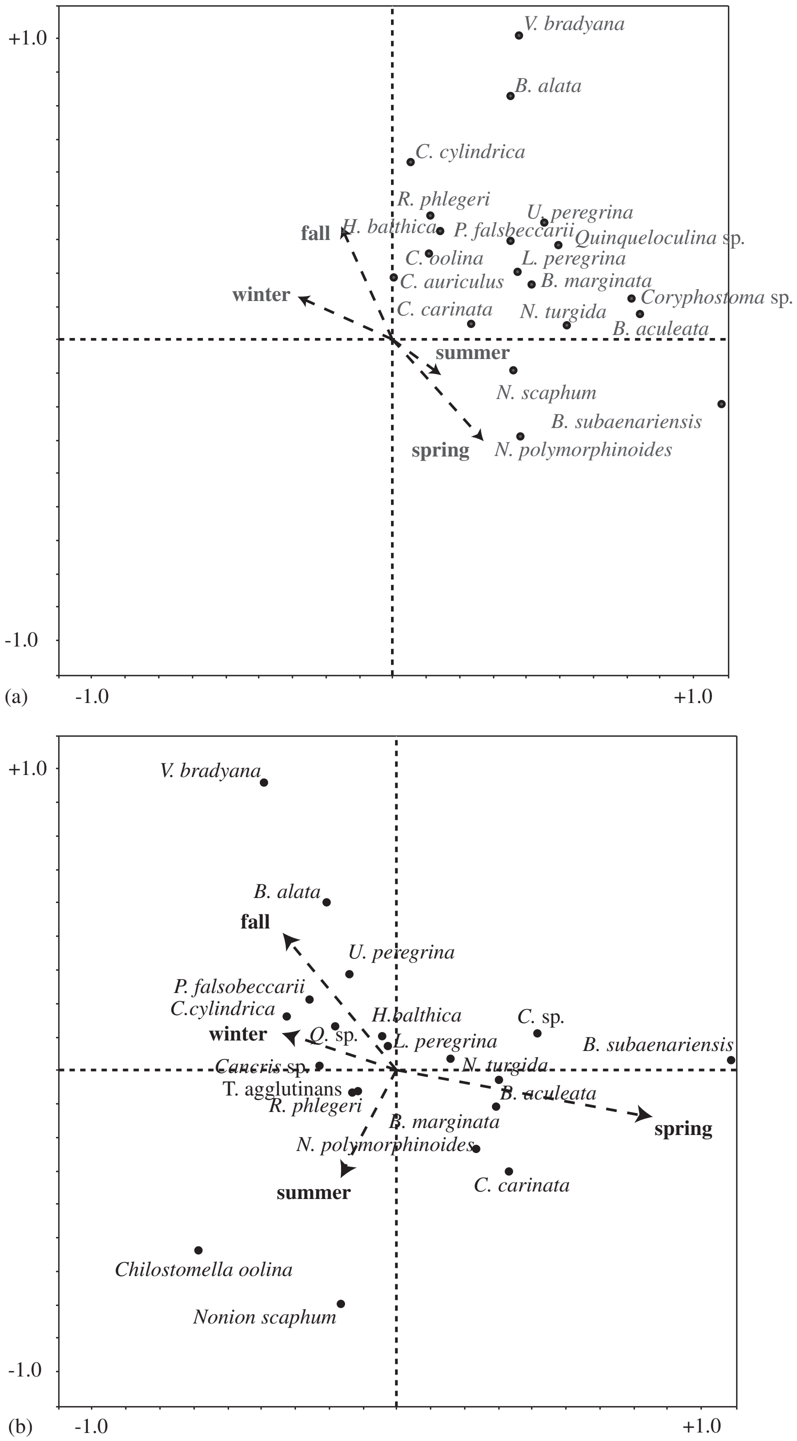

Fig. 6. (a) Principal component analysis (PCA) based on real numbers of the 20 most abundant species (>150 μm). Environmental variables introduced are: Spring, Summer, Autumn and Winter. The resulting eigenvalues for axis 1: 53.4, axis 2: 25.7, axis 3: 7.6. Only results obtained from the 0–1 cm interval were included in this analysis. (b) As (a) but based on percentile numbers. The resulting eigenvalues for axis 1: 42.4, axis 2: 30.3, axis 3: 14.1.

Table 2
Most abundant taxa in the larger and smaller size fraction

Most abundant species >150 μm	Most abundant species 63–150 μm
Bolivina alata	*Bolivina* confer *albatrossi*
Bolivina subaeanariensis	*Bolivina dilatata*
Bulimina aculeata	*Bolivina seminuda*
Bulimina marginata	*Bolivina subaeanariensis*
Cancris auriculus	*Bulimina aculeata*
Cassidulina carinata	*Bulimina marginata*
Chilostomella oolina	*Buliminella* sp.
Clavulina cylindrica	*Cassidulina carinata*
Coryphostoma sp.	*Chilostomella oolina*
Hyalinea balthica	*Coryphostoma* sp.
Lenticulina pergerina	*Gyroidina umbonata*
Nonion scaphum	*Nonion scaphum*
Nonionella turgida	*Nonionella* sp.
Nouria polymorphinoides	*Nonionella turgida*
Pseudoepomides falsobeccarii	*Rectuvigerina phlegeri*
Rectuvigerina phlegeri	*Sigmoilina* sp.
Uvigerina peregrina	*Stainforthia* sp.
Valvulineria bradyana	*Textularia porrecta*
Quinqueloculina seminuda	*Uvigerina peregrina*
	Valvulineria bradyana

Jakobsen, 1996). However, at station D, where the relative positions of reducing and oxidising sediment components was influenced by strong bioturbation (Hyacinthe et al., 2001), the time sequence of redox reactions does not always translate to a similarly recognisable depth sequence. The bioturbated sediment can be thought of as an environment where the distribution of oxidants and reductants evolves towards a steady state, without necessarily achieving it before the next event disrupts the process. Vertical profiles of redox species are therefore likely to represent a transient state rather than a steady state. The changes with time of vertical profiles observed at station D illustrate the dynamic nature of diagenesis in bioturbated sediments, as thoroughly described by Hyacinthe et al. (2001).

In the sediment at station D a well-developed classical vertical sequence of redox reactions linked to the bacterially mediated oxidation of organic matter was found only in January 1999. The sequence starts at the sediment surface with well-oxygenated bottom waters (200–250 μmol/l), followed by a rapid decrease until the zero oxygen level is reached between 5 and 8 mm depth. This strong decrease can be attributed to oxic degradation of organic matter, and the re-oxidation of the products resulting from anaerobic degradation of organic matter deeper in the sediment (Canfield et al., 1993). Slightly lower in the sediment column, a peak of nitrate and nitrite was present. The downward increase of nitrate is caused by the bacterial nitrification of organic N or ammonia that diffuses from below. The decreasing nitrate value slightly deeper in the core was due to bacterial denitrification. In all other cores, however, maximum nitrate + nitrite values were situated in the topmost half cm of the sediment, suggesting the co-occurrence of aerobic and anaerobic organic matter degradation pathways immediately below the sediment surface.

In January 1999, an increase of Mn^{2+} was found below the oxic layer. Deeper in the sediment this was followed by an increase in Fe^{2+}. Highest concentrations of Fe^{2+} were found deeper in the sediment than the highest concentrations of Mn^{2+}. The production of Mn^{2+} and Fe^{2+} in anaerobic sediments is attributed to the dissimilatory reduction of manganese and iron oxides by bacteria. In October 1998, December 1998, April 1999 and June 1999, on the contrary, Fe^{2+} and Mn^{2+} patterns were almost identical. The co-occurrence of high concentrations of Fe^{2+} and Mn^{2+} is contributed to simultaneous reduction of Fe^{2+} and Mn^{2+}.

Possible causes for these different patterns may be found in the amount of bioturbation and bio-irrigation. It has been shown that the presence of the sea-urchin *Brissopsis lyrifera*, of which several specimens were found in our cores, may influence

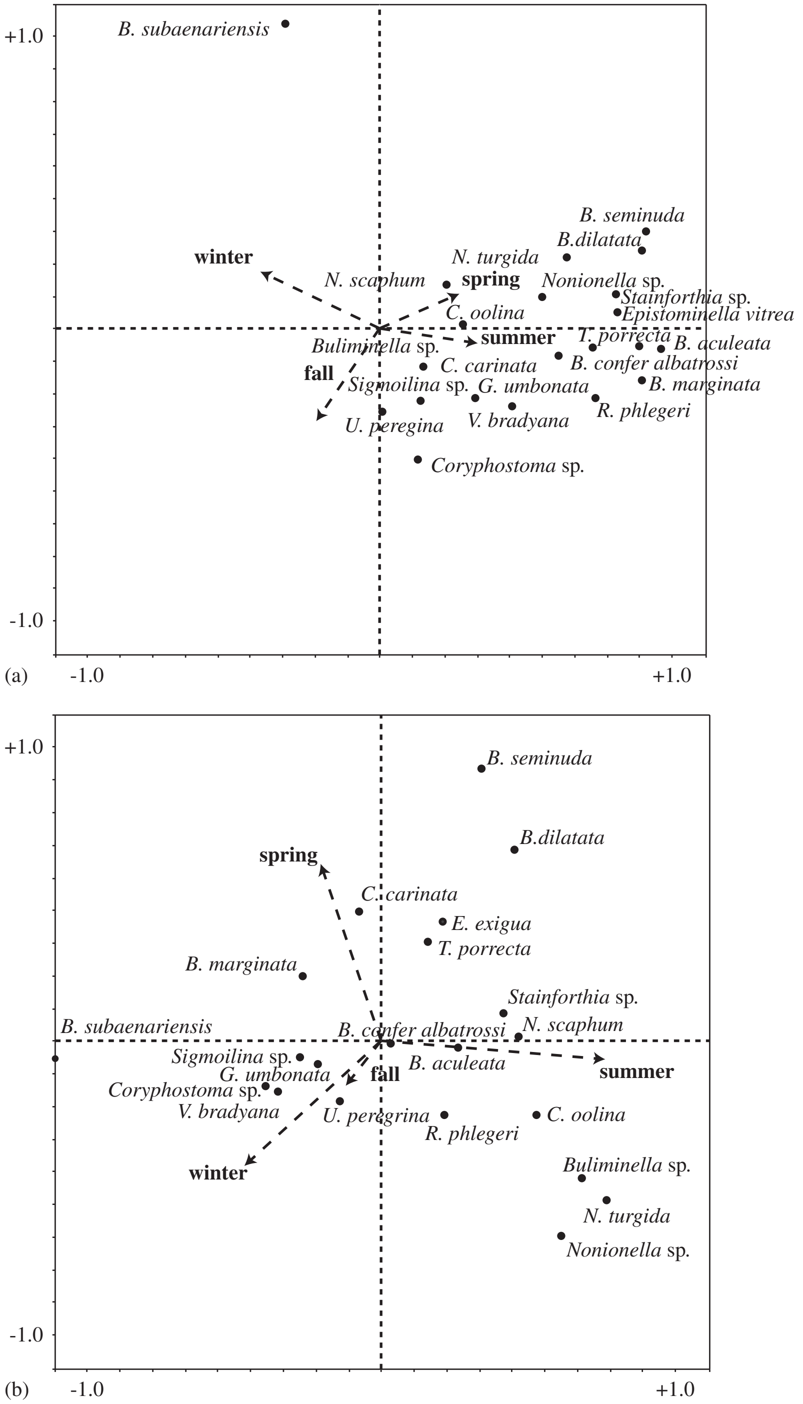

Fig. 7. (a) Principal component analysis (PCA) based on real numbers of the 20 most abundant species (63–150 μm). Environmental variables introduced are: Spring, Summer, Autumn and Winter. The resulting eigenvalues for axis 1: 44.7, axis 2: 25.0, axis 3: 11.1. (b) as (a), but based on percentile numbers. The resulting eigenvalues for axis 1: 65.4, axis 2: 13.7, axis 3: 6.2.

the sediment geochemistry significantly (Widdicombe and Austen, 1998). As a result of the spring bloom, high amounts of labile organic matter were deposited at the seafloor. Due to intensive bioturbation, the labile organic matter was rapidly mixed into the sediment, and ephemeral oxygenated microenvironments may have been created deeper in the sediment. This combination of an enhanced availability of organic matter and an increased sediment heterogeneity created by bioturbation caused the co-occurrence of multiple organic carbon degradation pathways (Koretsky et al., 2005). When the system returned to more oligotrophic conditions in autumn (and winter), bioturbational activity will probably decrease and the redox succession will become more prominent.

From 1998 to 2001 significant peaks in chlorophyll-*a* concentration were systematically observed in April. These peaks correspond to primary production maxima that probably caused a significant flux of labile organic matter to the ocean floor. This organic input should be responsible for an increased benthic oxygen demand, and thus a lower oxygen penetration into the sediment. Indeed, the oxygen penetration depth is minimal in the months where faunal density is maximal (June 1999, ~4 mm and April 2001 ~3 mm). However, the difference with other months (maximum penetration depth ~8 mm in October 1997) is rather limited. This may be caused by the fact that increased organic input triggers macrofaunal activity and bio-irrigation, counterbalancing the increased sediment oxygen demand.

4.2. Foraminifera

It is unclear to what extent apparent temporal variation can be attributed to spatial heterogeneity (Thiel et al., 1990, Barmawidjaja et al., 1992). It is known that a mosaic of organic-rich patches occurs on the seafloor (Grassle and Morse-Porteous, 1987; Grassle, 1989; Snelgrove et al., 1994, 1996), and that this patchiness may lead to spatially different foraminiferal standing stocks (Hohenegger et al., 1993). Gooday and Rathburn (1999) conclude that seasonal fluctuations of foraminiferal faunas, which react on seasonal input of organic matter, may be more obvious in bathyal systems than in the deeper abyssal systems. However, Ohga and Kitatzato (1997) report temporal variations in deep-sea foraminiferal communities, which can be be plausibly related to seasonal events. The presence of significant spatial variability in foraminiferal assemblages has been shown for the deeper (550 m) station B in the Bay of Biscay (Fontanier et al., 2003). The occurrence of sea-urchins in cores with high foraminiferal numbers (Langezaal et al., unpublished data) might point to the occurrence of patchiness driven by differences in availability of organic matter. However, the research performed on station B (Fontanier et al., 2003) shows that temporal variability is more important than spatial variability. Therefore, we attribute the strong variations that are found between cores taken at different times to seasonal variation of foraminiferal occurrences.

In each size fraction four abundant taxa always represented at least half of the population. In the >150 μm fraction these species were *B. subaenariensis*, *V. bradyana*, *C. oolina* and *N. scaphum*. The first two were living predominantly in the top sediment layer and are considered as shallow infaunal species. The latter two preferred a habitat deeper in the sediment, and are classified here as intermediate to deep infaunal.

In the smaller size fraction, a large part of the assemblage (at least 75% in the at 0–1 cm layer) lived in the upper 5 mm of the sediment. The four most abundant taxa showed a preference for the top sediment layers. In all autumn and winter and all but one (April 2001) of the spring samples, *B. subaenariensis* accounted for more than half of the foraminiferal individuals. In all summer samples and in April 2001, this species has a much lower percentage abundance, and other taxa such as *B. dilatata/spathulata*, *B. seminuda*, *B. marginata/aculeata* and *E. vitrea* become important faunal elements.

For the dominant species *B. subaenariensis*, a clear seasonal pattern was observed. In the >150 μm fraction, this species showed a strong correlation to spring; it was very abundant in April 2001, April 2000, April 1999 and June 1999, when the weak staining suggests that a part of the population was no longer alive. Rather surprisingly, in the smaller size fraction a different pattern was observed. Absolute densities are less variable throughout the year than that of other taxa, and *B. subaenariensis* shows maximal percentages in all autumn and winter samples, and in April 1999 and 2000. In April 2001, on the contrary, where the total faunal density is maximal, this species is much less prominent. This pattern suggests that the species has a reproductive response to the arrival of important amounts of phytodetritus in spring, quickly followed by a period of accelerated growth, explaining the paradox between its richness in the >150 μm fraction and its relative scarcity in the 63–150 μm fraction in April 2001 and in all summer months. This means that *B. subaenariensis* is an opportunistic species that remains small for a large part of the year, and shows a strong response to the input of organic matter in spring.

The shallow infaunal species *V. bradyana* shows a very different pattern. In the $>150\,\mu m$ size fraction it shows maximal absolute and relative densities in October 1997, October 1998, December 1998, and January 1999. In October 1998 it is even the dominant taxon. Also in the smaller size fraction, the highest percentages of this species tend to be encountered in autumn and winter. In spring, it is only frequent in April 1999, when *B. subaenariensis* has a low standing stock. The fact that *B. subaenariensis* and *V. bradyana* are both shallow infaunal taxa with an opportunistic tendency, that show population maxima in different periods of the year, could suggest that they rely on different types of phytodetritus. In the Bay of Biscay, the spring bloom is strongly dominated by diatoms (Lampert, 2001; Wollast and Chou, 2001), whereas during the less discrete production events taking place in autumn, dinoflagelates dominate the phytoplanktonic assemblage (Sellmer et al., 1998). *V. bradyana* has been found to inhabit riverine clay belts (Van der Zwaan and Jorissen, 1991). However, for the Gironde river the highest flux of the year is found in February 1998 and therefore, we assume that the relative abundance of *V. bradyana* is not caused by a significant increase in riverine material.

E. vitrea, *B. seminuda* and *B. dilatata/spathulata* are small species that were never found in the $>150\,\mu m$ fraction. They were particularly abundant in the 2 months with the richest foraminiferal faunas, April 2001 and June 1999. Apparently their increased numbers lasted only for a short period of time, since they are uncommon throughout the rest of the year. In many previous papers, *Epistominella exigua* (a close relative of *E. vitrea*) has been described as an extremely opportunistic taxon, capable to rapidly colonise freshly deposited phytodetritus (e.g. Gooday and Turley, 1990, Heinz et al., 2001, 2002; Fontanier et al., 2003; Ernst and Van der Zwaan, 2004). In view of its peak occurrences separated by periods in which the species is near absent, *E. vitrea* seems to have a similar ecological strategy. For *B. spathulata*, this response to phytodetritus input was previously described by Fontanier et al. (2003) for a station at 500 m depth in the Bay of Biscay. Also *B. dilatata/spathulata* and *B. seminuda* are taxa characteristic of eutrophic environments (Barmawidjaja, 1991; Barmawidjaja et al., 1992; Duijnstee, 2001). Gooday et al. (2000) reported *B. seminuda* in areas that are characterised by high (and highly seasonal) surface primary production, high organic carbon fluxes to the seafloor and high sediment TOC values and pigment concentrations, where oxygen concentrations are not extreme.

The intermediate to deep infaunal taxa *N. scaphum* and *C. oolina*, are both clearly related to summer conditions in the analysis based on percentage data. This could be due to a decrease in numbers of other species, rather than a reaction by *N. scaphum* and *C. oolina* to the summer conditions. However, in the case of *N. scaphum* which is also correlated to summer in the PCA of the absolute numbers this is probably caused by an increase in numbers of *N. scaphum*. For *C. oolina* the relative increase is more likely caused by a decrease in number of other species. As the PCA is only based on the top first centimetre of sediment, this absolute or relative increase might well be caused by a change in their depth distribution.

No clear correlation was found between the depth of the different redox zones and the migratory behaviour of *C. oolina* and *N. scaphum.* In January 1999, when the redox zones were well separated, both species had a relatively deep average living depth. This correlation was not found for other months in which *N. scaphum* occurred deeper in the sediment (e.g. October 1998, June 1999, and April 2000).

Results obtained by Heinz et al. (2001), Ernst, (2002), Ernst et al. (2002), and Fontanier et al. (2003) suggest that increased surficial biological activity is transmitted towards deeper layers. We assume that the input of large amounts of phytodetritus after the spring bloom provokes increased bioturbation. This would cause rapid mixing of labile organic matter into the topmost sediment. Apparently intermediate to deep infaunal species such as *C. oolina* and, to a lesser degree, *N. scaphum* react to the introduction of labile organic matter into the surficial sediment, by a shallowing of their microhabitat. This confirms suggestions of Kitazato et al. (2000) and Fontanier et al. (2003) that deep infaunal species such as *C. ovoidea* and *G. affinis* are able to profit from fresh organic matter, by migrating to the sediment surface and reproducing at the end of the spring bloom. Nomaki et al. (2005) showed that *C. ovoidea* rarely assimilated fresh algae in an experimental setting, while other deep infaunal species (such as *G. affinis*) did assimilate the offered algae. *C. oolina* was previously found to migrate only under specific conditions, which indicated a change in feeding strategy with changing trophic conditions (Langezaal et al., 2004).

The migratory response which follows the deposition of fresh organic matter on the sediment surface, may be aided by the more intensive overlap between redox zones, which occurs due to the increased amount of labile organic carbon in the system.

The benthic foraminiferal response to the spring bloom appears to be much more pronounced in April 2001 than in April 2000 and in April 1999. The slightly shallower oxygen penetration depth observed in April 2001 (3 mm versus ~5 mm in April 1999 and 2000) is indicative of a higher sedimentary oxygen demand. Possibly, the deposition of phytodetritus on the seafloor took place slightly later in 2001 than in 1999 and 2000. The weakly stained specimens observed in June 1999 are thought to represent individuals that died in the weeks before sampling. Their surprisingly high densities could be a response to the secondary chlorophyll-*a* maximum observed in the middle of May 1999.

4.3. Comparison with temporal patterns observed in margin environments in the Bay of Biscay

Fontanier et al. (2003) report results from a comparable study of seasonal and interannual variability at a deeper station (B; at 550 m). At the outer shelf station (D; at 150 m waterdepth), foraminiferal densities were much higher throughout the year than at bathyal depths in the Bay of Biscay (See also Fontanier et al., 2002). This is probably caused by the more eutrophic conditions of station D (Fontanier et al., 2002).

Fontanier et al. (2003) reported highest foraminiferal densities in October 1997 and April 2000 at station B. At the outer shelf station (D), however, highest densities were found in June 1999 and April 2001. This could suggest that the autumn bloom was more pronounced in deeper parts of the Bay of Biscay than at shallower areas. Another explanation is that a small increase in labile organic matter had less influence in the more eutrophic area at 150 m water depth. At both stations the number of foraminifera in the fraction 63–150 μm was more variable over the year than the number of foraminifera in the > 150 μm fraction. This is probably due to the fact that the more opportunistic taxa are rather small, and are exclusively found in the 63–150 μm fraction.

In a depth transect study performed in October 1997, Fontanier et al. (2002) indicated that completely different foraminiferal assemblages were found at station B and D (the latter being the one described seasonally in this study). However, a foraminiferal response to the autumn and spring bloom periods was found in both cases. At the deeper station B, some species (*E. exigua* and *U. mediterranea*) showed absolute and relative density increases after the spring and autumn blooms, whereas at the shallower station D, species reacted mostly either to the spring bloom or to the autumn bloom; no species were found to react strongly to both autumn and spring bloom conditions.

In contrast to species that reacted to both the spring bloom and the autumn bloom conditions, at both stations foraminiferal species were found that reacted only to the spring bloom conditions. At the deeper station B, the most important of these species were *Trochammina* sp. and *B. difformis*. At the shallower station, *B. spathulata/dilatata, E. vitrea* and *B. marginata/aculeata* showed a response only to the spring bloom. None of the species in the larger size fraction of station B, reacted strictly to the spring bloom. However, in this size fraction, *B. subaenariensis* showed a strong increase in densities only after the spring bloom at station D. In the larger size fraction *U. peregrina* increased after the putative autumn bloom at station B, whereas at station D this reaction was found for *V. bradyana.*

There was a migrational response by intermediate to deep infaunal species to spring bloom conditions at both stations. *C. ovoidea* and *G. affinis* migrated to the sediment-water interface at station B, whereas this behaviour was found for *C. oolina* (same species as *C. ovoidea*) and to a lesser extend for *N. scaphum* at station D. These species are probably able to profit from fresh organic matter, by migrating to the sediment surface and reproducing at the end of the spring bloom period (Kitazato et al., 2000; Fontanier et al., 2003).

According to the TROX model of Jorissen et al. (1995), in the eutrophic setting of our outer shelf station (Fontanier et al., 2002), oxygen availability should be the main parameter controlling the foraminiferal microhabitat. Since oxygen penetration is limited to the topmost 5–8 mm, the faunal penetration depth should be very limited as well. For most shallow infaunal taxa, that systematically show maximal densities in the topmost cm of the sediment, this seems indeed to be the case. The intermediate to deep infaunal taxa *C. oolina* and *N. scaphum*, on the contrary, appear to show a migrational behaviour in response to food availability in the sediment. These results fit well in the TROX II model (Van der Zwaan et al., 1999). However, increased knowledge of the degradation pathways of organic matter by bacteria make it clear that the variation in redox conditions is more complex than was proposed in the TROX II model.

5. Conclusions

A fairly obvious vertically redox zonation was observed only during January 1999. During spring months, when a high chlorophyll-*a* concentration was detected in the surface waters, various patterns of overlapping redox zones occurred. We conclude that organic matter was rapidly mixed into the sediment by bioturbation. In times of increased organic input, macrofaunal bioturbation is probably intensified, leading to an overlap of redox zones. In the Bay of Biscay, an area characterised by distinct spring blooms, the sediment column should therefore be most mixed in spring, whereas the best-developed succession of redox zones may be expected in winter.

Most foraminiferal species responded to the spring bloom either with rapid growth, as is inferred for *B. subaenariensis*, or with rapid reproduction, as in the case of *Epistominella vitrea*, *B. seminuda* and *B. dilatata/spathulata*. Shortly after the spring bloom period densities of the opportunistic taxa reduced rapidly. We suggest that species that reacted to the spring bloom feed preferentially on diatoms (see also Fontanier et al., 2003). However, the above mentioned taxa might also react to one of the distinct species of diatoms that occur. Food selectivity on different components of the deposited material by foraminifera has already been demonstrated by Suhr et al. (2003).

A few weeks to months after the spring bloom the intermediate to deep infaunal species *C. oolina* and to a lesser extent *N. scaphum*, migrated closer to the sediment surface where they probably profited directly from fresh organic matter. This migration is most likely triggered by the occurrence of fresh phytodetritus in the sediment, made available in slightly deeper sediment levels due to the increased bioturbation activity. However, the more intensive overlapping of redox zones that were perhaps better separated vertically in winter could have aided this migration.

In June 1998, Fontanier et al. (2003) observed a strong increase in numbers of juvenile specimens (63–150 μm) of the deep infaunal species *G. affinis* in the topmost half cm at a 550 m-deep station in the Bay of Biscay. Our data suggest a relative high number of juvenile specimens of *C. oolina* and *N. scaphum* in the summer. These observations suggest that intermediate and deep infaunal taxa have a delayed reproductive response to spring phytodetritus input, and also that they reproduce in rather superficial sediments, in contrast to the usually much deeper microhabitat preference of adult specimens.

Our results suggest a strong interaction between organic detritus input, macrofaunal bioturbational activity, the degree of separation of redox zones and the reproduction, growth and migrational response of benthic foraminifera. All these parameters appear to vary independantly on a seasonal scale.

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Appendix A. Supplementary Materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.csr.2006.05.005.

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